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SYMPOSIUM

New Dimensions for Animal Communication Networks: Space and Time

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Synopsis Communication is a social process and usually occurs in a network of signalers and receivers. While social network analysis has received enormous recent attention from animal behaviorists, there have been relatively few attempts to apply these techniques to communication networks. Communication networks have the potential to offer novel insights into social network studies, and yet are especially challenging subjects, largely because of their unique spatiotemporal characteristics. Namely, signals propagate through the environment, often dissociating from the body of the signaler, to influence receiver behavior. The speed of signal propagation and the signal's active space will affect the congruence of communication networks and other types of social network; in extreme cases, the signal may persist and only first be detected long after the signaler has left the area. Other signals move more rapidly and over greater distances than the signaler could possibly move to reach receivers. We discuss the spatial and temporal consequences of signaling in networks and highlight the distinction between the physical location of the signaler and the spread of influence of its signals, the effects of signal modality and receiver sensitivity on communication network properties, the potential for feedbacks between network layers, and approaches to analyzing spatial and temporal change in communication networks in conjunction with other network layers.

Introduction

The recent explosion of research into animal social networks has revealed that social structure plays a critical role in ecological and evolutionary processes including sexual selection, the evolution of cooperation, disease transmission, and the spread of innovations (Croft et al. 2009; Firth et al. 2015; McDonald and Pizzari 2018; Sah et al. 2018). Techniques for analyzing social networks are coevolving with increasingly sophisticated technology for tracking and recording the behaviors of large numbers of animals in space and time (Krause et al. 2013; Levin et al. 2015; Gill et al. 2016; Gernat et al. 2018; Smith and Pinter-Wollman 2021). This increased data availability enables partitioning social networks into layers based on specific behaviors, and examining links between these network layers (Finn et al. 2019; Smith-Aguilar et al. 2019). Communication regulates many social interactions, and so plays a key role in determining social structure. Nevertheless, and despite the fact that communication has long been recognized as occurring in a network (McGregor and Dabelsteen 1996), it is rare for studies of social networks to focus on explicit communication interactions, and for studies on communication networks to utilize the techniques of social network analysis to understand network-level properties of communication. The case for a better integration between communication network studies and social network analysis was recently made by Snijders and Naguib (2017), who describe many fruitful avenues of research. Our aim is to extend this argument, both encouraging new advances in studies of animal social and communication networks and indicating associated

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challenges, by emphasizing an aspect of communication that makes it an especially unique and interesting system with which to study animal social structure: its spatial and temporal characteristics.

The basis of any network analysis is to define connections ("edges") between individuals in the network ("nodes"; for a detailed review of techniques for constructing and analyzing animal social networks, see Farine and Whitehead 2015). Briefly, in animal social network analysis, edges represent either discrete dyadic interactions at close range (e.g., grooming, physical attack; Fig. 1B), or instead, under the "gambit of the group," edges are made between all individuals observed in a group at a given time (Fig. 1C; Whitehead and Dufault 1999). We define communication networks as networks of signalers and receivers, with edges generated between each signaler and any individuals that receive its signals. Communication networks are a subset of the networks found in animal groups, with each network representing a "layer" in the overall social structure, but communication networks have unique properties (Fig. 1). Specifically, in communication networks signals may be directed toward specific individuals, but because signals propagate more widely, they are likely to reach other individuals within the signal's active space (where, and for how long, a signal can be detected by receivers). To characterize the network, each individual interaction (e.g., each instance of signaling, although other sampling levels are possible) is recorded in a matrix quantifying all such interactions between all possible dyads of individuals over a period of sampling. These matrices can then be used to build visualizations of the network, with each node representing an individual and edges representing either that there is a connection between two individuals (unweighted networks), or quantifying the strength of the connection between two individuals (weighted networks). The edges in communication networks built from individual signaling interactions are directed, representing the asymmetry of the signaler and receiver roles in any given instance of communication, and depicted as arrows from signaler to receiver on network diagrams. Network statistics can be calculated that characterize an individual's position in the network, including the strength and number of its connections with others (Farine and Whitehead 2015).

Despite the challenge of quantifying connections in communication networks (see the section Measuring and constructing communication networks), we argue that communication will provide novel insights into the understanding of animal social networks, largely because of the spatiotemporal characteristics of signal propagation. First, aside from tactile signals, all signals propagate through space and/or time to reach receivers. The spatial pattern and speed of propagation, the rate at which the signal decays, and receiver detection abilities will determine both the number of connections with other individuals (i.e., edges) and, if the influence of the signal varies with distance, the strength of those connections (i.e., edge weights, in a weighted network). Second, the rapid spread and large spatial reach of many animal signals, combined with signals' influence on receiver behavior, generate potential for rapid feedbacks between individual behavior and social structure (Cantor et al. 2020), including not only communication interactions but also spatial positioning, group membership, and group density. Third, the communication network is not necessarily congruent with other social network layers. Among other reasons, this occurs because individuals' movements may be dissociated from the location and/or movements of their signals (particularly for long-lasting structures, chemical deposits, and long-distance signals; Schaedelin and Taborsky 2009). Furthermore, the short temporal scale and rapid repetition of many communication interactions imply that the time constant for network turnover is much smaller than for many other social processes. Below, we discuss these characteristics of communication networks in more detail, show how the spatiotemporal characteristics of communication raise challenges for network analyses, offer some approaches to deal with those challenges, and argue that explicit incorporation of communication interactions into studies of social networks will lead to advances in emerging areas of interest in the study of animal social structure.

