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EDITED AND REVIEWED BY
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SPECIALTY SECTION
This article was submitted to
Social Behavior and Communication,
a section of the journal
Frontiers in Ethology

RECEIVED 10 October 2022
ACCEPTED 31 October 2022
PUBLISHED 13 December 2022

CITATION
Freeberg TM (2022) Social behavior
and communication grand challenges
– Frontiers in Ethology.
Front. Ethol. 1:1066186.
doi: 10.3389/fetho.2022.1066186

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Social behavior and communication grand challenges – Frontiers in Ethology

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KEYWORDS

communication, cues, information, multimodal signaling, networks, noise, signals, social behavior

The ubiquity of social behavior and communication

All animals – indeed, all living things – communicate (e.g., [Diggle et al., 2008](#); [Bradbury and Vehrencamp, 2011](#); [Schaefer and Ruxton, 2011](#); [Babikova et al., 2013](#)). Communication is perhaps the key body-to-body or cell-to-cell interaction that makes fundamental biological processes possible. These processes include everything from biochemical changes on the surface of one cell that alter the metabolic activity of a nearby cell to the production of a mating signal by one individual that alters the likelihood of reproductive activity of another individual. Communication is therefore largely about changes induced in an individual by a perceived action or structure of another individual. It is thus the social behavior that lies at the foundation of all other social behavior and includes individuals producing visual displays that deter the pursuit of a predator, vocalizations that change the movement patterns of others in their midst, volatile chemical compounds that attract potential mates, and vibrational waves that pause the signaling behavior of nearby conspecifics.

Individuals of many species engage regularly if not constantly in social behavior – individuals in social species spend large parts of their lives in social groups, in close proximity and often engaging in interactions with conspecifics. Even in species in which individuals spend most of their lives solitary (e.g., orb weaving spiders), individuals still have to mate, and occasionally have to interact with others in ways that affect social proximity (e.g., territoriality: [Leyhausen, 1965](#); [Graw et al., 2019](#)). Furthermore, we are learning more about the importance to individuals of living in social groups composed of multiple species ([Dhondt, 2012](#); [Goodale et al., 2017](#)).

Living in social groups brings benefits such as an enhanced ability to detect and respond to predators and food resources ([Wilson, 1975](#); [Krause and Ruxton, 2002](#)). These benefits of group living are often thought to accrue to prey species, but predators clearly benefit from sociality as well ([Beauchamp, 2014](#)). Although we know a great deal about benefits of social living for both conspecific-only and mixed-species groups, we know less about the costs of such social living, and so more work on this question is needed ([Dhondt, 2012](#); [Goodale et al., 2017](#)). As a rule, social living will evolve when the benefits

outweigh the costs. The benefits of living in social groups often critically depend on the signals and cues of others (Hauser, 1997; Bradbury and Vehrencamp, 1998; D'Ettorre and Hughes, 2008; Bradbury and Vehrencamp, 2011).

Signals and cues

Individuals can gain considerable information about other individuals simply by assessing their non-signaling behavior – their cues. For example, small prey species typically respond with strong anti-predatory behavior to bird-hunting avian predators flying overhead, but may not display as much anti-predatory behavior if those same avian predators are actively courting one another. Likewise, by watching a pet dog sleep, we can predict with great certainty what its immediate subsequent behavior will be based upon these cues – more sleep. Most of the focus of research in communication has been on signals, however. Unlike cues, signals have evolved for the particular communicative function they serve. As a few examples consider the anti-predatory alarm signals in 3 vervet monkeys, *Chlorocebus pygerythrus*, mate attraction signals in stalk-eyed flies, *Cyrtodiopsis dalmanni*, and food detection signals in ravens, *Corvus corax* (for a key reference describing cues and signals, see Maynard Smith and Harper, 2003). Although the distinction between a cue and a signal is important, sometimes distinguishing cues from signals is not a trivial matter (Bradbury and Vehrencamp, 2011).

When we study the signals that animals use, we notice in many cases that the signals and signaling are quite complex. Dating back at least to Darwin (1872), fundamental questions in the study of communication relate to signal complexity. Why is there such incredible diversity in signal complexity across different species, or perhaps even across different populations of the same species? What factors select for the complexity of signals or of signal use? One of the hypotheses to explain signal complexity in animals is the idea that increased social complexity (larger groups, greater diversity of relationships within groups) drives a need for greater signaling complexity (Freeberg et al., 2012). More complex groups often demand increased social cognition in group members; therefore, in such groups we should expect strong selection for enhanced communicative systems that provide individuals diverse behavioral ways to assess and manage the behavior of others (Dunbar, 2003; Freeberg et al., 2012). This argument is relevant for all signaling modalities, and not just vocal and visual (e.g., delBarco-Trillo et al., 2012; Gebhardt et al., 2012). The relationships among social complexity, social cognition, and communication – and the neural bases underlying these – are currently a major focus of inquiry (Lucas et al., 2018; Freeberg et al., 2019; Roberts and Roberts, 2020; Roberts et al., 2022).

