COMMUNICATION: ANALYSIS OF ANIMAL COMMUNICATION

Communication Networks

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Abstract

Animal communication occurs when a signal passes from one individual to another, but in nature it is not uncommon for many different senders and receivers to interact, creating a network of individuals. A communication network explains the relationship among the different individuals who share the same signaling space. This article describes the extent of communication networks in terms of their abundance and taxonomic diversity, the different types of interactions between individuals, and the extent to which communicating within a network affects animal cognition. Taking a network approach to studying communication provides many insights not possible with more traditional didactic approaches.

Keywords

Audience effects; Chorusing; Collaborative signals; Deception; Duetting; Eavesdropping; Heterospecific recognition; Signal complexity; Signal perception; Social networks

Introduction

Animals use signals to communicate about all aspects of their lives, including attracting mates, locating food, and avoiding predators. The field of animal communication has blossomed in part because many of these signals are especially compelling: Nearly all of the bright colors, loud sounds, or strong smells we encounter in nature are signals used by animals to communicate (Bradbury and Vehrencamp, 2011). Animal communication requires information to be transmitted from a signaler to a receiver and textbooks stress that understanding these three aspects of communication (the sender, signal, and receiver) is necessary to determine that communication has actually taken place. Thus, it is not particularly surprising that much of the research in animal communication has focused on how a particular signal is transmitted by a sender and received by a receiver. While it may be tempting to focus on these didactic interactions for simplicity, the reality is that communication in nature often takes place not between just two individuals, but across many individuals, creating broad and diverse communication networks.

Communication networks are assemblages of animals that occur within a particular shared geographic range, so that they also share the same signaling space (McGregor, 2009). The specific geographic range can vary depending on the type of signal, from a few inches in the case of tactile communication in social mammals to many miles for the songs of whales. Yet in nearly any example of animal communication there are more than two parties involved, so considering the other individuals that share the signaling space is critical for understanding the evolution of signal design and the ecological implications of signaling behavior in animals.

Here, we apply a network perspective to the study of animal communication. We focus on the breadth of communication networks by briefly surveying the taxonomic representation of animals that signal within a network context and describing how researchers study communication networks. We then examine the major types of communication networks, including various types of intentional and eavesdropped networks, before ending by addressing how networks of signalers and receivers might affect not just the signals themselves, but also the cognitive abilities of the animals involved in these complex communication networks.

Taxonomy of Communication Networks

Communication networks have been documented in nearly every taxonomic group, from insects to whales (Fig. 1). Communication taking place across networks of individuals is common in both aquatic and terrestrial species and it is likely that this form of communication is more common than the traditional dyadic model involving only two individuals. Some of the earliest and most widely known communication networks were described in insects (e.g., crickets and cicadas) and anurans (toads and frogs) and take the form of choruses – synchronous signals of many individuals congregated in one place (McGregor, 2009; see below for more details). Birds too are famous for their own version of chorusing, which often occurs at twilight and is called the dawn chorus
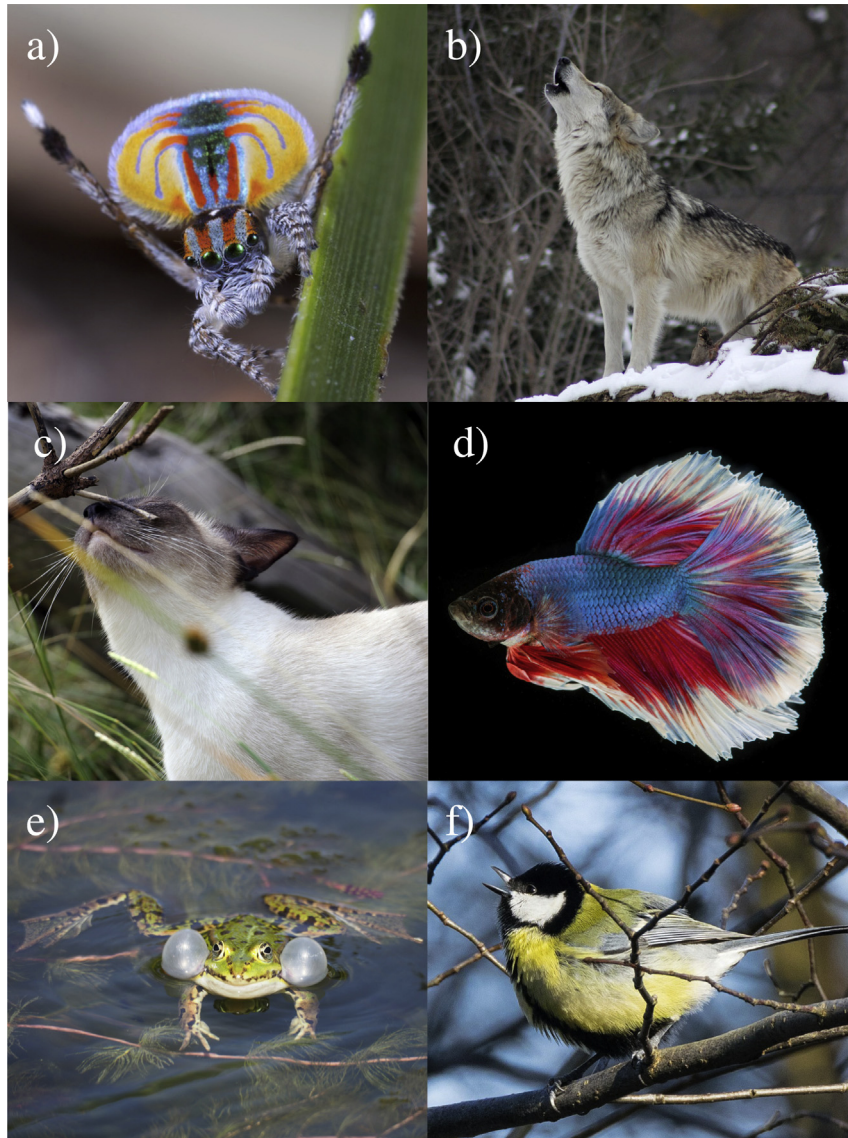
Fig. 1 Examples of species that communicate in a network context (a) Male peacock jumping spider (*Maratus volans*) posture during a targeted display to a female (photo by Jurgen Otto), (b) grey wolf (*Canis lupis*) howling to maintain contact with the rest of its pack, (c) domestic cat (*Felis silvestris catus*) smelling a sent mark left by another individual in its territory, (d) male Siamese fighting fish (*Betta splendens*) displaying to intimidate another male and/or court a female, (e) edible frog (*Rana esculenta*) croaking to attract a female, (f) a great tit (*Parus major*) calling to alert others about the presence of a predator.

