

- Collins S (2004). 'Vocal fighting and flirting: The functions of birdsong.' In Marler P & Slabbekoorn H (eds.) *Nature's music: The science of birdsong*. San Diego: Elsevier. 39–79.
- De la Torre S & Snowdon C T (2002). 'Environmental correlates of vocal communication of wild pygmy marmosets, *Cebuella pygmaea*.' *Animal Behaviour* 63, 847–856.
- Dodenhoff D J, Stark R D & Johnson E V (2001). 'Do woodpecker drums encode information for species recognition?' *Condor* 103, 143–150.
- Eberhardt L S (1997). 'A test of the environmental advertisement hypothesis for the function of drumming in yellow-bellied sapsuckers.' *Condor* 99, 798–803.
- Fought J G, Munroe R L, Fought C R & Good E M (2004). 'Sonority and climate in a world sample of languages: Findings and prospects.' *Cross-cultural Research* 38, 27–51.
- Garstang M, Larom D, Raspet R & Lindeque M (1995). 'Atmospheric controls on elephant communication.' *Journal of Experimental Biology* 198, 939–951.
- Heuwinkel H (1982). 'Sound pressure level and frequency spectrum in the song of *Acrocephalus arundinaceus*, *A. scirpaceus*, *A. schoenobaenus* and *A. palustris* and their relation to habitat acoustics.' *Ecology of Birds* 4, 85–174.
- Holland J, Dabelsteen T, Pedersen S B & Larsen O N (1998). 'Degradation of wren *Troglodytes troglodytes*-song: Implications for information transfer and ranging.' *Journal of the Acoustical Society of America* 103, 2154–2166.
- Lardner B & bin Lakim M (2002). 'Tree-hole frogs exploit resonance effects.' *Nature* 420, 475.
- Larom D, Garstang M, Payne K, Raspet R & Lindeque M (1997). 'The influence of surface atmospheric conditions on the range and area reached by animal vocalizations.' *Journal of Experimental Biology* 200, 421–431.
- Mack A L & Jones J (2003). 'Low-frequency vocalizations by cassowaries (*Casuaris* spp.).' *Auk* 120, 1062–1068.
- Mathevon N, Aubin T & Dabelsteen T (1996). 'Song degradation during propagation: Importance of song post for the wren *Troglodytes troglodytes*.' *Ethology* 102, 397–412.
- Naguib M & Wiley R H (2001). 'Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication.' *Animal Behaviour* 62, 825–837.
- Narins P (1995). 'Frog communication.' *Scientific American* 273, 62–67.
- Nettle D (1994). 'A behavioural correlate of phonological structure.' *Language and Speech* 37, 425–429.
- O'Connell-Rodwell C E, Arnason B T & Hart L A (2000). 'Seismic properties of elephant vocalizations and locomotion.' *Journal of the Acoustical Society of America* 108, 3066–3072.
- Penna M & Solis R (1996). 'Influence of burrow acoustics on sound reception by frogs *Eusophus* (Leptodactylidae).' *Animal Behaviour* 51, 255–263.
- Randall J A (2001). 'Evolution and function of drumming as communication in mammals.' *American Zoologist* 41, 1143–1156.
- Slabbekoorn H (2004). 'Singing in the wild: The ecology of birdsong.' In Marler P & Slabbekoorn H (eds.) *Nature's music: The science of birdsong*. San Diego: Elsevier. 178–205.
- Slabbekoorn H & Peet M (2003). 'Birds sing at a higher pitch in urban noise.' *Nature* 424, 267.
- Slabbekoorn H, Eilers J & Smith T B (2002). 'Bird song and sound transmission: The benefits of reverberations.' *Condor* 104, 564–573.
- Tellenbach Uttman M (2002). *Eine Untersuchung der Teiltonspektren bei Kulning- und Lockruftechniken anhand von Beispielen aus Schweden und Finnland*. STM-Online 5.
- Vilkman E, Alku P & Vintturi J (2002). 'Dynamic extremes of voice in the light of time domain parameters extracted from the amplitude features of glottal flow and its derivative.' *Folia Phoniatrica et Logopaedica* 54, 144–157.
- Wells K D & Schwartz J J (1982). 'The effect of vegetation on the propagation of calls in the neotropical frog *Centrolenella fleischmanni*.' *Herpetologica* 38, 449–455.
- Wiley R H & Richards D G (1982). 'Adaptations for acoustic communication in birds: Sound transmission and signal detection.' In Kroodsma D E & Miller E H (eds.) *Acoustic communication in birds 1*. New York: Academic Press. 131–181.

Animal Communication: Overview

M Naguib, University of Bielefeld, Bielefeld, Germany

© 2006 Elsevier Ltd. All rights reserved.

