

CHAPTER 20

Using the Senses in Animal Communication

Erica A. Cartmill

INTRODUCTION

Animal communication, like human communication, is a multimodal phenomenon. Just as humans entwine speech, gestures, bodily postures, noises, and facial expressions when they talk with one another, non-human animals use multiple modalities and senses when communicating with conspecifics (other individuals of the same species). Some animal species communicate primarily in one modality; others use several. Importantly, the timescales over which animals communicate can differ greatly from human communication. Some things described in the literature as animal signals are immutable traits (e.g., color or pattern), things that cannot be controlled by the individual. Other signals (e.g., pheromones) are deployed by animals and have a clear onset, but fade slowly over time in a way that is determined by the physical constraints of the modality rather than by the actions of the signaler.

Animals derive information about others from a wide variety of sources, but only some of these sources have evolved to communicate with others. Biologists studying animal communication make a distinction between *signals* and *cues* (Laidre and Johnstone 2013). Signals are traits or behaviors that have been shaped by natural selection to convey particular types of information to specific kind of audience. The evolution of signals impacts the *fitness* of both signalers and receiver i.e., how successful these animals are in passing their genes on to the next generation. Cues, by contrast, can be used to gain information about an animal but are byproducts of other behaviors and did not evolve to communicate information. For example, a pigeon with a leg injury might walk with a limp, and other pigeons or predators could use this as a cue to their health. However, this differs from the broken wing display that some species of birds have evolved as a signal to lead predators away from the location of their nests (Humphreys and Ruxton 2020). The distinction between signal and cue bears some resemblance to Erving Goffman's distinction between the expression a person *gives* and the expression they *give off*. The expression given involves a speaker's purposeful use of symbols to convey their conventionally agreed upon meanings. The expression given off includes many non-symbolic and potentially unconscious actions that others can use to infer things about the speaker (Goffman 1959). While there is no agreed-upon definition of *communication* used in research with animal, *signal* typically denotes a behavior that

The New Wiley Blackwell Companion to Linguistic Anthropology, First Edition. Edited by Alessandro Duranti, Rachel George, and Robin Conley Riner.

© 2023 John Wiley & Sons Ltd. Published 2023 by John Wiley & Sons Ltd.

alters the behavior of another and for which both the production and the comprehension have been shaped for that purpose by natural selection (Maynard Smith and Harper 2003).

Linguistic anthropologists and scholars of animal communication have little overlap in their theories or literatures. As the example above shows, however, they often play with similar concepts concerning the construction, expression, and interpretation of meaning in spontaneous interactions between the individuals they study. While the biological literature is more likely to cite Darwin and Dawkins than Goffman, Gumperz, and Grice, it is also concerned with questions of reference, relevance, social interaction, and meaning-making. In some ways, the job of the anthropologist is simpler, because we can interview people to gain insight into the meanings, intentions, and uses of unfamiliar expressions. In other ways, the biologist's job is simpler, because animal communication systems are not as multi-valenced and complex as human language.

My goal in this chapter is to provide an overview of the ways animals use different sensory channels in their communication. I also introduce the reader (most likely a linguistic or sociocultural anthropologist) to important biological concepts like *sexual selection*, *honest signaling*, *information theory*, and *mimicry*. Rather than attempt a comprehensive review of animal communication theory (for excellent overviews, see Bradbury and Vehrencamp 2011; Maynard Smith and Harper 2003; Searcy and Nowicki 2010), I provide examples from a wide variety of species to illustrate the different ways animals communicate, their different sensoria, and how different communicative modalities possess unique communicative opportunities and constraints. The chapter is organized according to three themes: **core biological concepts** in animal communication (e.g., *natural selection*, *honest signaling*, *information theory*, *mimicry*); **perceptual systems** used in communication (e.g., sight, hearing, touch, smell/taste), and **linguistic concepts** as they are applied in animal communication (e.g., reference, intentionality).

My hope is that this chapter provides a starting point to empower more anthropological scholars to undertake work on animal communication. Biologists simplify and categorize communicative interactions for the purposes of quantitative analysis and experimental manipulation. This is important in trying to understand the connections between signals, fitness, and selective pressures, but it greatly underestimates the complexity of animal interactions and may lead scholars to characterize animal communication as simpler than it is. Linguistic anthropologists could bring an important lens to studies of animal communication by bringing the features and complexities of interactions into focus. This might lead to a more complex and nuanced view of animals as social beings who can draw on a wide variety of sources in meaning-making.

Natural Selection

Animals and humans face many similar social challenges and use communication to make friends, attract mates, compete with rivals, and otherwise structure their social worlds. However, only humans possess an open-ended linguistic system that allows users to combine a finite set of learned items in new ways to convey an infinite set of meanings (von Humbolt 1836). This makes it possible for humans to communicate about things that they, their predecessors, or interlocutors have never encountered or imagined before. Language makes it possible to speak of unicorns tandem-riding Segways or teleporting skylarks with 40-year mortgages.

Animal communication systems are much more limited. Signals are typically genetically inherited rather than learned, and the contexts in which signals are given (sometimes called eliciting stimuli by biologists) are often fairly limited. That doesn't mean that animal signals

AQ1

can't be complex. Animals can perform elaborate displays incorporating many elements and involving multiple senses. However, the forms and deployments of most animal signals are not selected by the communicating animal during the interaction (as a human might decide whether to make and how to structure a request). Instead, they are shaped by *natural selection* over many generations.

There are different kinds of selective pressures that can shape animal signals over evolutionary time. *Sexual selection* is commonly invoked to explain the presence of complex courtship displays and sexually dimorphic traits. For example, an individual with the most impressive (read: attractive) mating display would win more mating opportunities and thus have more offspring. Assuming the mating display was at least partially heritable, that individual's offspring would have more attractive displays than the offspring of other individuals and they, in turn, would win more mating opportunities and have more offspring. Thus the trait would spread throughout the population and if there continued to be variation in how attractive the displays were, animals with the most attractive displays would likely have the most offspring and the features of the average display would become more and more pronounced over generations.

When a signal is pulled in one direction by sexual selection, it is often pulled in the opposite direction by energetic cost or predation risk. Larger, more ornate features or displays typically incur costs for the signalers, and thus only animals in peak condition can afford to have the showiest versions (Figure 20.1). This tradeoff has been called *honest signaling*—to convey the idea that the signal produced by an animal is an *index* (Peirce 1935) of the health, age, size, fertility or other qualities of the signaler (Zahavi 1975). These types of signals are difficult if not impossible to fake (though see Blackwell et al. 2000 for a study of fiddler crabs dishonestly signaling fighting ability by re-growing large but weak claws). Human language cannot be called an honest signaling system because there is very little that cannot be faked in human communication. To avoid deception, humans must instead rely on social norms, relationship strength, and reputational costs.