(McGregor, 2009). In addition, many bird songs sung at other times of the day also occur as part of communication networks, since these songs are received by many nearby individuals. Communication networks are also found in reptiles. Crocodiles, for example, produce signals that travel quite far in densely inhabited waters, thereby involving a number of receivers (Lang, 1977). Mammals often communicate in networks, especially in highly social species. For example, marmots call to alert others about predators (Blumstein, 1999) and many animals, including cats, use scent marking to transmit olfactory signals to a number of different individuals. In addition to terrestrial animals, many aquatic animals such as fish and marine mammals also commonly communicate in networks. Given that sound can travel much farther in water than in air, it is not uncommon for underwater acoustic signals to be heard by many different individuals and communicating over networks may be especially common in these systems. Social aggregations in many species also allow multiple receivers of (shorter range) visual and chemical signals in aquatic systems (Bradbury and Vehrencamp, 2011).

While communication networks are found in many different species, they are not constrained within a single species; heterospecific receivers commonly use signals produced by other species, increasing the population of receivers and dramatically increasing the potential scale of the communication networks (Magrath *et al.*, 2014). Heterospecific networks need not be restricted to similar species, with networks often occurring with unrelated species, sometimes differing by family or even class levels of taxonomy. Mule

deer (*Odocoileus hemionus*), for example, increase their vigilance in response to yellow-bellied marmot (*Marmota flaviventris*) alarm calls (Carrasco and Blumstein, 2011), while white-bellied copper-striped skinks (*Emoia cyanura*) respond with increased anti-predator behavior to the alarm calls of red-vented bulbuls (*Pycnonotus cafer*; Fuong *et al.*, 2014).

Measuring Communication Networks

Measuring and evaluating communication networks to try and understand which individuals and species are involved, what information is transmitted and received, and how this information travels between individuals is difficult within a traditional dyadic model, and becomes exponentially more difficult as more individuals are added to the network. To try and understand how information travels through these networks, one of the first hurdles is to understand which individuals are involved in the networks. One of the more common methods to achieving this goal is to conduct experiments to identify the signaler and receivers. By presenting a stimulus that elicits a signaling event (e.g., a predator model), signalers can be identified by the production of the signal (e.g., alarm call). Similarly, by conducting playbacks of specific signals, receivers become evident by their response to these signals. This approach has been, and continues to be used, across studies of communication networks. For example, many studies examining the individuals involved in mobbing networks will use playbacks of a specific species' mobbing calls (i.e., black-capped chickadees; Hurd, 1996) to determine the other species involved in the network. This type of approach has been employed in a number of different networks to determine the types of information that is transmitted through different signals. In bottlenose dolphins (*Tursiops truncatus*) for example, playback studies were used to determine that the signature whistles that individuals use in social interactions (both between two individuals and groups of individuals) contain information about a specific individual King and Janki, 2013). While these approaches continue to be informative, new technologies and mathematical modeling techniques are also beginning to add new ways of addressing information networks and how information flows between individuals.

New technology has allowed for a closer examination of some of the more difficult to quantify questions in communication networks. Recent advances in computing have allowed the development of new statistical methods of examining relationships between individuals in a group, such as network-based diffusion analysis (Hoppitt and Laland, 2013). Many examinations into communication networks use social networks as a proxy, under the assumption that information will flow in similar patterns (i.e., that information flows though association patterns). Social networks are often constructed based on temporal-spatial association patterns between individuals as in many social species, associations between individuals are not random and individuals preferentially spend time associating with some individuals over others (Snijders and Naguib, 2017). While these data allow for the analysis of the social structure of a group of individuals, their usefulness for understanding communication networks could be more limited since many forms of communication happen when individuals are not actually in physical proximity (such as eavesdropping) and therefore could be overlooked using social networks alone (Snijders and Naguib, 2017). As new technologies are developed, however, researchers are finding new ways to integrate social and communication networks, for example, backpack transmitters with built-in microphones can now record individual movements and vocalizations. Anisimov *et al.* (2014) used small backpacks with accelerometers and microphones to record an individual bird's vocal production and its flock mates' vocal production concurrently and then used statistical techniques to examine the patterns of vocal interactions among individuals within the network. The use of advanced network analyses also extends to using models of interactions from other systems to understand communication networks. For example, Stowell *et al.* (2016) adapted neural network models, typically used to explain temporal patterns of neuron firing, to describe patterns in communication networks within flocks of zebra finches.

Types of Signals Found in Communication Networks

When discussing communication networks, one of the first steps is to determine the type of signal the signaler is generating as this has different repercussions on the types of networks that can arise. In general a signal will fall into one of two broad categories: directed or broadcast signals (**Fig. 2**).

Directed signals are signals directed specifically at one (or in some cases) a few individuals, and have traditionally been used to explain classical dyadic models of communication (**Fig. 2a**). Directed signals are most often used in close interactions between individuals, such as during contests, fights, or during courtship between two individuals. In addition to producing long-range signals to attract the attention of females, male jumping spiders (*Habronattus pyrrithrix*) use specific short-distance courtship signals after they approach a receptive female (Echeverri *et al.*, 2017; **Fig 3**). Males position themselves directly in front of the female during this phase of courtship as this is the best location to capture the females visual field, suggesting that these signals are directed specifically at this particular female (Echeverri *et al.*, 2017; **Fig. 3**).