Animals, like humans, communicate with one another, often in strikingly complex ways. Despite obvious differences between human communication and communication in animals, there are many fundamental similarities in the underlying principles. Anticipating

how and why animals communicate makes an important comparison to human communication and provides a broader background for understanding human speech and language. Communication in animals and humans has a shared evolutionary history and thus understanding animal communication also helps to elucidate the biological basis of human language. Communication in animals has deep implications for their social life, survival, and fitness; thus,

communication systems are among the key research models to elucidate biological processes from within a mechanistic and an evolutionary perspective. It allows the integration of questions raised in, for instance, psychology and very different biological fields, including physiology, neurobiology, genetics, development, and cognition as well as population biology and evolution. Communication, in general, is one of the most fundamental issues in life, as it is crucial at all organismal levels. Cells must communicate within an organism and there are specific adaptations for signals, such as hormones and transmitters, that act as information carriers at these levels. When talking about animal communication, however, we refer to communication among individuals, which is the topic of this article.

Definitions

In many cases such as the melodious song of songbirds and whales and the fascinating body patterns and color traits that are displayed during social interactions, it is undebated that animals communicate. However, there are cases such as a mouse rustling in the leaves and by this behavior attracting a predator that we generally do not interpret as meaning that the mouse is communicating with the predator despite influencing its behavior. For such cases, definitions are helpful and necessary to set the stage even though one must keep in mind that there are numerous definitions that differ in subtleties and in their focus and that it is more important to deal with the issues and questions of interest rather than with coarse definitions. The most common and most widely accepted definition is that animal communication is behavior involving signals as information carriers. Signals in animal communication are understood as behaviors or traits that have evolved **specifically** to provide information from a sender to one or more receivers. Thus, birdsong or frog calls are signals, whereas coughing is not a signal (unless it becomes ritualized to act as signal) even though it provides information about the signaler (e.g., possibly its health status). If information is derived from traits that are not signals, these traits are usually referred to as cues. Signals also cause a change in the state of the receivers without providing the physical energy for this change, another definition that is frequently used. Pushing someone off a cliff is not a signal; telling him or her to jump off is a signal. The nature of a specific communication system then is characterized by a broad range of factors, such as the species, the social system and context in which communication takes place, the function of signals, the interests by senders and receivers (which commonly differ between them), and the

sensory modalities used as well as the abilities to produce signals and to perceive and to process them.

What Is Communicated

One of the central questions in animal communication is related to the information that is communicated. Animals communicate information often by using complex signals that simultaneously carry different kinds of information or by using compound signals that carry information in several sensory modalities. In general, animals communicate information about themselves, such as their individuality, species and population identity, age, motivation, genetic background, developmental history, physiological condition, and intentions. In contrast, evidence that animals communicate about external events (referential signaling) is limited to some very specific cases. The best evidence that animals use referential signals comes from honeybees (*Apis mellifera*), presumably the most famous case, where the waggle dance on the hive provides information to group members about the location and direction of a food source. Also, alarm and warning calls by birds and primates have been shown to be functionally referential, i.e., that specific signals are used in response to specific types of predators. In general, when dealing with communication, the message, as coded by a sender, must be distinguished from the meaning, as decoded by a receiver, of a signal. A sender codes information in a signal and the signal as information carrier then will carry this information as a specific message. The meaning of a signal, however, depends not only on the sender and the coded information but also on the receiver. For different receivers, a signal that carries the same message may have a different meaning, or even no meaning at all (Figure 1).

An advertisement signal by a male may attract a female, as the meaning to a female may be *I am a high-quality and attractive male*, whereas the same signal with the same message may mean to a rival male *I'd better stay away as this is a strong male* and to an individual of a different species that signal may have no meaning at all.

Sensory Modalities

Animals have evolved an enormous variety of highly specialized communication systems across all sensory modalities, such as acoustic signals, visual signals, chemical signals, electric signals, and tactile signals. Each sensory modality has its own advantages and disadvantages in information transfer and there are many intrinsic and extrinsic factors that have favored and shaped the particular communication system in a

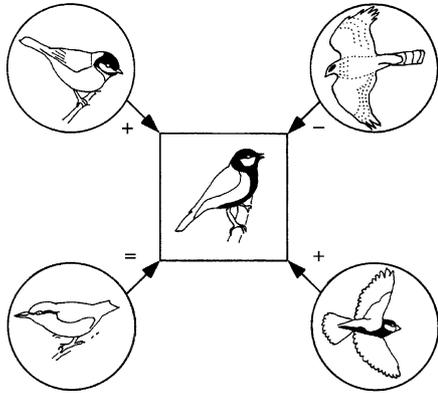


Figure 1 Schematic illustration of the message and the meaning of a signal. A visual or acoustic signal by a sender (center) contains a message to its conspecifics. For a rival male (bottom right), the meaning will be different than for a female (top left). Rivals may be repelled by the signal, whereas females may be attracted. The message is not directed at individuals of other species and may have no meaning to such an individual (bottom left). However, even though the signals and its message are not directed at individuals of other species, the signal may have meaning to a predator that uses such a signal to localize its prey. Drawn after Slater (1999), *Essentials in Animal Behaviour*, Cambridge University Press, Cambridge.