Figure 20.1 Peacocks are a classic example of sexual selection and the ways predation risk limits that selection. Males with the most feather eye spots (biggest tails) attract the most mates and have more offspring, who also have larger tails. However, tail size cannot keep increasing indefinitely because larger tails make it more difficult for peacocks to fly, perch, and avoid predators. These two competing pressures keep tails large but place an upper bound on size. *Source:* Tezzstock/Adobe Stock.

“Information”

Animal communication research has been strongly shaped by the model of information transfer formalized by Claude Shannon in the 1940s, now seen as foundational to information theory. In Shannon’s model, “information” is conceptualized as a set of messages that must be encoded, sent over a noisy (or leaky) channel, and then received and decoded at the other end (Shannon 1948). It resembles de Saussure’s (2011 [1916]) concept of a *speech circuit*, particularly in emphasizing the articulation between a psychological processes (the concept) and a physiological one (the telling). The Shannon model has been applied to certain aspects of human language (e.g., efficiency of encoding information across languages: Coupé et al. 2019), but is generally regarded as being too simple to explain all the complex inferences humans make when communicating.

Animal communication, however, is often analyzed through the lens of information. Animals involved in a communicative exchange are described as signalers and receivers or recipients, and much attention is paid to how the signals are transmitted and whether the signals (rather than the contexts) contain the communicative message. When the signal alone is enough to convey the message, it is deemed to be meaningful and context-independent, in the sense that it continues to carry meaning even when separated from its original context. For example, a pointing gesture directed at a dog loses its meaning when it is removed from its physical context (and has nothing to point to). The word “dog” carries at least some of its meaning when used across a wide range of contexts.

Human languages can communicate many things in ways that scholars of animal communication would consider “context independent,” for example, by recording things in writing or by retelling an event to another person after it has happened (e.g., “toads emerge after it rains”). However, as many linguistic anthropologists have shown, much of the information in human communication is carried outside of the semantics and syntax of the linguistic system. Speakers convey many kinds of information through extra-linguistic and paralinguistic features of interaction. Vocal elements like accent, pitch, speed, breath, and vocal fry all convey meaning (e.g., Gal 1995; Mendoza-Denton 2011; Sicoli 2015). So do situated bodily movements like gesture, gaze, posture, and facial expression (e.g., Duranti 1992; Müller et al. 2013; Sidnell 2006). The physical and social contexts surrounding a communicative act are also critical in understanding its full meaning (e.g., Goodwin 2018). Gumperz (1992) described these types of extra-linguistic features as “contextualization cues.” He argued that rather than being seen as peripheral to linguistic communication, they should be recognized as necessary for interpreting the content of a speech act and for relating it to what precedes or follows.

The distinction in animal communication between the signal alone and the signal plus its social and environmental context can be thought of in terms of de Saussure’s notions of *langue* and *parole* (2011 [1916]¹). Here, *langue* would be the ideal structures and meaning of a signal in the abstract and *parole* would be the signal as it is used in a natural communicative exchange. Take, for example, a male song sparrow singing to defend his territory against rivals. The species-typical ideal song (estimated from recordings of many individuals), including the pitches of the notes and the patterns of the song phrases, could be considered *langue*. The way that particular male sings his song on that day, including the small variations, deviations, and other “imperfections” he makes when singing could be considered *parole*. Additionally, the broader social and environmental contexts of his singing all

¹ Note the Gumperz (1982) argument contra Saussure that we should not label some communicative elements central and some peripheral.

add to the full meaning. These could include: the way he hops from branch to branch along one side of his territory while singing, to direct his song to a rival neighbor; his individual identity (e.g., Chuck not Henry), his age and fitness; the identity of his neighbor; the size and location of his territory; the time of day and of year; the presence of eavesdroppers; and the threat of predation during his song. All of these factors (and more) could play a role in understanding and interpreting the full meaning of his communicative act, for analysts and fellow sparrows alike.

Animal communication researchers tend to search for and privilege signals that can be understood outside of their original context(s). While it is not possible to test context-independence in all types of signals, many studies of animal communication record and present signals outside of the context in which they were recorded in order to see whether the signal itself carries the full meaning, or whether it is only one of many clues to meaning that occur within the signaling context. Auditory signals are perhaps the easiest to experimentally isolate from their original contexts. They can be recorded and then played back to animals outside of the original context. These so-called “playback” studies form a cornerstone of animal communication research and are the dominant method for testing meaning of animal signals. Because perception of auditory signals does not depend on seeing the signaler, it is possible to fool animals into believing that the signal is made by a conspecific and not a group of researchers crouching in the bushes with a speaker. Acoustic signals also lend themselves to experimentation because it is relatively easy to measure, manipulate, and reproduce them. You can change the pitch, duration, or phrase order in a recording of bird-song using a laptop, but it is much more difficult to identify, let alone manipulate, the volatile compounds in an olfactory signal.

Who’s Who?

Some animal signals are *directed* towards a particular individual; others are *broadcast* for detection by any individuals within the perceptible range. This leads to several types of signal recipients, echoing the distinctions Goffman makes between kinds of hearers and other participants in his discussion of footing in human communication (1981). While broadcast signals are not directed at a particular individual, they may have the goal of reaching a particular kind of audience. They might be “designed” (through natural selection) to attract mates, declare ownership over a territory to potential rivals, or raise an alarm for group members when a predator is detected. Directed signals can use the full range of senses, but broadcast signals are typically limited by the range and detectability of the signal medium. For example, it is difficult to broadcast a tactile signal to many others (though it might be possible by vibrating a shared substrate). Broadcast signals are most likely to rely on sound (e.g., songs) or smell/taste (e.g., urine marking). The substrate within which a signal is transmitted can also impact its perceptibility. Sound travels well through the air, but only certain frequencies can travel long distances in the water. Many aquatic animals instead rely on chemical signals to communicate at a distance.

For both directed and broadcast signals, the recipient is typically another individual of the same species (i.e., a conspecific). However, there are some cases where the recipient is an animal of another species (i.e., a heterospecific). This can be seen when prey species vocalize in the presence of a cryptic (hidden) predator to indicate that they have been spotted and the animal is no longer an easy meal. Designating a recipient does not imply intentional communication on the part of the signaler, but, rather, that a predator is present when the signal is produced, the animal does not hide when signaling, and the predator responds to the signal by changing its behavior.