Broadcast signals, on the other hand, are, by design, intended for multiple receivers (**Fig. 2b**), automatically precluding the traditional dyadic models of communication to describe the evolution and use of this type of signal. These signals are frequently long-distance signals, which are often produced to defend a territory, attract mates at a distance, or warn others about danger. While these signals are intended for specific types of receivers (i.e., females in the case of male advertisement calls or kin in the case of alarm calls), they are not directed at a specific individual per se. However, while not intended for specific individual receivers, broadcast signals are often intended for a specific type of audience, and are more likely to be emitted in certain circumstances such as when kin are nearby (in alarm signals), or at times of day females are likely to be looking for a mate (in courtship signals). Bird song is an
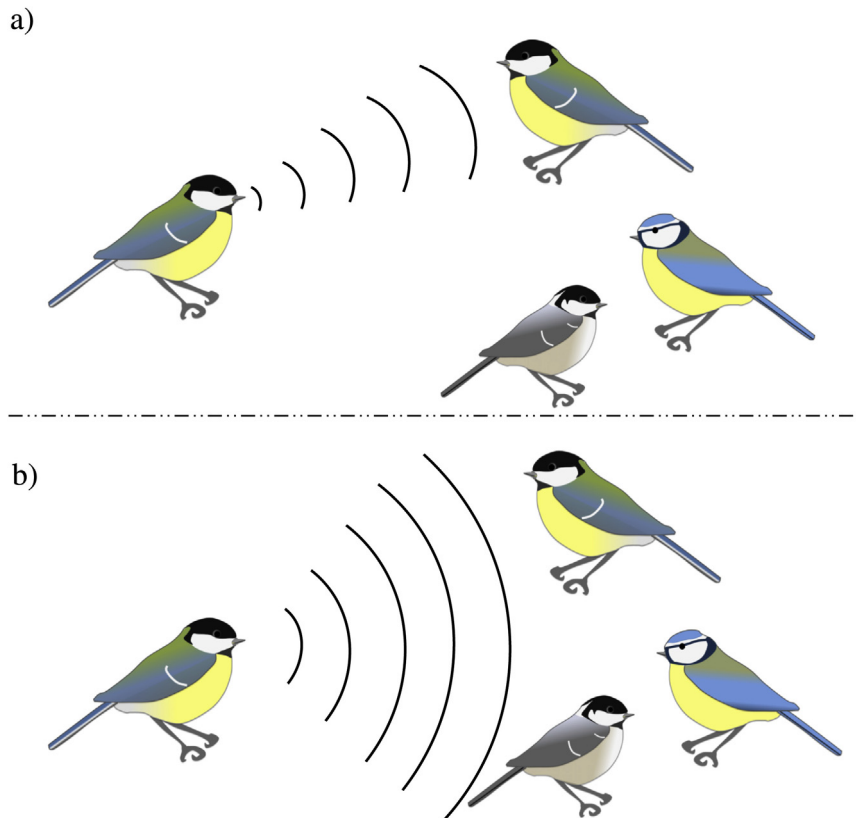
Fig. 2 Two type of signals: (a) a directed signal, with the sender directing a signal to a specific receiver/category of receiver and (b) a broadcast signal with the sender sending out a signal to many or all receivers in the area.

excellent example of this type of signal, as songs are, for many species, a broadcast signal meant for neighboring males or females looking for mates. Many of the songs used for either territory defense or mate attraction are specifically designed to travel long distances in order to reach any pertinent receivers (Catchpole and Slater, 2008).

Bird songs also are a good example of how many signals, even if they are designed for a specific purpose, often serve multiple purposes. For example, many birds produce songs that are sung at high amplitudes and used primarily as broadcast signals, but these same signals can also be produced at low amplitude ('soft songs'). Soft songs are typically directed at specific individuals that are very close in proximity (e.g., a female during a short-range courtship or even more commonly a rival male that has escalated a territorial interaction), and the relatively soft amplitude presumably allows the signals to be received by intended receivers without being overheard by other individuals that could eavesdrop if the song was sung at full volume (Reichard and Anderson, 2015). In fact, there are many circumstances, both in courtship and territory defense/conflict, where broadcast signals are used for part of the interaction, but more directed signals are used as the interaction escalates to reduce the chances of eavesdropping and aim the communication directly at one specific receiver (Fig. 3a).

Types of Networks

Communication networks are immensely variable, involving any number of senders and receivers, but all networks have the potential to include both 'intended' and 'unintended' receivers of the signals. Because communication is often framed in the context of signaler and 'intended' recipient, different communication networks typically fall into one of two general categories: intended networks and eavesdropping networks (Fig. 4).

Intended Networks

When returning to the original dyadic view of communication, between one signaler and one receiver, this interaction can often be perceived as an 'intended' one, where the signal is clearly directed at a specific recipient (Fig. 4(a)). This idea of directed signals can also apply within a communication network framework, with certain receivers being the intended recipients of a sender's signal (Fig. 5). Convict cichlids (*Cichlasoma nigrofasciatum*), for example, will signal the presence of a predator by rapidly flicking their pelvic fins, but they only do so in the presence of their young, suggesting that the information is intended specifically for these
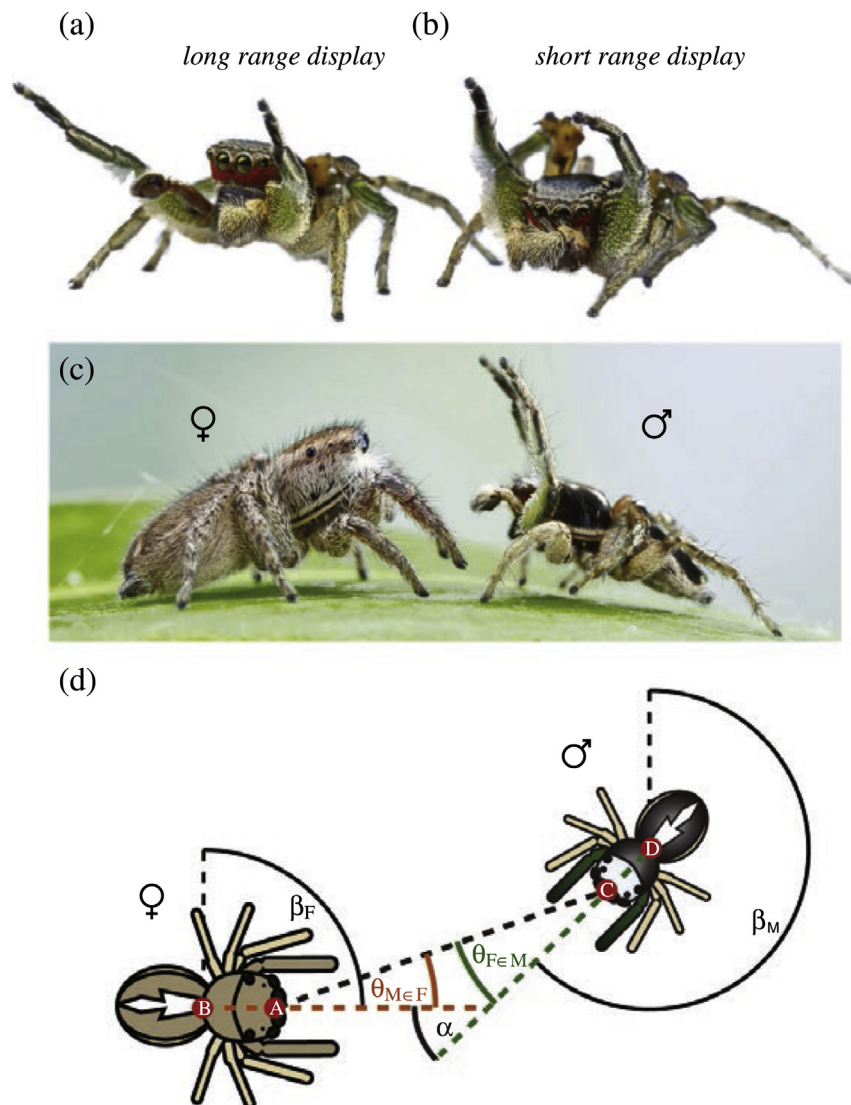
Fig. 3   Male posture during (a) long-range and (b) short-range phases of courtship, (c) side view of short-range courtship interaction (photo by Colin Hutton), and (d) a male positioning itself directly in front of the female's line of sight to ensure she has received the signal. Reproduced from Echeverri, S.A., Morehouse, N.I., Zurek, D.B., 2017. Control of signaling alignment during the dynamic courtship display of a jumping spider. Behavioral Ecology 28(6), 1445–1453. Available at: http://doi.org/10.1093/beheco/arx107.