given sensory modality within a species. Among these factors, there are phylogenetic and morphological constraints, and constraints imposed by the environment through which the signals must travel from a sender to a receiver. Which sensory modality is used obviously also depends on the kind of information that is signaled and its biological significance. Advertisement signals for mate attraction need to transmit far and omnidirectionally, e.g., acoustic signals. They also need to be conspicuous, e.g., acoustic signals or visual signals when the habitat does not constrain sight; signals need to be persistent, even in the absence of the sender, e.g., chemical signals used in many mammals for territorial marking. Short-range interactions, such as communication between close group members or parent–offspring communication during feeding or nursing, require a different set of signals that often are soft and subtle. Many of the basic principles of communication apply in one form or another to several sensory modalities. For those interested in language and linguistics, vocal communication presumably will be of most interest. Thus, this article, in addition to focusing on general issues and providing an overview about the three best studied sensory modalities, draws several examples from vocal communication as well because it provides key examples of major issues in animal communication. Despite separate treatment of the sensory channels, it should be mentioned that often communication involves a

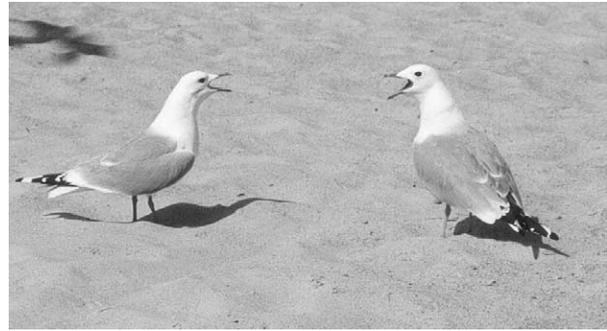


Figure 2 Communication often involves concurrent and compound signaling in different sensory modalities, as in these common gulls, in which calling is associated with specific body postures.

simultaneous combination of different modalities (Figure 2).

Acoustic Communication

Acoustic communication is found across the animal kingdom and in most cases is characterized by its conspicuousness, even though acoustic signals can also be subtle and soft. Some animals even communicate acoustically outside our hearing range, such as bats or rats, which use ultrasound, or elephants, which communicate in the infrasonic range. Birds and whales sing, frogs and insects call, deer roar, and there are many other examples making us wonder what the functions of these complex and diverse behaviors are. In most cases, the loud and conspicuous signals are advertisement signals used for resource defense, such as a food source or a nesting place, or to attract a social mate or a mate for extrapair copulations. Acoustic signals are ideal for such advertisement as they allow rapid coding of complex information and most importantly the signal with its information transmits almost omnidirectionally. Thus, acoustic communication is less ‘private’ than visual or even tactile communication, as in most cases the signal cannot be sent exclusively to a specific receiver. In long-range communication, which often occurs over distances of 100 m or more in birds or even occurs over distances of kilometers in whales or elephants, the signals degrade and attenuate over a distance, leading to signals being different in structure at the position at which a receiver makes a decision compared to the signal structure at the source. Thus, the information available to a receiver, the transmitted information, can differ from the coded information, an issue of increasing interest in studies on animal acoustic communication. Selection by conspecific receivers has led to signals being adapted to the acoustic properties of the habitat by favoring lower frequencies and slower repetition rates of similar

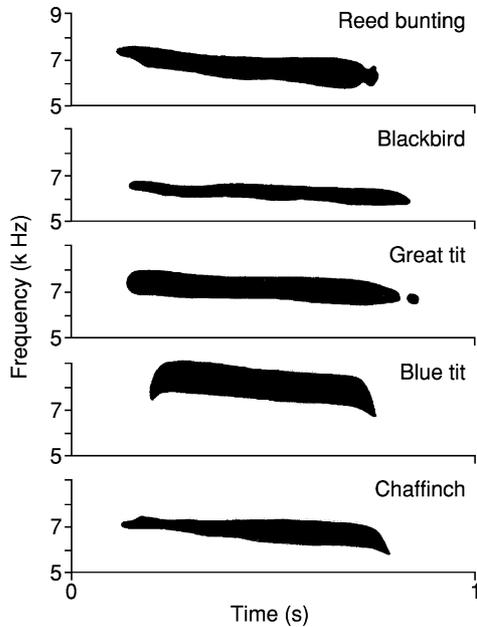


Figure 3 Sound spectrograms of alarm calls of five different species of European songbirds. Calls are very similar in structure. Due to the narrow frequency bandwidth and the lack of strong frequency modulation, the caller will be difficult to localize by a predator. High frequencies also do not travel very far so that they are well suited to warn nearby conspecifics without alerting distant predators. Drawn after Slater (1999), after original source in Thorpe (1961), *Bird song*, London: Cambridge University Press.