Just as in human language, when an individual other than the targeted audience perceives and acts on a signal, they are said to be *eavesdropping* (Valone 2007). For example, a male chickadee might eavesdrop on a broadcast song contest between two other males and modify his subsequent behavior to more aggressively defend his territory against the winner of the overheard exchange (Mennill and Ratcliffe 2004). Eavesdropping can also happen between species. There are many examples of animals learning to respond to the alarm calls of another species though they may be quite different from the calls of their own species (Magrath et al. 2015).

Production vs. Perception

Many species have evolved particular features or behaviors that improve their ability to perceive signals. These may be static traits like large ears or better color vision, or they may be postures or behaviors that help an animal use a particular sense more effectively (Figure 20.2). For example, one animal might sweep its head side to side, thereby increasing its perceptual field in sight, electroreception, or smell, while another might stop moving and angle its ears, allowing it to better locate the source of a sound. Robert Seyfarth and Dorothy Cheney detail the different challenges for signal production and comprehension in their 2003 paper “Signalers and receivers in animal communication.”

Mimicry

Some species evolve markings, calls, or displays that resemble (“mimic”) those of other species (see Endler 1981 for an overview). This is often seen when a prey species (A) evolves a signal that resembles a species (B) that preys on their predators (C). When C sees A’s signal, it may mistake A for B (i.e., it might mistake its prey for its predator). Since B preys



Figure 20.2 This male horse is improving its ability to smell by raising its front lip and displaying its teeth in a smelling posture called flehmen. This posture helps animals pull pheromones and other scents into the Jacobson’s organ (also called the vomeronasal organ), a patch of specialized cells located in the nasal cavity that detect liquid organic compounds. The flehmen response is found in many mammals (those with a Jacobson’s organ), but is absent in African primates and great apes (including humans). *Source:* Kimberley/Adobe Stock.



Figure 20.3 The caterpillar of the *Hemeroplanes triptolemus* moth strongly resembles a snake when it raises the front half of its body into the air. The area resembling top of the snake's head is actually the underside of the caterpillar. The caterpillar's mimicry of a snake is effective at deterring its main predators (birds), which are prey for many snake species. *Source:* Atelopus/Adobe Stock.

on C, C might become fearful and leave A alone. Of course, as the mimicked signal evolves in A, the ability to detect mimicry evolves in C, in what is often referred to as a predator-prey arms race (Dawkins and Krebs 1979; Thompson John 1994). Importantly, none of this is conscious! It evolves very slowly over many generations with no end goal in mind and no intention in the signaler. Figure 20.3 illustrates an example of this type of mimicry.

A few species have evolved behavioral mimicry, produced by copying sounds or movements rather than static traits. This is most salient in birds that can replicate the vocalizations of other species (heterospecific signals) as well as other sounds in their environment. Heterospecific vocalizations are learned rather than inherited by mimicking birds, and what has evolved is the ability and tendency to copy rather than the resemblance to another species. The motivations for vocal mimicry are debated. Some studies suggest that birds mimic the calls of other species to elicit their aid in mutual predator defense (Goodale and Kotagama 2006). Others suggest that birds mimic alarm calls of other species to deter competitors (Kelley and Healy 2012). While the ability to mimic by copying sounds may seem familiar to us because many of the bird species kept as pets are vocal mimics, this type of behavioral mimicry is much rarer across species than mimicry in static traits like the caterpillar in Figure 20.3. Heterospecific vocal mimicry is limited to a handful of species: humans, some bird species, cetaceans, pinnipeds, elephants, and bats, species also considered intelligent and flexible in their behaviors (Dalziell et al. 2015; Janik and Knörnschild 2021).

PERCEPTUAL SYSTEMS

We tend to think of there being five major senses: sight, hearing, touch, smell, and taste (Finnegan 2002). This categorization and the way senses are described differs somewhat across societies (Majid and Levinson 2011) and human perception includes other types of sensory behavior like proprioception (knowing where one's body is in space). However,

these five senses provide a useful starting point to consider and compare sensory worlds across species. Some animal species have abilities that humans lack (e.g., magnetic perception, echolocation, sensing heat or electricity), while others lack one or more of the “human five.” Though there are many differences between the sensoria of different species, the senses typically used in animal communication can essentially be clustered into these familiar five categories. The definition of each sense, however, has to be broadened to account for abilities of animals that fall outside of human perception (e.g., seeing ultraviolet light, producing bioluminescence, hearing/feeling infrasonic vibrations). Table 20.1 provides a rough overview of the major perceptual channels and gives examples of the types of animal signals that make use of them. Of course, many signals are multimodal and involve more than one sense. Birds often produce visual displays along with their calls. Many kinds of touch also include the exchange of chemical signals perceived through smell or taste. I have tried to organize the examples below according to the dominant sense involved in their perception.

Table 20.1 Comparison of different perceptual senses and the ways they are commonly used in communication across animal species

Sense	Perceived element	Physical contact	Typical sensing organ(s)	Example(s)	
Sight (vision)	Light waves	no	Eyes, photosensitive cells	Visual marking, Gesture, Lumination, Movement	
Hearing (audition)	Sound waves or vibrations in water or ground	no	Ears, jaw, swim bladder, body	Vocalization, Hitting body part or substrate	Some vibrations may be felt with the whole body rather than just the jaw or bones in the ear. These could be thought of as either hearing or touch.
Touch (taction)	Pressure or temperature changes on body	yes	Body, whiskers	Pushing, Pulling, Fanning, Licking, Embracing	
Smell (olfaction)	Chemical signals	no	Nose, antennae, other chemoreceptors	Urine, Sweat, Pheromones	Smell and taste are closely related forms of chemoreception; animals may sample the same signal through either sense. There may be no practical difference in some environments (e.g., water).
Taste (gustation)	Chemical signals	yes	Tongue, skin, antennae, other chemoreceptors	Urine, Sweat, Pheromones	
Sensing Electricity (electroreception)	Electrical signals	no	Electroreceptors	Weak electrical pulses	

SIGHT

Animal communication relying on sight falls into two broad categories: *static traits* and *dynamic behaviors*. Traits are features of the animal itself rather than behaviors the animal produces. They are long lasting and may be permanent. Feather coloration and antler size are examples of traits that serve as signals. Individuals with more brightly colored plumage or larger antlers are typically in better health and are thus more formidable opponents and more attractive mates. Individual animals can't do much to alter these traits, but the traits might change slowly over time as an individual becomes more or less stressed or well-fed. Traits can be considered passive signals because they are not deployed, displayed, or turned on by the signaling animal; instead they are continuously present. They can be considered broadcast signals in that they aren't directed at a particular individual, but can be picked up by any recipient within range.