individuals (Shennan *et al.*, 1999; **Fig. 5a**). Within this intended receiver framework, there are multiple types of signaling categories based largely on the context in which the signals are sent and to whom the signals are intended. Aside from classic sender-receiver dyads and the more common broadcast signals described above, intended networks commonly take the form of choruses and collaborative signals.

Choruses

Choruses are communication events in which multiple individuals signal at the same time and place (**Fig. 5(b)**). Individuals often compete against one another to transmit their signals to receivers, though some choruses can instead involve cooperative signals. The most common examples of chorusing use the auditory modality and occur in insects (such as crickets and cicadas) and anuran amphibians (primarily frogs). Though the most common examples of choruses are acoustic, they are not limited to this modality; for example, the evening light displays of fireflies also function as choruses (McGregor, 2009). Due to the collective participation in these events, employing a communication network perspective is necessary to understand the function of chorusing.

By its very nature, chorusing is a signaling strategy that is highly competitive, as males compete with many neighbors to be 'overheard', while simultaneously listening for a response to their signal. One theory about why individuals will engage in this highly competitive signaling strategy is that chorusing is actually an epiphenomenon resulting from individual males competing with each
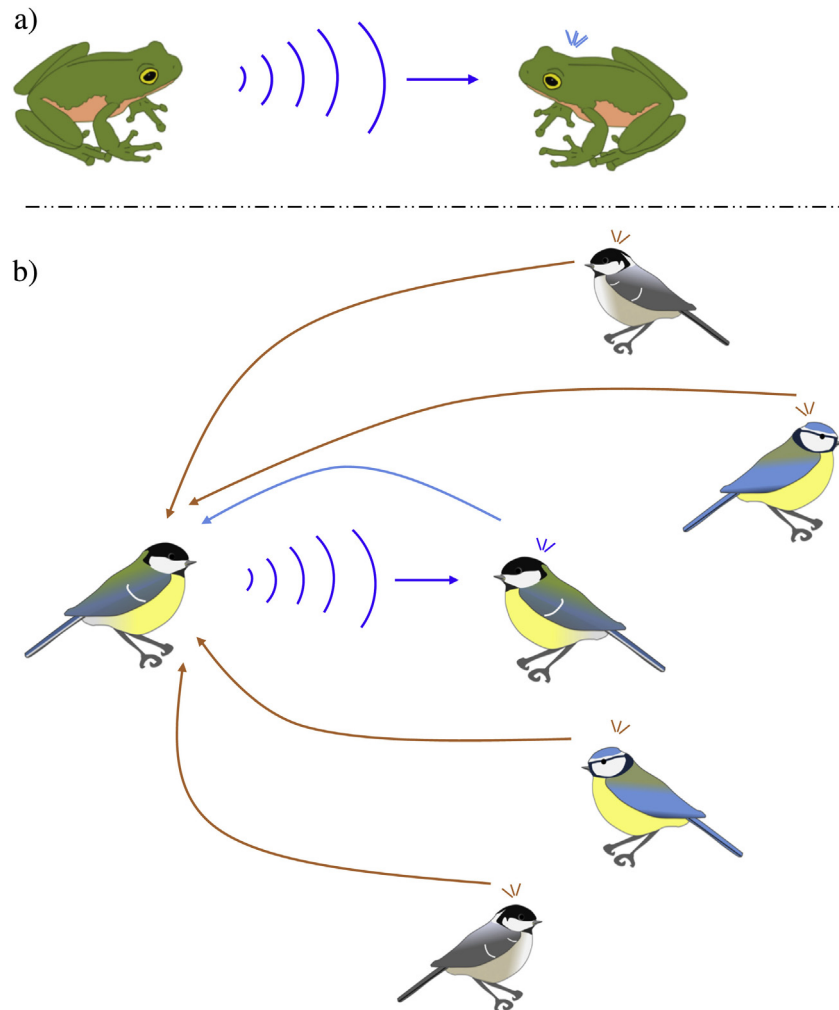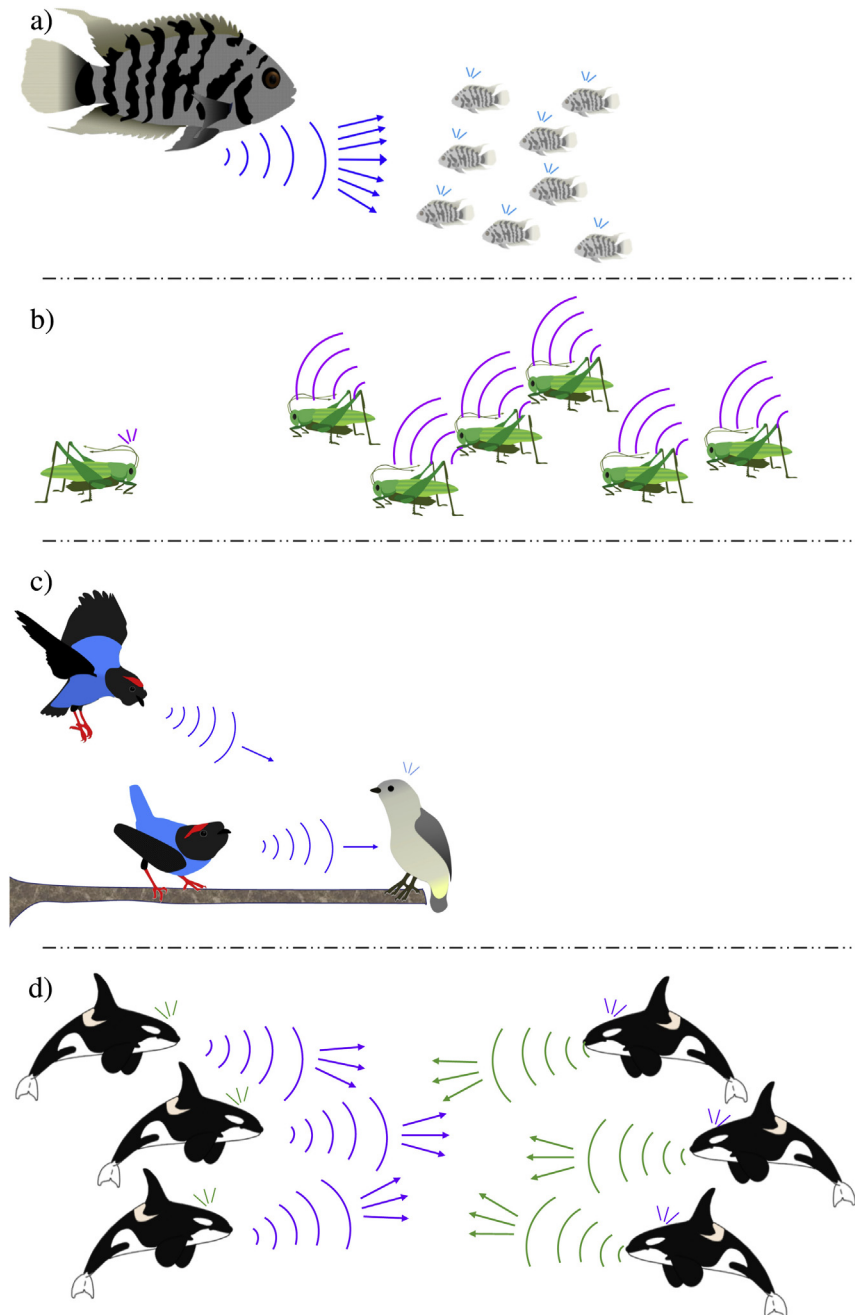
Fig. 4 Two types of networks: (a) an intended network, with a signaler(s) sending a signal directed at a specific individual(s) who receive that signal, and (b) an eavesdropping network where the sender sends a directed signal (dark blue) to intended recipients who receive and respond to the signals (light blue) but nonintended recipients also receive to the signal (orange).