frequencies in closed habitats that lead to strong attenuation and reverberation compared to those of signals of species that settle in open fields. Such adaptations reduce ambiguities and increase the efficiency of communication over long distances. Striking examples of adaptations of acoustic signals to the acoustic properties of the environment and receivers' hearing and perception are the high-pitched 'seep' alarm calls given by many songbirds in response to predators (Figure 3). The lack of strong frequency modulation makes the signal difficult to localize and as high-pitched sounds they do not transmit far and thus the sender avoids the risk of being heard and attacked by a predator while still warning nearby group members. A classic study on this topic has shown that songbirds hear significantly better in the frequency range of these calls than do predators (Figure 4).

In addition to alarm calls and advertisement signals, there are many other, often subtle, vocal signals, such as contact calls, food calls, or begging calls.

For those interested in language and linguistics, it is of particular interest that acoustic signals make the best and most direct comparison to human language. Like human language, acoustic signals permit rapid coding of information and thus varying information content rapidly over time. Most interestingly, acoustic

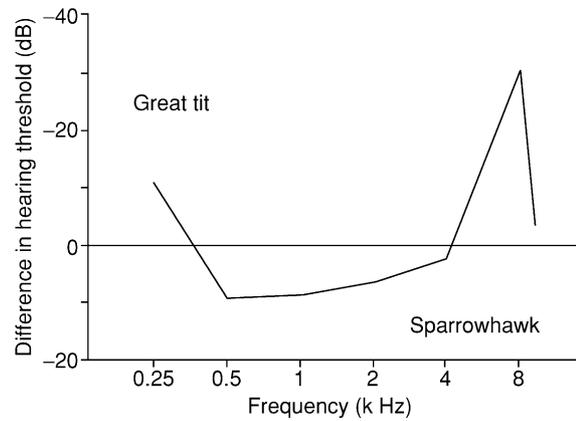


Figure 4 Differences in the hearing curves of great tits and sparrow hawks. The lines above the x-axis indicate that the hearing of great tits is superior to that of a sparrow hawk. The alarm calls are centered in the frequency range where hearing by great tits and other songbirds is most superior to that of sparrow hawks. Thus, the high pitch is well adapted to warn nearby conspecifics by minimizing the risk of being heard by a predator. Drawn after Klump *et al.* (1986), *Behavioural Ecology and Sociobiology* 18, 317–323.

communication systems in some animals bear striking similarities to human language even though this may not be evident at first sight. Birdsong makes the best comparison. Like language, it develops under the influences of vocal learning with a key sensory period early in life and it requires a period of vocal practice. There is striking geographic variation, even with discrete dialect boundaries, similar to that which occurs in human language. Birdsong is also learned without specific instruction being required and on a neurobiological level, song is controlled by specific brain regions that are lateralized, as is known for the regions for speech production and comprehension. Birds, like humans, even assess the distance to a source of sound using the same set of cues provided by environmental attenuation and degradation resulting from sound propagation.

Visual Communication

As in humans, vision in general is a key sensory modality in the behavior of many species so that communication is also of central importance in this sensory modality. Transmission distance and direction of visual signals obviously depend on the structure of the habitat. In dense vegetation, such signals are suitable only for short-range communication, whereas in open habitats, they may well be used for long-range communication, even though communication distance in general will be shorter than if using acoustic signals. Visual signals also are more directional than acoustic signals so that they are well suited to address a specific individual but are less well suited to general

omnidirectional advertisement. Two kinds of visual signals need to be distinguished: Those that are always 'on' and those that can be turned 'on' and 'off' like acoustic signals. Visual signals that are always on, such as specific body coloration, allow the individuals to signal continuously with these markings without making a specific active signaling investment in addition to having produced the signal and maintaining it. Such signals that are always on are thus not suitable for transmitting information about any aspect of an individual that varies on a short time scale, such as motivational aspects of behavior. Well-known examples of such visual signals are fur marks in mammals, colorful feather ornaments in birds, and antlers in deer. Other kinds of visual signals can be turned on or off and such signals are visual displays, such as the waggle dance in bees, the zigzag mating display in sticklebacks, and the peacock's train. Such visual behavioral displays in which specific body postures are used to transmit information, or in which specific color or body patterns are displayed actively, can be used to signal additional information that varies on a short time-scale, i.e., motivational aspects of behavior, as the peacock does with its train or some butterflies do by opening their wings when detected by a predator. The information transmitted by visual signals can be directed more specifically at certain receivers. Such directional signaling can be advantageous as it reduces the probability that unintended receivers intercept and extract information that is not in the sender's interest. In addition, directed signaling can attract and maintain attention by intended receivers, leading to specific signaling interactions as is well known for the classic example of mating displays in sticklebacks. Of course, acoustic signals also can be used to specifically address an individual but here it is more difficult to exclude other individuals from receiving the signal. Visual signals may code information about the nutritional state of an individual when the colors or metabolic precursors that are deposited in the fur or the feathers are not easily obtained. Visual signals also may reveal information about age, such as antlers in deer, or developmental history, as has been reported for symmetric ornaments, such as tail streamers in birds. Such signals may be used in decisions on mate choice as they are linked to current nutrition or the nutritional history during development, revealing honest information about aspects of an individual's quality.