As with other types of signals, visual signals can target conspecifics or heterospecifics. One type of static visual signal targeting heterospecifics is bright coloration suggesting that a potential prey species is poisonous or distasteful. Most prey species are "cryptic" (camouflaged against the background), and only the most fit individuals can display bright colors or other noticeable markings since it makes them easier to see and thus incurs an increased risk of predation. However, some prey species have evolved a different strategy by displaying bright colors that make them highly visible to predators. These traits lower predation risk by communicating to would-be predators that the animal would make an unpleasant meal. This type of coloration is called "aposematic" and is sometimes described as warning coloration. Species with aposematic traits evolved their bright markings alongside toxins in their skin or other predator deterrent features (Figure 20.4). Predators quickly learn to avoid those colors or patterns after a few unpleasant encounters with poisonous prey. The bright colors might not help the first animal a predator samples, but they are likely to help its relatives, and thus the trait remains in the population. Some palatable prey species have evolved to mimic the colors or patterns of poisonous or otherwise unpalatable species, though they do not have the predator-deterrent features themselves. This is called Batesian mimicry (Bates 1862) and could be considered an example of dishonest signaling. A classic example is that of the drone fly (*Eristalis* spp.), which closely resembles the honeybee, though it does not have a stinger (Brower and Brower 1965).



Figure 20.4 Many animals, like this poison dart frog, have evolved bright colors along with toxic or noxious compounds that make them distasteful to predators. This is known as aposematic marking or coloration. *Source:* Alcuin/Adobe Stock.

Visual Behavioral Displays

Animal signals relying on vision include many types of dynamic behaviors as well as static traits. Gestures, displays, dances, facial expressions, and postures are all primarily visual signals. Humans typically think of movements and body postures as the main types of dynamic behaviors and bodily coloration/ and markings as the main types of static signals, but some = animals usedynamic visual signals that humans cannot produce. Some insects and fish communicate using light (bioluminescence), broadcasting visual signals to others at long range when there is very little environmental light (Herring 2000; Lloyd 1983). Some cephalopods (octopus, cuttlefish, and squids) communicate by changing patterns of color on their body using specialized pigment sacs called chromatophores (Mather 2016; Packard 1995). These color changes can be subtle, similar to blushing, or fast-moving bright patterns almost like a wearable video screen.

In some cases, the information transmitted in dynamic visual signals are only perceptible during the act itself. Gestures, facial expressions, and some postures and dances have this property. The information they are attempting to convey disappears when the signaler finishes the movement. In other cases, dynamic displays are used to draw attention to a static trait, like the color or size of a part of the body. In these cases, the trait persists after the movement has ended. For example, fiddler crabs wave their large claws above their heads when threatening a rival. This display posture allows both competitors to see and compare the size of their claws. Claw size is a good indicator of fighting ability (Jennions and Blackwell 1996), and so the crab with the smaller claw may retreat rather than risking injury in a fight. Many fight displays have evolved to facilitate comparison of size, strength, or agility and thus allow competitors to avoid risking injury in physical combat (Laidre and Johnstone 2013). Dynamic display of static traits is common in courtship as well. The intensity of blue on the feet of blue-footed boobies is an indicator of health and vigor and is a preferred trait in selecting a mate (Torres and Velando 2003). The mating display of the blue-footed booby is a relatively simple dance in which each foot is lifted and shown off in turn (Nelson and Nelson 1978, Figure 20.5). This movement highlights the brightness of the bird's feet and allows others to better examine them.

Many signals targeting heterospecifics are dynamic behaviors emphasizing static traits. Prey species frequently use heterospecific signaling to deter or deflect predators. In some cases, the prey species will display a conspicuous marking when a predator starts to attack causing the predator to startle and delay, withdraw, miss, or attack a non-vital body part. In other cases, the prey species will burst out of hiding when a predator draws near and display a conspicuous marking while fleeing. Sometimes these anti-predator markings are visible all the time, but may become more salient during an escape maneuver or defensive posture. The sudden change between crypsis and aposematicism is often referred to as a *startle display*, causing the predator to startle or recoil at the abrupt sensory overload (Umbers et al. 2017).

Perhaps the most well-known anti-predator markings are so-called eye spots: bright circular markings commonly found on many insects and fish that stand out from the background colors of the animal (Figure 20.6). Historically, scholars have believed that these markings resemble the eyes of the predator's predator (Stevens 2005). This would serve as a strong deterrent to attack, and could provide the prey species time to escape, even if the predator only hesitated for a split second. Recent studies, however, have questioned whether these markings really mimic the eyes of dominant predators (Stevens and Ruxton 2014).



Figure 20.5 The bright blue feet of the blue-footed booby are highlighted during courtship displays. While they have no control over the color of their feet, the birds can make the color more visible by raising and showing off each of their feet in turn. This display illustrates how a dynamic behavior can make a static signal more prominent. *Source:* Dennis/Adobe Stock.



Figure 20.6 The Io or peacock moth (*Automeris io*) has large, prominent eye spots on its back wings. *Source:* Jim and Lynne Weber/Adobe Stock.

HEARING

Sound is a critical modality in many animal communication systems. It is particularly important for communicating across long distances, in environments with low visibility, and for locating out-of-sight group mates. Much of the research on acoustic communication focuses on vocalization, but animals use many other types of sounds to communicate as well. Insects create sound by rubbing their legs or wings together or by vibrating sound-making organs (Figure 20.7). Birds are known for their calls and songs, but many also communicate by rhythmically tapping on trees or by clapping their wings together. Primates use a wide range of vocalizations, but also frequently communicate with oral noises that don't engage the vocal chords (like smacking their lips together) (Fedurek and Slocombe 2011). Many animals also make communicative sounds by striking, shaking, slapping, or scratching objects in their environment.

Vocalizations can be directed or broadcast. Directed vocal signals are typically softer and less noticeable at a distance. They may be particularly important in negotiating and strengthening close social bonds (e.g., during nursing, grooming, or comforting). Broadcast vocalizations are designed to be perceptible by many individuals or by certain types of individuals at a distance. These calls are frequently used to mark territory boundaries, advertise for mates, and raise alarms when threats are detected.