other to be the lead signaler (McGregor, 2009). In many anuran and insect species, leading males that call first are preferred by females, driving all males to attempt to be the first to signal which in turn results in a near synchronous chorus (Snedden and Greenfield, 1998). However, chorusing may also be an effective anti-predator strategy. Many chorusing species have predators that use these signals to locate their prey. Fringe-lipped bats (*Trachops cirrhosus*), for example, use the calls of the male tree frogs (*Smilisca sila*) to locate and eat them, and are more likely to move toward asynchronous or solitary calls compared to chorusing individuals (Tuttle and Ryan, 1982).

Collaborative Signals

Collaborative signals are communication events where multiple individuals signal in concert in order to send one cohesive signal to other individual(s) (**Fig. 5(c-d)**). Similar to chorusing, these are collective behaviors that cannot be sufficiently explained by the single signaler –receiver dyad. While collaborative signals are less common than choruses, there are multiple contexts in which multiple individuals signal together to create one cohesive signal. One commonly observed type of collaborative collective signal is found in duetting, when multiple individuals sing coordinated songs often either alternating or overlapping (Hall, 2009; Logue and Krupp, 2016). For example, mated pairs of happy wrens (*Pheugopedius felix*) sing large repertoires of highly-coordinated duets that include pair-specific 'duet codes' (Logue, 2006), necessitating that both males (Templeton et al., 2013a) and females (Templeton et al., 2013b) pay close attention to their mate to coordinate the precise timing and song selection to properly coordinate their songs (**Fig. 6**). Like in happy wrens, plain-tailed wren (*Thryothorus euophrys*) males and females sing different parts of a complete song. However, plain-tailed wrens are more social and live in groups of up to 7 individuals, with all members of the group participating in the 'duet' to produce an elaborate, highly-synchronized chorus (Mann et al., 2006). Thus, in this case a large group of individuals collaborates, rather than competes, to produce a complex vocal chorus.

Fig. 5 Types of intended communication networks: (a) an intended network with one sender (adult convict cichlid) and multiple receivers (its young), (b) a chorus with all individuals signaling at the same time directed to a specific audience (females) who receive this signal, (c) a collaborative signal with multiple signalers (a pair of male swallowtailed manakins) signaling together for one receiver (female swallow-tailed manakin), and (d) a collaborative signal with multiple signalers and receivers, seen often in circumstances where two different groups or populations of individuals (purple and green) encounter one another, like in these Orcas.

While vocal duetting is widespread in animals, it is not the only type of collaborative group signal. Collaborative visual displays are also used during mate attraction (Foster, 1981). These signals often involve multiple (often unrelated) males engaging in a collaborative courtship display to attract a female (Fig. 5(c)). While the whole collaborate effort is necessary to attract the female, she typically only mates with one of the males (the alpha) suggesting that the other males gain delayed benefits from the arrangement. Swallow-tailed manakins (*Chiroxiphia caudate*), for example, use collaborative displays during courtship. Groups of 4–6 males will come together to 'help' an individual dominant male attract and court a female by engaging in a collaborative 'jump dance' involving multiple males (Foster, 1981). While dominant males also engage in solitary dances, males that perform collaborative jump dances are more likely to successfully acquire matings (Foster, 1981).
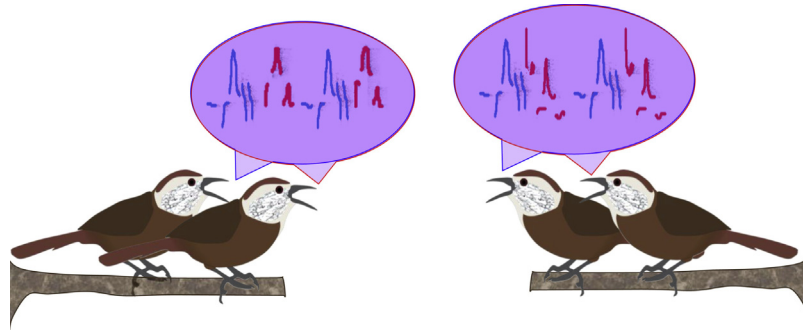
Fig. 6 Several species of neotropical wrens sing antiphonal duets that are often used as part of a coordinated territorial display in a network context. Two pairs of happy wrens countersing at their territory border with males singing part of the duet song (blue) while females sing the other part (red). The unique duet codes of each pair create situations in which individuals must carefully select their song phrases to type match an intruder (to signal aggression) or follow their partner's duet code (to signal collaboration).