Olfactory Communication

Olfactory signals are widespread in the animal kingdom. Even though they are generally less variable and complex than acoustic and visual signals, there are situations in which the use of olfactory signals is

advantageous to the signaler. Olfactory signals that are produced specifically to provide information to other individuals are called pheromones but animals can also obtain information about other individuals by perceiving odors from body glands or urine that are not classified as pheromones. Olfactory signals have the major advantage over other signaling modalities in that they can be present even when the sender is absent. Thus, they seem to be ideal for marking territories or home ranges that are too large to be patrolled continuously. Many mammals have specific glands to produce pheromones that they deposit on the vegetation to mark a site as being part of their home range or territory. Compared to acoustic and visual signaling, such marking is considerably cheaper in terms of the energy invested, both in producing the signal and in the time spent signaling. Once the chemical is produced, a persistent pheromone can be used as a marker that is effective for many days and subsequent decay can give a measure of time. Acoustic signals and visual displays, in contrast, require continued signaling and thus are time- and energy-consuming. Furthermore, olfactory signals are important in mating decisions as females can signal their receptivity to males and recent research has shown that olfactory signals are used to assess genetic similarity on which decisions on mate choice are based. Chemical signals that are not deposited on vegetation or on the ground may be released into the air and attract mates. One of the most striking examples here is the wax moth, which releases a pheromone called bombycol, even single molecules of which can be detected by males. Thus, even though chemical signals do not permit coding of highly complex information that can vary rapidly over time, as is the case for acoustic signals and visual displays, they are an important sensory modality for communication in certain contexts.

Cognition and Communication

Cognitive capabilities in communication are among the most fascinating areas in animal communication. The complexity of animal signaling and the range of response strategies to signals clearly show striking cognitive capabilities in animals. Famous examples are the comprehensive capabilities of apes, dolphins, and parrots when being trained with sign language or spoken language. Animals possibly withhold information and may use signals to mislead others, which requires complex information processing that goes far beyond simple stimulus-response systems, as animal communication sometimes was seen in early psychological studies. Animals must continuously update their information about their social environment

and by doing so memory also plays a key role. The information that an animal extracts from a signal then may be processed by integrating it with previous information to even generate specific expectations about future communication events. Recent studies have shown that animals often establish communication networks in which they not only extract information from single signals directed to them but also through transitive inference extract information by attending to others' interactions (eavesdroppers). Combining their own information obtained through signaling interactions with information obtained by observing signaling interactions among others requires a sophisticated system of information processing. In social animals, individual recognition on the basis of signals often is fundamental to enable complex relations and again there is evidence that long-term memory is involved, so that animals remember specific individuals and their relation to them even after a year or more of separation. Animals also have striking capabilities in production, usage, and comprehension learning of communication signals, and examples again are found in the well-studied songbirds, parrots, and marine mammals.

Cooperation and Deception in Communication

Often, superficial observations of animals and their communication behavior suggest that communication serves to bring about cooperation, for instance, in defending a territory, as duetting bird species do, where males and females jointly sing complex and melodious songs, or in animals where parents communicate in raising their young, or when groups of animals peacefully move along without any form of aggression being noticeable. Such apparent cooperation in reality often involves a strong conflict between the communicating individuals. Individuals often have conflicting interests as selection will favor those individuals that maximize their reproductive fitness. Cooperation thus is stable in those communication systems in which both interacting individuals have a benefit on their own. Males that signal to attract a female benefit by appearing better and more attractive than they are, whereas females benefit by not being fooled and from using honest indicators of male quality in their assessment. Selection by receivers is thus a leading force in making communication systems on average honest as receivers will be selected to not respond to signals carrying false information. However, as with any system of information transmission, there is uncertainty and noise and thus the probability of correctly rejecting a signal with false information must be traded off with the probability

of incorrectly rejecting a signal with accurate information. These basic features of signal detection theory open room for error and deception in animal communication.