In a now classic example, researchers found that vervet monkeys produce unique alarm calls in the presence of leopards, eagles, and snakes (Struhsaker 1967). Playback studies



Figure 20.7 Animals produce sounds in many ways, not only through vocalization. Insects, like this Brood X cicada (*Magicicada septendecim*), often make communicative sounds with specialized organs or by rubbing their legs or wings together. Male cicadas have an organ under each of their wings called a tymbal, which produces a loud sound when it is vibrated.

demonstrated that the calls themselves produced different predator-defense behavior in the listeners. Leopard calls led to monkeys running up into the trees, eagle calls to monkeys crouching low or taking cover, and snake calls to monkeys standing up on their hind legs and scanning the ground (Seyfarth et al. 1980). This finding led some to describe the vervet calls as words for leopard, eagle, and snake. However, it is important not to default to our own linguistic and conceptual categories when describing animal communication. The alarm call system of domestic chickens illustrates this point. Chickens produce different calls for raccoons and raptors (Figure 20.8). In playback studies, these calls elicited different defensive postures (standing tall and looking around vigilantly for raccoons, crouching down for raptors). This might lead to the assumption that chickens have one call that means “raccoon” and one that means “raptor.” However, when the researchers presented chickens with videos of raccoons above their heads, chickens produced the call normally given to raptors. It became clear that chicken alarm calls communicate the direction of likely attack (terrestrial vs. aerial) rather than the type of animal (Evans et al. 1993). Of course, we shouldn’t conclude that chickens have a call that exactly means “terrestrial predator” or one that means “aerial predator,” but these types of clever experiments, combined with detailed observations of animals in the wild, bring us closer to understanding how animals conceptualize and communicate about their worlds.

The frequency of an auditory signal presents both affordances and constraints. It is easier to locate the source of a low-pitched sound than a high-pitched sound. So, while low-pitched sounds may be more effective at attracting conspecifics, they also run the risk of allowing eavesdropping predators to more easily discover the signaler. Sexual selection may also influence pitch if one sex (typically females) demonstrates a pitch preference in the calls of the other sex. One classic example of this is found in Tungara frogs (*Physalaemus pustulosus*). Male frogs produce both high-pitched whines and lower-pitched chucks. Females are able to locate males using the whines alone, but prefer males who produce more chucks (Ryan and Rand 1993).



Figure 20.8 Many animals, like this chicken, produce alarm calls when they detect predators or other types of danger. Typically, these are loud “broadcast” type calls that are not directed to a particular individual but instead can be heard by any members of their group who are within range. Chickens have different calls for predators attacking from the ground vs. the air. *Source:* Shediva/Adobe Stock.

Some animals are able to use very high acoustic frequencies to navigate, using echolocation. During echolocation, animals produce very high-pitched sounds in one direction. Some of the sound waves reflect off objects in the environment and are perceived by the echolocating animal. Many animals have evolved specialized organs for producing or sensing these sounds. Echolocation is mostly used to navigate and locate prey, but there is evidence that it can also be used in communication (at least as cues) by some bat species (Knörnschild et al. 2012).

When the frequency of a sound is low enough, it is more likely to be perceived through the body as vibration. This blurs the line between hearing and touch. In one such case, elephants communicate with one another using infrasonic (frequency below 20 Hz) “rumble” vocalizations that can be heard up to 10 km away. These vocalizations travel through both the air and the ground, though it is thought that they are perceived most effectively through the ground. Elephants detect these seismic vibrations using special nerve endings in their feet (Bouley et al. 2007).

TOUCH

All animals perceive touch, which it is critical in navigating social relationships, particularly during intimate interactions like nursing, play, fighting, and mating. Touch is, however, notoriously difficult to study at a distance and without interviewing subjects about their first-hand experiences. It can be hard to tell whether two animals are touching. It is even more difficult to assess the quality and strength of touch at a distance. It is possible to measure the force of touch on inanimate objects by placing pressure sensors on the objects. This is how the strength of animal bites is measured (Anderson et al. 2008). But when touch is directed towards another animal, it is not possible to intercept and measure the strength or quality of touch without disrupting the interaction.

The difficulty of studying the communicative role of touch is compounded by the inability to perform experiments in which touch can be manipulated. It is possible (though never easy) to play auditory signals to groups of animals to see how they will respond. It is also possible to manipulate some types of visual signals by painting colors on animals or by augmenting or attenuating ornaments like plumage or antlers (e.g., swallow tail length: Møller et al. 1998). It might be possible to simulate communicative touch in very particular circumstances, but a researcher probably can't encourage a female kingsnake to mate by biting her on the neck like male snakes do during copulatory behavior (Lewke 1979).

Instead, researchers are limited to describing the aspects of tactile communication that they can see at a distance. Since most tactile behaviors also have visual signatures (a poke can be seen as well as felt), it is possible to document them in this way, but there are limitations to what can be inferred about the tactile experiences of the animals involved. For example, elephants touch each other with their trunks in many social interactions (Langbauer 2000; Lee 1986). These trunk touches can be seen by human observers (Figure 20.9). The elephants would be able to receive many kinds of tactile information during these touches that are not accessible to human observers, including pressure, tension, and temperature. They also receive olfactory and auditory information during these interactions, making these highly multisensory signals.



Figure 20.9 African elephants use their trunks to touch one another in many types of interactions. When greeting one another or affiliating with close contacts, elephants reciprocally entwine their trunks and undoubtedly receive tactile and olfactory information that are not perceptible by human observers. *Source:* Sichkarenko_com/Adobe Stock.

SMELL/TASTE

Human communication has not been shown to make much use of smell or taste (see Wyatt 2020 for an analysis of the reproducibility of research on human pheromones). However, chemical communication is a critical communicative channel for most other species. Animals use chemical signals to mark territory, find mates, lay down or follow routes to resources, signal danger, call for help, stimulate lactation, and induce many other behaviors. Chemical signals are perceived as smells or tastes in humans, so I have grouped them in this way here. However, animals detect these signals using many types of sensors, including antennae and receptors in the skin on different parts of the body.

Animals have evolved a range of organs, sensors, postures, and behaviors to help them better detect and interpret chemical signals. Jacobson's organ (described earlier in the chapter) is just one example of a specialized area packed with chemoreceptors for receiving and processing chemical signals. Some chemoreceptors are specially tuned to only detect a particular compound. Other receptors are "broadly tuned" in that they pick up a range of different chemical signals.

Chemical signals that have evolved to communicate with conspecifics are called *pheromones*. Many animals have specialized areas for producing as well as receiving pheromones and other chemical compounds. Chemical compounds can be released into the air or water, deposited onto an environmental substrate, or placed directly onto the sensing organ of another animal. Pheromones and other chemicals decay over time. These signals are strongest when they are first produced; they fade over time. Compounds may decay at different rates and the substrate onto which the compounds are placed will also affect how long they last. Chemical signals can be affected by temperature and exposure to other environmental elements. Unlike auditory and visual signals, chemical signals persist long after the signaler



Figure 20.10 Dogs, like many other animals, signal using the chemical compounds in urine. These signals are long-lasting but fade over time, so others can use their potency to estimate the time that has elapsed since they were produced. They can be interpreted by multiple audiences, serving both as an advertisement to potential mates and a warning to rivals. Urine can also be used to detect the presence of predators or prey species.

has produced them. The rate at which these signal fade can be used by other animals to estimate temporal or physical distance to the signaler. For example, a dog urinating on a patch of grass marks the location with volatile compounds in her urine. Other dogs who pass by the spot will be able to identify not just the sex of the signaler, but also to estimate her health and how much time has passed since she marked the fence (Figure 20.10).