Aside from mate attraction, collaborative signals are also often used in territorial defense when one group encounters another (**Fig. 5(d)**). Green woodhoopes (*Phoeniculus purpureus*), for example, will produce a rallying 'kek-ek-ek-ek' call when confronting a neighboring group on their territory boundary (Radford and Plessis, 2004). These calls display the stamina of the respective groups, as those able to produce the longest bouts of calling often win the contests. It is also thought that many duets and synchronized choruses produced by wrens, including the happy wren and plain-tailed wrens discussed above, are also used as territory defense signals (Mann *et al.*, 2006).

Finally, collaborative signals are not only used in situations related to sexual attraction and mating, but can also be used in other circumstances where groups need to communicate with individuals or other groups (**Fig. 5(d)**). Wolves, for example, will use synchronous howling to communicate territory boundaries with neighboring packs as well as making a pack appear larger than it is due to the Beau Geste effect (Harrington, 1989).

Eavesdropping Networks

In addition to the 'intended' receivers described above, signals can also be received by 'unintended' individuals, or eavesdroppers (**Fig. 4(b)**). Eavesdropping is commonly defined as an individual receiving information from communications between two or more other individuals, when that individual is not intend to be a receiver (McGregor and Peake, 2000). By its very definition, communication that involves the possibility of eavesdropping falls outside of sender – receiver the dyadic model of communication, and therefore requires a network approach to understand the evolution and function of these types of communication interactions. Eavesdropping networks are especially common for broadcast signals, as by definition, broadcast signals involve multiple receivers over a large distance, which provides many opportunities for eavesdropping. Eavesdropping networks are not only a result of broadcast signals, however, and can also occur in more directed communication interactions. Eavesdropping strategies are diverse, in terms of the type of information that is gleaned from eavesdropping and the effect of the eavesdropper on the signaler, but in general most can be placed in one of two categories: Interceptive and social eavesdropping (McGregor, 2009; **Fig. 7**).
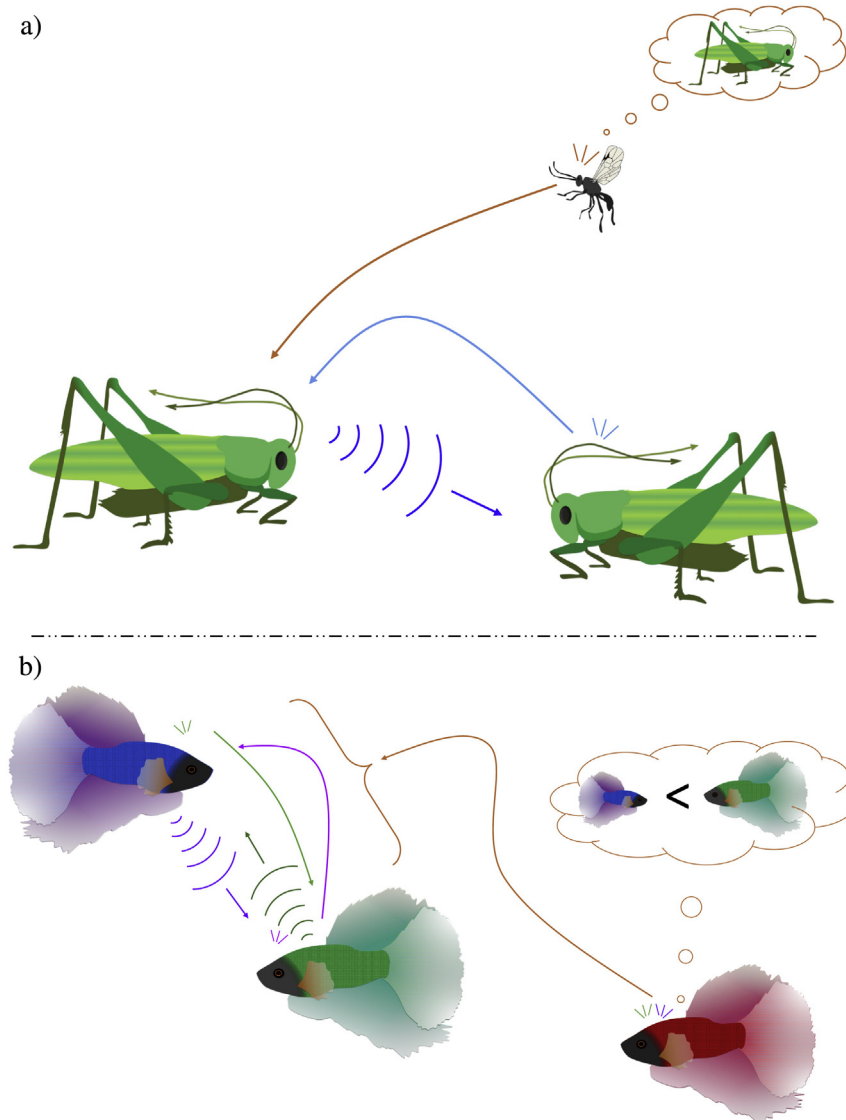
Interceptive Eavesdropping

Interceptive eavesdropping occurs when an individual eavesdrops on a communicative signal that is designed and intended for another specific individual. Any information obtained from this form of eavesdropping is typically the same that the intended receiver would extract from the signal. Often, the interception of this type of signal can be detrimental to the signaler (**Fig. 7a**).

One common example of interceptive eavesdropping occurs in predator-prey interactions. In many species, predators will use the signals produced by prey animals to locate and capture their prey (**Fig. 7(a)**). Like the frog-eating bats discussed above, Mediterranean house geckos (*Hemidactylus tursicu*) eavesdrop on the sexual signals of their prey. These geckos use the mate attraction calls of decorated crickets (*Groylldes supplicans*) to locate their burrows, allowing the geckos to intercept and eat female crickets attracted to the source of the calling (Sakaluk and Belwood, 1984). Femme fatale fireflies (*Photuris*) go one step further: In addition to eavesdropping on the bioluminescent visual signals that other firefly species produce in order to attract mates, they lure males towards them by mimicking the signals of receptive females and then prey on the males that are attracted to these 'female' signals (Lloyd, 1975).