Costs and Benefits of Signaling

Animal signals can carry substantial costs to a sender. The costs may lie in the energetic or other physiological costs of producing the signals, in the time devoted to signaling, or in the social costs when signals elicit specific responses by other members of the species or even attract predators. There are often conflicting interests in communication between an animal emitting a signal and those animals that are receiving the signal and that must decide whether or not and how to respond. This conflict of interest is especially evident in signals that are used to advertise and defend resources, such as food, space, or mates. Also, in parent-offspring communication, there can be substantial conflict of interest. An individual offspring that begs for food will have a different interest than that of its parents, which must invest time and energy to provision the offspring and may have to feed several offspring at the same time. As a result, selection on signalers in such a case will favor signals that exaggerate the quality or need of the signaler (cheating or deception), whereas selection on receivers will favor them to extract accurate information from the signal about the sender, i.e., not to be cheated. Thus, if signals consistently provide misleading information, receivers should stop responding to such signals. As the effectiveness of a signal will depend on the receiver's response, communication systems at equilibrium are expected to be honest on average but at least some cheating can persist. This principle was first coined by Zahavi (1975) as handicap signaling, which is meant to indicate that receivers should respond only to those signals or signal components that carry costs to the sender. Such costs would ensure honesty as only those individuals in good quality will be able to produce such a signal or only for them it will pay to produce such a signal. There is ample evidence in the animal kingdom that signal expression indeed is costly and is linked to an individual's quality. But it also needs to be noted that not all signals can be viewed as handicaps, in particular when they are cheap to produce and when the cost/benefit ratio of a signal is low.

Functions of Signals

Animals communicate, like humans, in many contexts. Information signaled will be different in different contexts and different contexts also impose

different constraints on information transfer. As a result, signals can differ strikingly depending on the context in which they have evolved. Advertisement signals are loud and conspicuous, whereas other signals may be soft and subtle and thus inherently more difficult to study. The best studied signaling systems in animals are those that are linked to resource defense, such as territorial advertisement; mate attraction; parent–offspring communication; and alarm calling. Signals in these contexts are usually not only of central biological relevance but also are conspicuous, which permits good access for scientific investigations. Apart from the specific context of alarm calling, signals in these contexts contain information about an individual's state, motivation, or quality. Thus, by and large, animals communicate information about themselves and evidence for referential signaling, i.e., signaling about external environmental events, is limited mainly to some specific examples, such as some cases of alarm calling.

Mating Signals

Many of the most conspicuous signals used in animal communication are mating signals, i.e., signals that are used to attract a partner for reproduction. Many of the loud vocal and visual displays found in birds, insects, frogs, toads, and primates are related to mating. In these cases, commonly only the males display and they do so often to attract females and to repel rival males. Also, many color displays, such as feather ornaments in birds or colors in fish, are related to mating contexts. Why have mating signals evolved to be elaborate and conspicuous? First, animals are often spaced far apart so that advertising individuals need to be conspicuous to attract potential mates from a distance. Second, mating and reproduction provide material for natural selection to work on and those individuals that are most successful in reproduction will leave more and often better offspring to the next generation. Individuals, and in particular the males, compete for access to reproduction so that selection should favor those individuals that are most successful in gaining reproductive partners of high quality or in large numbers. Thus, signals that are used to make reproductive decisions should provide information about the quality of the signaler. The resulting sexual selection leads to signals that are largely resistant to cheating, i.e., that do not allow an individual to signal better condition than it actually has. Elaborate signals have been shown often to carry costs in terms of production and maintenance as well as the likelihood of attracting predators. Such costly signals maintain the average honesty of a communication system.

Communication for Defending Resources

A second key issue in animal behavior and thus animal communication is the defense of resources. Key resources are space, such as territories, nesting sites, or food sources (and also mates, as discussed above). In order to defend resources, animals often need to signal aspects of their quality, e.g., fighting ability or resource-holding potential. As the same information is often important in mate choice, in many cases we find signals with dual functions – on the one hand, to serve to attract and maintain mates and, on the other hand, to repel rivals. Within this broad classification of signal functions, there are, however, important subtleties in the use of different signals that are relevant in only one or the other context. A male bird sings to attract a mate and to repel rival males but it then may sing differently depending on which function predominates. It may sing a soft complex song at a slow rate to a female nearby and a loud simple song at a high rate to rivals that threaten the territory. It may sing differently when nondirectionally advertising a territory but suddenly may switch to a very different singing mode with different singing patterns and timing of song once his territory is threatened by a rival. Siamese fighting fish (*Betta splendens*) may use the same signaling behaviors when courting a female as they do when trying to evict a rival. The way the pattern is displayed and integrated with other traits in behavior and communication then affects the value of the signal so that it is effective in either context.