Pheromones are critical to insect communication, particularly in hymenoptera (i.e., ants, bees and wasps). Ants famously use pheromones to mark trails from food resources back to their nest. Other ants then follow these trails to the resource, using receptors in their antennae to detect and follow the signal. But ants and other social insects use pheromones to communicate about a broad range of things (Jackson and Ratnieks 2006). Some release pheromones when they encounter danger to marshal support and defend the colony from attackers. Some release a specialized pheromone to attract other foraging ants if they locate a large prey item that they are unable to retrieve themselves. Pheromones can also be combined with signals in other modalities to produce more specialized signals.

DETECTING ELECTRICITY

The senses discussed above use different organs, mechanisms, or channels to produce and receive signals. A visual gesture produced by the hands or body but perceived with the eyes. A contact call is produced with the vocal tract but perceived by the ears. Electrical signals are



Figure 20.11 South American knifefish (Order Gymnotiformes) are one of the most well-known examples of animals using electrical signals to communicate. This group of fish (including the infamous “electric eel”) produces electrical pulses that contain information about their species, sex, age, and (at least in some species) social rank (Smith 2013). They produce and perceive electrical signals using electric organs composed of muscle or nerve tissue. *Source:* Reimar/Adobe Stock.

unique in that they are produced and received by the same specially evolved electric organ(s). More types of animals can detect electrical signals (electroreceptive species) than can produce them (electrogenic species). Electroreception is found in monotremes (mammals that lay eggs), dolphins, insects, and fish (Bullock et al. 2006). Electrogenesis (producing electricity) is only found in fish. This ability appears in only a few species, but they are not all closely-related and electrogenesis has evolved at least six different times (Gallant et al. 2014). Electrogenic fish species primarily use electroreception to navigate and hunt and electrogenesis to stun their prey, but they can also communicate using weak electrical pulses in different durations and patterns (Figure 20.11). Electric fish typically live in murky water where visual communication is difficult, and so electrocommunication may be efficient, though costly to produce.

LINGUISTIC CONCEPTS

Reference

When observing a group of animals interacting spontaneously in their natural environment, it can be very difficult to tell whether a behavior by one and a subsequent action by another are causally related. Is the behavior in the first a signal communicating something about the environment to the other individual who receives the signal and reacts to the information? Or are both the original behavior and the later action independent responses to a shared environmental feature? Experimenters often try to record and isolate the signal and then present it to animals to see how they respond (using the playback method). If the responses in the experiment mirror the responses seen in the original context of the signal, then experimenters conclude that the signal itself communicates information that leads animals to respond in a particular way. This is taken as evidence of the *referentiality* of the signal. However, it is impossible to fully assess the communicative intent or interpretation of the signal, so many researchers have adopted the term *functionally referential* to describe signals that function as if they have reference (Blumstein 1999; Macedonia and Evans 1993; Townsend and Manser 2013).

Intentionality

There is no evidence that most of the signals I discuss in this chapter are produced *intentionally* by the signaling animal (i.e., with the goal of communicating a specific meaning to a specific audience). In the case of static traits, intention is not a useful concept because animals do not produce the signal, it just exists. However, even for behavioral signals with clear starts, scholars do not typically engage with the question of intentionality, instead asking whether a signal is “under volitional control” of the signaler (i.e., can the signaler choose whether or not to signal).

Many animal signals show *audience effects*, meaning that animals produce signals only when conspecifics are around, and sometimes only when certain types of conspecifics are around. This provides evidence that the signals are directed towards a particular type of audience, but also suggests that the animal does not reflexively produce the signal in response to an internal state like fear, surprise, or hunger. Some argue that the presence of a conspecific audience, even a specialized one, could be merely one of the “eliciting stimuli” for the signal. In other words, that a prey animal would need to detect both the presence of a predator and the presence of conspecifics in order to give an alarm call. This perspective views animals as more similar to algorithms than agents, playing different programs when given the right input.

Perhaps the best evidence for intentionality in animal communication is found in the gestural communication of great apes (Figure 20.12). Ape gesture researchers have adopted and adapted criteria from developmental psychology used to argue for the presence of intentions in preverbal infants (Bruner 1981). Apes direct gestures to other individuals, adapt their gestures to whether or not the other is looking at them, wait for a response from the other, and demonstrate goal-directedness and flexibility in meeting communicative goals (Call and Tomasello 2020; Cartmill and Byrne 2010). In many ways, ape gestures are flexible, complex signals. Some scholars have used their sophistication to argue for a gestural rather than vocal evolutionary origin of language (e.g., Arbib et al. 2008).



AQ2 **Figure 20.12** An orangutan mother directs a manual gesture towards her adolescent son, shooing him away. Apes adjust the modality of their gestures to the visual attention of their recipient, so if her son were looking in another direction, this mother orangutan would likely have reached over and produced a tactile pushing gesture, waited to signal, or moved to where she could be seen.

But ape gesture might not be as unique as previously thought. As the intentionality criteria from ape gesture work find their way into studies of other species and other modalities, more intentional signals are identified (Ben Mocha and Burkart 2021; Schel et al. 2013; Townsend et al. 2017; Vail et al. 2013). For example, Schel et al. (2013) presented chimpanzees with partially-hidden models of pythons (a predator) and examined their subsequent alarm vocalizations. The authors found evidence for multiple markers of intentionality: chimpanzees called more in the presence of friends, their calling involved visual monitoring of the audience, and their calling only stopped when recipients were distant from the predator. Perhaps, in a few years' time, we will have many examples of intentional communication across animal taxa.

DISCUSSION

Linguistic anthropology has only just begun to approach animal communication as an area of study. But this is changing quickly, both within anthropology and across the social sciences and humanities. Scholars are attempting ethnographies of animal groups (Kirksey and Helmreich 2010) and studying the many roles animals and humans play in one another's lives (Brown and Nading 2019). Philosophers and legal scholars are debating the personhood of animals and the ethics surrounding the way humans treat them (Varner 2012). Humanists are reflecting on the ways humans portray animals, and are bringing a deeper knowledge of animal behavior and ethology to their work (Parrish 2021). The study of animals is having a renaissance across many disciplines. Though linguistic anthropologists have not traditionally engaged with the theory and methods of animal communication, anthropologists have an opportunity to make a substantial contribution to this literature. By combining careful observation of social interaction and nuanced understanding of communicative theories with core ideas from evolutionary biology and ethological data on the social structures and sensoria of animal species, linguistic anthropologists could shed light on the overlooked complexities of quotidian animal life.