Social behavior and communication: Where we've come from and where we might go

As with so many things in biology, one of the earliest major treatments of social behavior and communication was carried out by Darwin in his foundational *The Expression of the Emotions in Man and Animals* (Darwin, 1872). A century after that book was first published, three founders of the field of ethology won the Nobel Prize for Physiology or Medicine in part for their work on social behavior and communication – Niko Tinbergen, Karl von Frisch, and Konrad Lorenz (Burkhardt, 2005). In the last several decades, researchers in social behavior and communication have continued to make major advances. There was a sustained consideration of the value (or damage) of the term “information” in the study of communication (Shannon and Weaver, 1949; Burkhardt, 1970; Smith, 1977; Dawkins and Krebs, 1978), and the information debate reared again recently (Owings and Morton, 1998; Hailman, 2008; Owren et al., 2010; Seyfarth et al., 2010; Fischer, 2013; Wiley, 2013a). For some the ‘communication as information’ vs ‘communication as manipulation’ debate is largely one of semantics, for others communication involves both information and manipulation, and for others the debate raises some fundamental ideas about how communicative interactions actually influence behavior and shape interactions and relationships among individuals. Game theory models helped advance our understanding of signaling both in cooperative/pro-social and in competitive/contest situations as, unlike in basic optimality models, frequency dependence and what signaling behavior other individuals are using are important (Maynard Smith, 1982; Bergstrom and Lachmann, 1998; Maynard Smith and Harper, 2003; Hurd and Enquist, 2005).

Over the last few decades, it has become clear that the standard dyadic way of thinking about communication is too limiting. The *sender* → *signal/cue* → *receiver* relationship almost always occurs within a complicated social milieu of both conspecifics and heterospecifics and of both cooperators and competitors – individuals commonly communicate within complex communication networks (Cheney and Seyfarth, 1999; McGregor, 2005). Recent advances in social network approaches are now putting us in a position to understand better how networks of signaling relate to networks of other social behavior (such as affiliations or agonistic interactions: Snijders and Naguib, 2017), and this should help us better understand how social interactions build into the social relationships that create the structure of groups (Hinde, 1976; Croft et al., 2008; Wey et al., 2008; Barrett et al., 2012; Farine et al., 2015). Over the last few decades it also became clear that

our unimodal way of observing and experimenting with animal signaling greatly oversimplified the ways in which individuals actually communicate with one another in natural settings. For example, decades of study revealed the developmental and functional implications of variation in songs of songbirds using analyses of the recorded acoustic signals. But the songs of many songbird species are often produced in conjunction with visual displays that can range from relatively simple changes in body posture to relatively ornate changes in feather and wing placement and movements. These visual displays that are produced with songs are important signals to receivers, and it is increasingly clear that communication in animal species is regularly multi-modal, and this has important implications for our proximate and ultimate understanding of animal communication (Partan and Marler, 1999; Cooper and Goller, 2004; Partan and Marler, 2005; Higham and Hebets, 2013; Partan, 2013; Peckre et al., 2019). Furthermore, multi-modal signaling is seen in a wide range of taxa (e.g., Narins et al., 2005; de Luna et al., 2010).

Outside of the realms of studies of mate choice related to signal variation and studies of predator behavior related to prey cue variation, most of the focus of research on animal communication had traditionally been on the sender and the signal it produces. Increased work on the receiver side of the equation is needed for a wider range of signaling modalities, a wider range of communicative contexts, and a wider range of taxa. What kinds of proximate and ultimate factors influence signal perception by receivers (King et al., 2003; Schmidt and Romer, 2011; Sheehan et al., 2014; Henry et al., 2016)? In any channel of communication, noise distorts or diminishes the chances of successful communication – the ability of a receiver to pull a signal or cue out of the background becomes more difficult the more noise exists in the system (Wiley, 2017). Given the prevalence of noise in most every channel of communication – and the increasing presence of human noise in non-human animal communication – more research on signal and cue perception in the contexts of acoustic, chemical, visual noise is needed (Grafe et al., 2012; Naguib, 2013; Wiley, 2013b; Wiley, 2017). Going back to the sender, furthermore, we know that signals are frequently produced in streams of signals. How important is the particular sequence of signals to receivers? We have developed sophisticated analytical approaches to analyzing signal sequences (Kershenbaum et al., 2016), but now need to devote more effort to understanding how variation in sequences maps on to variation in sender and receiver behavior. We are also beginning to understand how variation between signal presentations can be meaningful to receivers, but much more work is needed.