Responses to Predators: Alarm and Mobbing Calls

Many animals produce loud and conspicuous vocalizations when they detect a potential predator. These warning signals can be either alarm calls that are given without approaching the predator (usually such calls are given immediately before a flight response) or so-called mobbing calls, which are used in combination with an approach to a predator. Both kinds of calls are interesting from an information theoretical perspective as they have been used as key models to investigate referential aspects of animal communication. Alarm and mobbing calls usually encode information about the urgency of the situation, such as the kind, threat, or distance of the predator. In addition, there is growing evidence that they are functionally referential, i.e., that specific call types or variants are given with high probability in response to specific predators. The classic example for such predator-specific calling is vervet monkeys, which use different calls in response to different types of predators and which also respond differently to the different calls in adaptive ways to avoid particular types of predators (Figure 5).

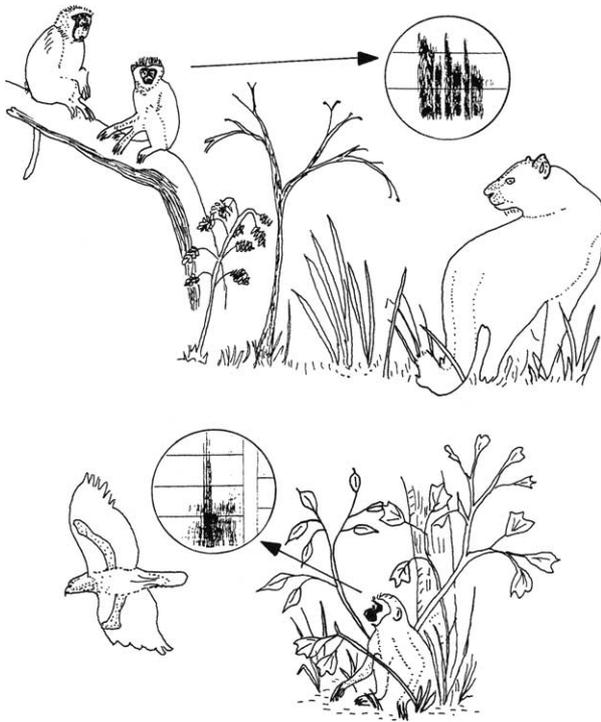


Figure 5 Alarm calling of vervet monkeys. Different calls (shown as sound spectrograms) are given in response to different predators. Playback studies have shown that the different calls elicit different flight reactions that are adaptive with respect to the type of predator for which the calls are given. Drawn after Slater (1999), *Essentials in Animal Behaviour*, Cambridge University Press, Cambridge.

In vervet monkeys, calls given in response to aerial predators elicit hiding responses, calls given in response to mammalian ground predators, such as leopards, elicit flight up into trees, whereas calls given in response to a snake elicit attention to the ground. In other species that do not have separate flight reactions to different predators, the evidence for functionally referential calls is less clear and current evidence suggests that calls vary with differences in urgency rather than differences in type of predator even though these two possibilities are not fully mutually exclusive.

Studying Animal Communication

The information available about all aspects of animal communication is in part constrained by the techniques that allow us to study these communication systems. Animals cannot be asked directly which information they have coded in a signal and which information they have extracted from a signal so we must rely either on inferences from descriptive studies on animal communication systems or on experiments. From these, we then can obtain insights into the information signaled, received, and evaluated by the

animal's behavior under controlled experimental conditions. Depending on the questions involved, data are collected in the field either through observational studies or by conducting field experiments. Laboratory studies in general allow much better control of the context but these studies are often limited by animals not communicating in the laboratory as they would under natural conditions in the field. Laboratory studies using operant conditioning regimes, for instance, are ideal to test 'just noticeable differences' in signal structures, an issue that is important to obtain insights into the perceptual capabilities of animals. Field studies in natural settings, in contrast, test for 'just meaningful differences' in signals or signaling strategies, as animals may respond similarly to signals that they perceive as being different but that still have equal salience to them. Playback techniques using sound, or increasingly also video, have been among the most powerful experimental tools in experimental research on animal communication. Often, animals readily react to such stimuli in a natural manner and by clever experimental designs and manipulation of stimuli, responses of animals to playback reveal insights into the information and its biological value decoded from the signal. The continuous refinement of possibilities to digitally manipulate signals (visual and acoustic) opens up exciting areas for future research, which should allow the unraveling of subtleties in animal communication that in many cases still remain a secret.