While animals may lack many of the rich complexities of human language and culture, they face many of the same communicative challenges: meeting strangers, negotiating status, attracting mates, competing with neighbors and rivals, building and maintaining friendships, warning others of danger, and correcting others' behavior. They do so through a rich tapestry of different signals and sensory modalities. Sensoria vary widely across species. Considering the physical and social environments of animals together with their social goals and available senses brings us one step closer to understanding their *umwelt* (von Uexküll 2010 [1934]) and lived experiences.

REFERENCES

- Anderson, R.A., McBrayer, L.D., and Herrel, A. (2008). Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society* 93 (4): 709–720.
- Arbib, M., Liebal, K., and Pika, S. (2008). Primate vocalization, gesture, and the evolution of human language. *Current Anthropology* 49 (6): 1053–1076.
- Backwell, P.R., Christy, J.H., Telford, S.R., Jennions, M.D., and Passmore, J. (2000). Dishonest signalling in a fiddler crab. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267 (1444): 719–724.

- Bates, H.W. (1862). Contributions to an insect fauna of the Amazon valley (*Lepidoptera: Heliconidae*). *Transactions of the Linnean Society of London* 23: 495–556.
- Ben Mocha, Y. and Burkart, J.M. (2021). Intentional communication: Solving methodological issues to assigning first-order intentional signalling. *Biological Reviews* 96 (3): 903–921.
- Blumstein, D. (1999). The evolution of functionally referential alarm communication: Multiple adaptations; multiple constraints. *Evolution of Communication* 3 (2): 135–147.
- Bouley, D., Alarcon, C.N., Hildebrandt, T., and O’Connell-Rodwell, C.E. (2007). The distribution, density and three-dimensional histomorphology of Pacinian corpuscles in the foot of the Asian elephant (*Elephas maximus*) and their potential role in seismic communication. *Journal of Anatomy* 211 (4): 428–435.
- Bradbury, J. and Vehrencamp, S.L. (2011). *Principles of Animal Communication*, 2e. Sinauer Associates.
- Brower, J.V.Z. and Brower, L.P. (1965). Experimental studies of mimicry. 8. Further investigations of honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis* spp.). *The American Naturalist* 99 (906): 173–187.
- Brown, H. and Nading, A.M. (2019). Introduction: human animal health in medical anthropology. *Medical Anthropology Quarterly* 33 (1): 5–23.
- Bruner, J.S. (1981). Intention in the structure of action and interaction. In: *Advances in Infancy Research* Lipsett, L. (ed.)
- Bullock, T.H., Hopkins, C.D., and Fay, R.R. (2006). *Electroreception*, vol. 21. Springer Science & Business Media.
- Call, J. and Tomasello, M. (2020). *The Gestural Communication of Apes and Monkeys*. Psychology press.
- Cartmill, E.A. and Byrne, R.W. (2010). Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition* 13 (6): 793–804.
- Coupé, C., Oh, Y.M., Dediu, D., and Pellegrino, F. (2019). Different languages, similar encoding efficiency: comparable information rates across the human communicative niche. *Science Advances* 5 (9).
- Dalziel, A.H., Welbergen, J.A., Iqic, B., and Magrath, R.D. (2015). Avian vocal mimicry: a unified conceptual framework. *Biological Reviews* 90 (2): 643–668.
- Dawkins, R. and Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205 (1161): 489–511.
- de Saussure, F. (2011 [1916]). *Course in General Linguistics*. Columbia University Press.
- Duranti, A. (1992). Language and bodies in social space: Samoan ceremonial greetings. *American Anthropologist* 94 (3): 657–691.
- Endler, J.A. (1981). An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society* 16 (1): 25–31.
- Evans, C.S., Evans, L., and Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour* 46 (1): 23–38.
- Fedurek, P. and Slocombe, K.E. (2011). Primate vocal communication: A useful tool for understanding human speech and language evolution? *Human Biology* 83: 153–173.
- Finnegan, R. (2002). *Communicating: The Multiple Modes of Human Interconnection*. London: Routledge.
- Gal, S. (1995). Language, gender, and power. In: *Gender Articulated: Language and the Socially Constructed Self*. Hall, K. and Bucholtz, M. (eds). 169–182.
- Gallant, J.R., Traeger, L.L., Volkening, J.D., Moffett, H., Chen, P.H., Novina, C.D., Phillips, G.N., Anand, R., Wells, G.B., Pinch, M., and Güth, R. (2014). Genomic basis for the convergent evolution of electric organs. *Science* 344 (6191): 1522–1525.
- Goffman, E. (1959). *The Presentation of Self in Everyday Life*. New York: Doubleday Anchor.
- Goffman, E. (1981). Footing. In: *Forms of Talk* (eds. E. Goffman), 124–159. Philadelphia: University of Pennsylvania Press.
- Goodale, E. and Kotagama, S.W. (2006). Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. *Animal Behaviour* 72 (2): 471–477.
- Goodwin, C. (2018). *Co-operative Action*. Cambridge University Press.
- Gumperz, J.J. (1982). *Discourse Strategies* (No. 1). Cambridge University Press.