Individual behavior can be heavily influenced by variation in social context – contextual variables like the density of individuals and the composition of different personalities or behavioral types of individuals within groups or populations. These influences can be both proximate factors impacting

individuals over their lifetimes, but can also be powerful selective pressures shaping behavior patterns in populations over generations (e.g., lizards: Cote et al., 2008; birds: Roth et al., 2021; fish: Almany and Webster, 2004). More work is needed that integrates assessments of social contextual factors like density and variation in social roles with assessments of individual behavior to increase our understanding of behavioral variation across populations and across generations (Wright et al., 2019).

Social grouping and social behavior are often constrained by environmental factors, including predation pressure and physical habitat structure (Orpwood et al., 2008; Griesser and Nystrand, 2009; Cenni et al., 2010; Bettridge and Dunbar, 2012; Goodale et al., 2014; Gentry et al., 2019). Increased sociality is important for anti-predatory benefits and may help individuals deal better with habitat disturbance. Although increased mixed-species group sociality is also thought to be important for anti-predatory benefits, the stability and composition of mixed-species groups often breaks down with habitat disturbance (Lee et al., 2005; Mokross et al., 2014; Mammides et al., 2018). Why habitat disturbance might impact social behavior and communication of single species groups differently from mixed-species groups is an important question to try to answer given the ubiquity of anthropogenic disturbance in non-human animal systems – urbanization and hard reflective surfaces, light and noise pollution, climate change, etc.

Beyond the question of how mixed-species groups respond to habitat disturbance, our understanding of the proximate and ultimate factors driving mixed-species grouping is still in its infancy (Goodale et al., 2017; Goodale et al., 2020). What factors cause an individual of one species to join with individuals of another species, what factors keep it in the group for minutes, hours, or days, and what factors cause it to leave the group (Sridhar et al., 2009)? We do know that individuals regularly eavesdrop – they perceive and attend to the signals of other species (e.g., Templeton and Greene, 2007; Goodale and Kotagama, 2008) and such heterospecific communication can influence the structure of mixed-species groups (Goodale et al., 2010). We also know that mixed-species group size and composition can impact the ways in which individuals communicate (Coppinger et al., 2020). The dynamics and determinants of signaling and mixed-species group composition will prove to be an important area of future research.

Researchers in a wide range of fields have long been interested in the similarities and differences between non-human animal communication on the one hand and human language on the other hand (Cheney and Seyfarth, 2010; Collier et al., 2014). For non-human animal communication systems beyond bird song, how (in)flexible are signaling systems with regard to variation in social experience during development? Recent evidence suggests more plasticity in vocal development than had been appreciated (Lemasson et al., 2011; Koda et al., 2013). We are also beginning to understand better the significance of syntax-like structure in communicative systems

outside of human language (Bohn et al., 2009; Ouattara et al., 2009; Collier et al., 2014; Suzuki et al., 2016; Griesser et al., 2018). Most of this work has been carried out in systems of vocal communication, but recent research is pointing to the importance of visual communication with regard to the ‘communication → language’ transition (Roberts et al., 2019; Roberts and Roberts, 2019; Damjanovic et al., 2022). Circling back to earlier discussion, how important is the complexity of the social milieu to the complexity of signals and signal sequences, and how might social complexity explain the evolutionary transition to language (Dunbar, 1993; Dunbar, 2003; Freeberg et al., 2012)?

The “Social Behavior and Communication” specialty section seeks to address these, and many other, questions in this field. We are at a particularly interesting and exciting time in the field as technological and statistical advances have made the study of signal use and social behavioral metrics incredibly sensitive and sophisticated. There are enormously important questions remaining to be addressed in animal social behavior and communication, some of which are raised here, and this specialty section is an ideal home for articles that describe work aimed at addressing those questions. We welcome both experimental and descriptive/correlational studies and approaches at all levels of analysis – mechanistic, ontogenetic, functional, and phylogenetic. Furthermore, studies that integrate more than one of these levels are

particularly needed to help push our understanding of social behavior and communication forward.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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