Comparison to Human Language

In general, finding a unique and specific difference between communication in humans and animals is not easy. Most of the traits that were believed for decades to be unique to human language have been shown to be part of one or another communication system in animals. Animals may communicate intentionally and they may withhold information on purpose even though these aspects remain difficult to study empirically. They can cheat and mislead one another. Animal signals can provide information about the past (signals reflecting quality) and the future (signals indicating intentions) and be functionally referential (alarm calls). On the other hand, the complexity of message coded in human language and its flexibility clearly go beyond what we know about animal communication. As such, human communication differs from animal communication not so much in specific traits but rather in its complexity and flexibility. Moreover, even though animals have been shown to produce referential signals, i.e., signals that label external objects, the examples are restricted mainly to certain contexts and are of limited

flexibility. A striking aspect is that our closest relatives, the apes, are very restricted in their vocal communication. Their sound repertoire is limited and calls in primates in general are not acquired under the influence of vocal learning as is the case in humans and other animals, such as songbirds or some marine mammals.

See also: Alarm Calls; Animal Communication: Deception and Honest Signaling; Animal Communication: Dialogues; Animal Communication: Long-Distance Signaling; Animal Communication Networks; Animal Communication: Parent–Offspring; Animal Communication: Signal Detection; Animal Communication: Vocal Learning; Apes: Gesture Communication; Bats: Communication by Ultrasound; Bee Dance; Birdsong; Categorical Perception in Animals; Cognitive Basis for Language Evolution in Non-human Primates; Communication in Grey Parrots; Communication in Marine Mammals; Development of Communication in Animals; Dialects in Birdsongs; Fish Communication; Frog and Toad Communication; Individual Recognition in Animal Species; Insect Communication; Non-human Primate Communication; Production of Vocalizations in Mammals; Traditions in Animals; Vocal Production in Birds.

Bibliography

- Barnard C (2004). *Animal behaviour: Mechanisms, development, function and evolution*. Harlow: Pearson, Prentice Hall.
- Bradbury J W & Vehrencamp S L (1998). *Principles of animal communication*. Sunderland, MA: Sinauer Associates.
- Catchpole C & Slater P J B (1995). *Bird song: Biological themes and variations*. Cambridge, England: Cambridge University Press.
- Cheney D L & Seyfarth R M (1990). *How monkeys see the world*. Chicago: University of Chicago Press.
- Endler J A (1993). 'Some general comments on the evolution and design of animal communication systems.' *Philosophical Transactions of the Royal Society of London Series B* 340, 215–225.
- Espmark Y, Amundsen T & Rosenqvist G (2000). *Animal signals: Signalling and design in animal communication*. Trondheim: Tapir Academic Press.
- Halliday T & Slater P J B (1983). *Animal behaviour*. New York: W. H. Freeman.
- Hauser M D (1996). *The evolution of communication*. Cambridge, MA: MIT Press.
- Hauser M D & Konishi M (1999). *The design of animal communication*. Cambridge, MA: MIT Press.
- Janik V M & Slater P J B (1997). 'Vocal learning in mammals.' *Advances in the Study of Behaviour* 26, 59–99.
- Klump G, Kretschmar E & Curio E (1986). 'The learning of an avian predator and its prey.' *Behavioural Ecology and Sociobiology* 18, 317–323.
- Krebs J R & Dawkins R (1984). 'Animal signals: Mind-reading and manipulation.' In Krebs J R & Davies N B (eds.) *Behavioural ecology: An evolutionary approach*, (2nd ed.). Oxford: Blackwell Scientific Publications. 380–402.
- Maynard Smith J & Harper D (2003). *Animal signals*. Oxford: Oxford University Press.
- McGregor P K (2005). *Communication networks*. Cambridge: Cambridge University Press.
- Naguib M & Wiley R H (2001). 'Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication.' *Animal Behaviour* 62, 825–837.
- Slater P J B (1999). *Essentials of animal behaviour*. Cambridge, UK/New York: Cambridge University Press.
- Wiley R H (1983). 'The evolution of communication: Information and manipulation.' In Halliday T R & Slater P J B (eds.) *Animal behaviour—Communication*, Vol. 2. Oxford: Blackwell Scientific Publications. 156–189.
- Zahavi A (1975). 'Mate selection: A selection for a handicap.' *Journal of Theoretical Biology* 53, 205–214.

Animal Communication: Parent–Offspring

F Trillmich and A Rehling, University of Bielefeld, Bielefeld, Germany

© 2006 Elsevier Ltd. All rights reserved.

Communication between parents and offspring ensures offspring survival, growth, and successful development to independence. Parents invest time and provide food, protection, and – in endothermic organisms – warmth. This costly brood-care behavior can evolve only if the donor obtains fitness benefits for its actions. Such benefits arise if the receivers of parental

care share genes with the care-giving individual. Consequently, care should be expended only on own offspring or those of close relatives, and not on unrelated individuals. This is ensured by recognition mechanisms.

Beyond recognition, parental care should be allocated in such a way that the costs incurred lead to maximal benefits (fitness) achieved through offspring. This makes communication about the needs of offspring necessary. However, offspring compete for the limited, precious resource of parental care whether directly with siblings in a brood or indirectly with