- Gumperz, J.J. (1992). Contextualization and understanding. In: *Rethinking Context* (eds. A. Duranti and C. Goodwin), 229–252. Cambridge University Press.
- Herring, P.J. (2000). Species abundance, sexual encounter and bioluminescent signalling in the deep sea. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 355 (1401): 1273–1276.
- Humphreys, R.K. and Ruxton, G.D. (2020). Avian distraction displays: A review. *Ibis* 162 (4): 1125–1145.
- Jackson, D.E. and Ratnieks, F.L. (2006). Communication in ants. *Current Biology* 16 (15): R570–R574.
- Janik, V.M. and Knörnschild, M. (2021). Vocal production learning in mammals revisited. *Philosophical Transactions of the Royal Society B* 376 (1836): 20200244.
- Jennions, M.D. and Backwell, P.R. (1996). Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society* 57 (4): 293–306.
- Kelley, L.A. and Healy, S.D. (2012). Vocal mimicry in spotted bowerbirds is associated with an alarming context. *Journal of Avian Biology* 43 (6): 525–530.
- Kirksey, S.E. and Helmreich, S. (2010). The emergence of multispecies ethnography. *Cultural Anthropology* 25 (4): 545–576.
- Knörnschild, M., Jung, K., Nagy, M., Metz, M., and Kalko, E. (2012). Bat echolocation calls facilitate social communication. *Proceedings of the Royal Society B: Biological Sciences* 279 (1748): 4827–4835.
- Laidre, M.E. and Johnstone, R.A. (2013). Animal signals. *Current Biology* 23 (18): R829–R833.
- Langbauer, W.R., Jr. (2000). Elephant communication. *Zoo Biology: Published in Affiliation with the American Zoo and Aquarium Association* 19 (5): 425–445.
- Lee, P.C. (1986). Early social-development among African elephant calves. *National Geographic Research* 2 (3): 388–401.
- Lewke, R.E. (1979). Neck-biting and other aspects of reproductive biology of the Yuma kingsnake (*Lampropeltis getulus*). *Herpetologica*, 35 (2):154–157.
- Lloyd, J.E. (1983). Bioluminescence and communication in insects. *Annual Review of Entomology* 28 (1): 131–160.
- Macedonia, J.M. and Evans, C.S. (1993). Essay on contemporary issues in ethology: variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* 93 (3): 177–197.
- Magrath, R.D., Haff, T.M., Fallow, P.M., and Radford, A.N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews* 90 (2): 560–586.
- Majid, A. and Levinson, S.C. (2011). The senses in language and culture. *The Senses and Society* 6 (1): 5–18.
- Mather, J.A. (2016). Mating games squid play: Reproductive behaviour and sexual skin displays in Caribbean reef squid. *Sepioteuthis sepioidea*. *Marine and Freshwater Behaviour and Physiology* 49: 359–373.
- Maynard Smith, J. and Harper, D. (2003). *Animal Signals*. Oxford University Press.
- Mendoza-Denton, N. (2011). The semiotic hitchhiker’s guide to creaky voice: Circulation and gendered hardcore in a Chicana/o gang persona. *Journal of Linguistic Anthropology* 21 (2): 261–280.
- Mennill Daniel, J. and Ratcliffe, L.M. (2004). Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour* 67: 441–450.
- Møller, A.P., Barbosa, A., Cuervo, J.J., Lope, F.D., Merino, S., and Saino, N. (1998). Sexual selection and tail streamers in the barn swallow. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265 (1394): 409–414.
- Müller, C., Cienki, A., Fricke, E., Ladewig, S., McNeill, D., and Teßendorf, S. (2013). Body-language-communication. *An International Handbook on Multimodality in Human Interaction* 1 (1): 131–232.
- Nelson, S. and Nelson, B. (1978). *The Sulidae: Gannets and Boobies*. Oxford: Oxford University Press.
- Packard, A. (1995). Organization of cephalopod chromatophore systems: A neuromuscular image generator. In: *Cephalopod Neurobiology* (ed. N.J. Abbott, R. Williamson, and L. Maddock), 331–367. Oxford, UK: Oxford University Press.
- Parrish, A.C. (2021). *The sensory modes of animal rhetorics: A boot in the light*.
- Peirce, C.S. (1935). *The Collected Papers of Charles S. Peirce*, vol. 2. Cambridge: Harvard University Press.

- Ryan, M.J. and Rand, A.S. (1993). Sexual selection and signal evolution: The ghost of biases past. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 340 (1292): 187–195.
- Schel, A.M., Townsend, S.W., Machanda, Z., Zuberbühler, K., and Slocombe, K.E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS One* 8 (10): e76674.
- Searcy, W.A. and Nowicki, S. (2010). *The Evolution of Animal Communication*. Princeton University Press.
- Seyfarth, R.M. and Cheney, D.L. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology* 54 (1): 145–173.
- Seyfarth, R.M., Cheney, D.L., and Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour* 28 (4): 1070–1094.
- Shannon, C.E. (1948). A mathematical theory of communication. *Bell Systems Technical Journal* 27:379–423.
- Sicoli, M.A. (2015). Voice registers. *The Handbook of Discourse Analysis* 2: 105–126.
- Sidnell, J. (2006). Coordinating gesture, talk, and gaze in reenactments. *Research on Language and Social Interaction* 39 (4): 377–409.
- Smith, G.T. (2013). Evolution and hormonal regulation of sex differences in the electrocommunication behavior of ghost knifefishes (Apteronotidae). *Journal of Experimental Biology* 216 (13): 2421–2433.
- Stevens, M. (2005). The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biological Reviews* 80: 573–588.
- Stevens, M. and Ruxton, G.D. (2014). Do animal eyespots really mimic eyes? *Current Zoology* 60 (1).
- Struhsaker, T.T., 1967. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). *Social Communication among Primates*.
- Thompson John, N. (1994). *The Coevolutionary Process*. Chicago: The University of Chicago Press.
- Torres, R. and Velando, A. (2003). A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxi*. *Behavioral Ecology and Sociobiology* 55 (1): 65–72.
- Townsend, S.W., Koski, S.E., Byrne, R.W., Slocombe, K.E. et al. (2017). Exorcising Grice's ghost: An empirical approach to studying intentional communication in animals. *Biological Reviews* 92 (3): 1427–1433.
- Townsend, S.W. and Manser, M.B. (2013). Functionally referential communication in mammals: the past, present and the future. *Ethology* 119 (1): 1–11.
- Umbers, K.D.L., De Bona, S., White, T.E., Lehtonen, J., Mappes, J., and Endler, J.A. (2017). Deimatism: A neglected component of antipredator defence. *Biology Letters* 13 (4): 20160936.
- Vail, A.L., Manica, A., and Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nature Communications* 4 (1): 1–7.
- Valone, T.J. (2007). From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology* 62 (1): 1–14.
- Varner, G.E. (2012). *Personhood, Ethics, and Animal Cognition: Situating Animals in Hare's Two Level Utilitarianism*. Oxford University Press.
- von Humboldt, W. (1836/1999). *On Language: The Diversity of Human Language Construction And its Influence on the Mental Development of Mankind*. Translated by Peter Heath, Cambridge Texts in the History of Philosophy, Cambridge: Cambridge University Press.
- von Uexküll, J. (2010 [1934]). *A Foray into the Worlds of Animals and Humans with a Theory of Meaning*. Minneapolis, MN: University of Minnesota Press.
- Wyatt, T.D. (2020). Reproducible research into human chemical communication by cues and pheromones: learning from psychology's renaissance. *Philosophical Transactions of the Royal Society B* 375 (1800): 20190262.
- Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of Theoretical Biology* 53 (1): 205–214.