While predator-prey examples of interceptive eavesdropping highlight the potential detrimental effects of this type of eavesdropping, the consequences are not always life-threatening. In cases related to reproduction, individuals can use the signals of conspecifics to become satellite males, an alternative mating tactic in which males that invest less in ornamentation, weaponry, or courtship effort will stay near other males with more highly developed secondary sexual traits and then intercept and mate with the females that approach these males. In Hawaiian field crickets (*Teleogryllus oceanicus*), for example, many of the males cannot

Fig. 7 Types of eavesdropping strategies: (a) interceptive eavesdropping, where one individual (parasitoid wasp) intercepts the signal of another individual (the male cricket) and uses that signal for its own information/benefit (in this case to parasitize the signaler), and (b) social eavesdropping where an eavesdropper (red Betta fish) will observe the signaling interaction between to other individuals (blue and green signaling Betta fish) and will gather information (i.e., that one fish is stronger than the other) from the interaction rather than from the signal.

sing due to a mutation in their wings (a response to a parasitoid that itself eavesdrops on singing males and then targets them as hosts for its eggs) and therefore cannot attract females. However, these silent males will move towards the song of other males and thereby increase their chances of encountering and mating with females attracted to those same males (Zuk *et al.*, 2006).

While many examples of interceptive eavesdropping show that eavesdropping is detrimental to the signaler, this is not always the case. Anti-predator signals, such as mobbing alarm calls, are one type of signal where the interception by others either has no effect or is actually beneficial to the signaler. For example, interceptive eavesdropping on alarm calls can provide a benefit through kin-selection mechanisms as seen in Siberian jays (Griesser and Ekman, 2004). In the case of mobbing, interceptive eavesdropping could lower the chances of attack by recruiting other individuals to mob the predator along with the original signaler and intended receivers (Curio, 1978; Carlson *et al.*, 2017). Considering mobbing from a network perspective is particularly useful because these signals are not only eavesdropped on by both conspecific and heterospecific receivers, but mobbing also may play a large role in forming an maintaining mixed-species flocks (Goodale and Kotagama, 2005). Black-capped chickadee mobbing calls, for example, can recruit many other species to a mobbing event, lowering the chance of predation for the signaler(s) (Hurd, 1996) and there is evidence that at least one of these species extracts information about the degree of predatory threat by eavesdropping on the fine-scale acoustic structure of these signals (Templeton and Greene, 2007).

Social Eavesdropping

Social eavesdropping occurs when an individual eavesdrops on the information generated from a signaling interaction between third parties, rather than the information exchanged itself; i.e., the information acquired includes information about the signalers and the outcome of the interaction between the signalers (McGregor, 2009; **Fig. 7b**).

A clear example of social eavesdropping occurs in Siamese fighting fish (*Betta splendens*). After observing two males producing aggressive signals and fighting, other males adjust their response to these same individuals in subsequent encounters depending on whether they observed that individual win or lose the contest (**Fig. 7b**). Eavesdropping males will approach and signal more quickly to males they have observed losing compared to those that they observed winning (Oliveira *et al.*, 1998). Many bird species have similar eavesdropping networks during territorial confrontations. Male great tits (*Parus major*), for example, eavesdrop on vocal contests between neighboring and 'intruder' (playback) males, and treat each male differently in subsequent encounters depending on the overheard interaction (Peake *et al.*, 2001). In response to non-aggressive 'intruder' males, eavesdropping males are more likely to quickly and aggressively instigate a singing contest, while eavesdroppers take longer to respond and are less aggressive when encountering the aggressive 'intruder' male (Peake *et al.*, 2001). Similar results have been observed in song sparrows (*Melospiza melodia*), with males paying close attention to the singing interactions of their neighbors. Like many species of birds, song sparrows tend to treat long-term neighbors with less aggression than unfamiliar individuals, a phenomenon known as the 'dear enemy' effect. However if a male overhears one of his neighbors intruding within the territory boundary of another neighbor, this male is treated with increased aggression during future interactions (Akçay *et al.*, 2010).

Females also eavesdrop on male dominance interactions and can use the information obtained from eavesdropping on these interactions to assess male quality. For example, in addition to male fighting fish eavesdropping on fighting contests of other males, females also eavesdrop on these contests and base their initial stages of mate choice at least in part on the information gleaned by eavesdropping (Doutrelant and McGregor, 2000). Female chickadees also assess the quality of males from eavesdropping on their song contests and use this information to inform their social mate selection. Chickadees are socially monogamous, but females continue to eavesdrop on the song contests of males even after they have made their choice of social mates, and they use the information they glean from eavesdropping to adjust their extra-pair mating patterns; after hearing their current mates lose a (simulated) vocal exchange with another male females are more likely to pursue extra pair copulations with more dominant males (Mennill *et al.*, 2003).

Many animals must learn to produce their vocal signals and there is some evidence that social eavesdropping is also a mechanism by which vocal learning can take place. For example, (Beecher *et al.*, 2007) showed that young song sparrows raised in the lab learned more songs from adult males that they heard interacting with another bird than those that they were able to interact with directly and Templeton *et al.* (2009) used radio telemetry to track young and inconspicuous song sparrows in the wild to show that they moved closer to males engaged in interactive singing contests (but not males singing alone), presumably to better eavesdrop on these interactions. These results suggest that social eavesdropping is a powerful mechanism that promotes learning.

Audience Effects

Audience effects occur when a signaler changes its signaling behavior based on the presence of particular receivers. Individuals might vary a signal depending on the chance of eavesdroppers receiving it, with signaling behavior often dependent not just on the potential presence of receivers but on the specific sex of the eavesdroppers present (McGregor, 2009). Eavesdropper effects vary with the costs or benefits associated with non-target individuals receiving the signal. For example roosters (*Gallus gallus*) are much more likely to signal about both the presence of food and predators if a female is present than if they are alone or with other males as this may increase their chances to mate with that female (Wilson and Evans, 2012).

In addition to affecting the likelihood of producing a signal, audiences can also affect the type of signal produced. Siamese fighting fish, for example, will change their signaling behavior during aggressive fights with other males depending on the presence and sex of an audience. When the audience is female, males will change their display behavior to include more conspicuous visual displays that can also be used during courtship (Doutrelant *et al.*, 2001). Males that have previously won contests do not change their behavior in the presence of a male audience, but looser fish do alter their displays, possibly in an attempt to decrease the chance of further aggressive interactions from the audience member(s) (McGregor, 2009).

Changes in signaling behavior do not only occur in the presence of conspecifics, but can be affected by heterospecific audience members as well. Fork-tailed drongos (*Dicrurus adsimilis*), for example, produce a specific sentinel call (signaling an 'all-clear' after a predator encounter) when foraging with sociable weavers (*Philetairus socius*), but not when alone (Baigrie *et al.*, 2014). In addition to modifying a signal in the presence of other potential receivers, the response to heterospecifics can also be to cease signaling altogether. In White-browed scrubwrens (*Sericornis frontalis*), for example, nestlings will beg in response to conspecifics, but in the presence of a predator, the pied currawong (*Strepera graculina*), the nestlings will stop begging, presumably in order to avoid detection by the predator (Magrath *et al.*, 2007).

Effects of Networks on Animal Cognition

Communication pathways have historically been studied as the dyadic interactions in part because trying to understand the complexities of communication from a network perspective is exceptionally challenging. Assessing the function of a signal,

including understanding the types of information or influence exerted, from both a signaler's and receiver's perspective is challenging enough when the two parties might not always have the same motivations or aligned interests. Therefore, adding another two (or twenty or two hundred!) potential receivers, and the effects of their presence on the signaler and other potential receivers, creates a dizzying level of complexity that few researchers are able to effectively tackle. These types of communication networks – often vast, variable, or complex in their structure and dynamics – must create similar types of cognitive challenges for the animals producing and receiving signals in nature.

Perceptual Challenges of Communication Networks

Perception of animal signals by receivers can be cognitively challenging (Shettleworth, 2010), and the difficulty of decoding relevant information presumably becomes considerably more difficult when the signaling space grows to include a variety of signals within a communication network. Signal detection theory (Wiley, 2006) describes the problem receivers face when encountering a variety of signals: How does a receiver detect biologically important signals in an environment filled with other irrelevant or unimportant signals? Some specific criteria must be set in order to discriminate the (important) signal from background noise, but the difficulty of getting this response threshold just right inevitably leads to either false alarms (responses to unimportant signals) or missed opportunities (failure to respond to important signals). Background noises or anthropogenic sounds can mask important signals by making detection more difficult (Brumm and Slabbekoorn, 2005). To avoid having their signals masked by other sources, some animals modify their signals by shifting the frequency, amplitude, or timing of vocal signals, for example, to help facilitate perception of the signal from the background noise (Brumm and Slabbekoorn, 2005).

Like background noise, conspecific communication networks can also cause masking and because of their high degree of similarity in signal design, conspecific signals also create special problems for signal perception. Conspecifics tend to produce relatively similar signals; in fact selection tends to favor relative uniformity in signals to help facilitate recognition by receivers. For example, male sexual signals – be they color patterns in butterflies or songs of birds – need to be similar enough for a female to identify the male as belonging to the appropriate species. This level of similarity in signals between individuals in a network results in competing signals with very similar frequency spectrum, resulting in heightened levels of masking compared with other types of unintended noise.

In addition to similarities in signal design among individuals within a network, the spatial associations of individuals within a network also create perceptual challenges for receivers. For many different types of signals, a receiver needs to extract information not just about the properties of the signal, but also about the location of the signaler. For example, in regards to sexual signals, an animal that is searching for a mate needs to not only know that a potential mate is in the general area, but also determine its exact location before copulations (or even courtship in many species) can take place. Similarly, localizing the source of an alarm call could provide important information about the location, and even potential future trajectory, of a moving predator. Signal localizability, like signal detection, is also affected by acoustic masking of signals. A receiver's ability to detect a signal depends on the spatial arrangement of the different sound sources in the network (Wiley, 2006). For example, in acoustic signals, many animals use small temporal differences between the two ears to perceive distance and signal location. Acoustic interference from calling individuals (real or simulated) that are located at different distances or angles away from the signaler differentially impact the ability to correctly perceive the location of the signal. Thus, when animals communicate across complex networks of signalers and receivers there are considerable challenges for signalers to make themselves stand out and receivers to find the source of the signal.

Social Complexity and Signal Complexity

The social complexity hypothesis (Jolly, 1966) posits that complex social interactions, including networks, may have spurred high levels of intelligence in humans and other animals because of the demand for cognitive abilities necessary to keep track of different social interactions and relationships. A successful social animal should keep track of the interactions of other individuals it is likely to encounter and many of the examples discussed above (e.g., eavesdropping on aggressive interactions in fighting fish or songbirds) indicate that animals pay attention to the social relationships among other individuals. The ability to eavesdrop on the interactions of one or two other individuals, and infer likely competitive ability, demonstrates some level of cognition (Shettleworth, 2010). However, some animals, such baboons, hyenas, dolphins, or parrots, live in much larger groups, sometimes with a fission-fusion group structure. Keeping track of the complex network of interactions and signals in groups this large clearly requires considerable cognitive ability, but there is evidence that individuals within these groups also eavesdrop on and carefully monitor the social interactions of other individuals within their social group (McGregor, 2009).

In addition to assessing relationships between specific individuals, communicatory signals can be used to assess the number of individuals present. A variety of species of social animals, including elephants, lions, and birds, have been shown to exhibit behaviors that suggest this type of numerical cognition. For example, spotted hyaenas (*Crocuta crocuta*) use the vocalizations of rival groups to assess the number of individuals present. They then use this information to determine their relative numerical advantage, necessarily levels of vigilance, and likelihood of winning future aggressive interactions (Benson-Amram *et al.*, 2011).

The social complexity hypothesis discussed above has also been directly applied to the evolution of communication signals, using a similar rationale. The general idea is that increased levels of social complexity could in turn drive increased levels of vocal complexity (Freeberg *et al.*, 2012). Clearly if an animal uses vocal signals to recognize specific individuals in its social group, then larger groups would necessitate a larger number of distinct signals to accommodate all of the individuals. The idea that social

complexity could drive communicative complexity can be extended significantly further than this by thinking about the structure of larger social groups. As a social network increases in size, so too does the variation in its composition. From the perspective of a particular animal, for example an adolescent male, a large group might contain some individuals that are females (potential mates) and some that are males (potential competitors). Of these males, some might be dominant and others might be subordinate to our male, still others might be kin or other allies. It is not hard to imagine how the evolution of different acoustic signals (e.g., those used to advertise courtship to females and dominance vs. subordination to males) would be favored to more efficiently communicate information or intention to individuals in each of these diverse categories. As a social network continues to increase in size so does the number of potential relationship categories for each individual. It follows then that this increase in the number of important second and third-party relationships an individual must understand in order to safely navigate social interactions should in turn increase the complexity of signals (Freeberg et al., 2012). Because of the relationship between social and vocal complexity, it has been suggested that in a similar way our own extensive communication networks are one of the key drivers by which humans evolved such complex language abilities.

See also: **Social Behavior:** Collective Intelligence in Social Animals; Group Movement.

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