Active space and communication networks

Communication networks are characterized by connections between signalers and receivers, which are determined by physical relationships between individuals, how signals propagate in space and time, and receiver sensory capabilities. Different signal modalities have different transmission properties, and therefore may be received by different individuals. For instance, the spatial reach of many broadcast acoustic signals can be quite large (Payne and Webb 1971; McComb et al. 2003), while some chemical signals, though also detectable over long distances, generally propagate more slowly and are limited by water or wind speed (Dusenbery 1989). Electrical and vibratory signals usually have a very limited

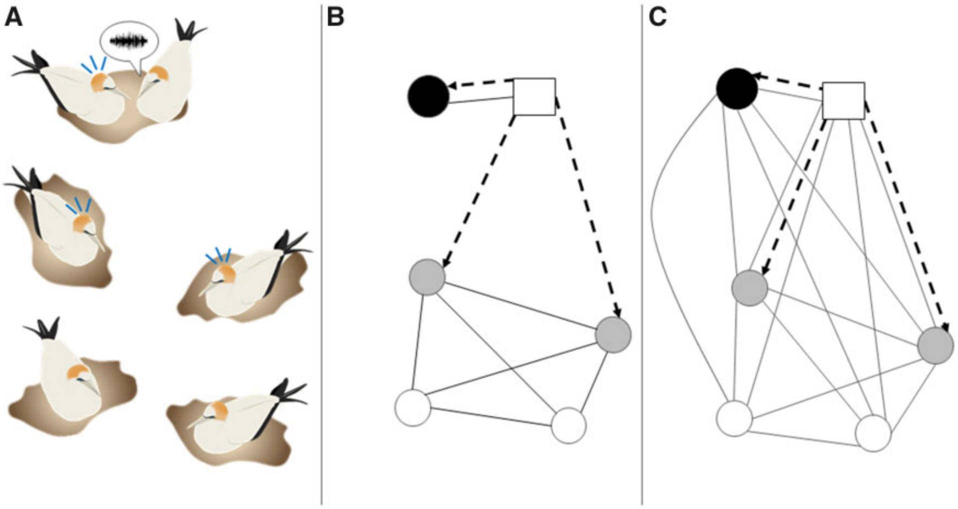

Fig. 1 Illustration of edge placement in communication networks and traditional social networks. (**A**) shows the actual spacing of organisms. The individuals in the top row are a signaler and intended receiver. Those in the middle row are unintended receivers. (**B**) Edges in a hypothetical social network (solid lines) based on physical interactions. Edges in a hypothetical communication network would instead be placed between the signaler and all receivers within the active space of the signal (dashed arrows). The white square represents the signaler, the black circle the intended receiver, and the grey circles unintended receivers. (**C**) As in (B), but here the social network is depicted based on the gambit of the group approach, with edges between all individuals.

active space (Hopkins 1999; Čokl and Virant-Doberlet 2003). Acoustic and electrical signals and visual displays are often temporally ephemeral, while many chemical deposits can persist for much longer periods of time (Soso et al. 2014; Brahmachary and Poddar-Sarkar 2015). Although deposited chemical signals may not propagate as far or as fast as many other signal types, they may nevertheless reach many individuals, due to the movement of individuals toward a relatively fixed long-term signal (as can some visual signals e.g., bowerbird bowers; Diamond 1986; fiddler crab burrow hoods; Christy et al. 2001). Thus, there is often some dissociation between the signaler and its signals in either space or time, which raises a challenge for comparisons of communication networks with other network layers based on proximity. In principle, an animal could be interacting physically with one individual (forming an edge between nodes representing the two individuals in a social interaction network), at the same time that one or more signals it produced in the past affect other individuals elsewhere (in which case it may be appropriate to consider the signal itself as the node, with a second layer in the communication network connecting the individual signaler to all of its signal nodes).

All of these patterns of signal propagation will vary depending on heterogeneity in the transmission characteristics of the environment (Richards and Wiley 1980). For instance, noise may reduce the active space of acoustic signals (Römer 2001), while turbidity and vegetation structure could do the same for visual signals (Wong et al. 2007). Thus, communication network structure (i.e., the pattern of connections between individuals) will vary with environmental conditions, even for the same spatial configuration of individuals.

Receivers have received less attention in spatio-temporal studies of communication because it is less straightforward to quantify their behavior than it is the propagation of a signal. Ultimately, to determine signal active space and characterize edges in communication networks, it is not sufficient to show that the signaler produced a signal in some place and time when the receiver could have detected it; we must also show that the receiver was in fact influenced by that signal, and how it was influenced, a considerably greater challenge (but not an insurmountable one, e.g., Lohr et al. 2003). Receivers' abilities to detect and evaluate signals are limited by the sensitivity and tuning of their sensory systems. We discuss approaches for defining receivers in communication networks in the section Measuring and constructing communication networks, below. Receiver characteristics will also have more subtle effects by influencing how information percolates within communication networks (Halupka 2014; Hare et al. 2014). For instance, many receivers exhibit selective attention toward only a subset of the nearest signalers or a subset of signal components, even if others may also be close enough to be detected (Greenfield and Snedden 2003; Yorzinski et al. 2013). Temporal processes such as memory, sampling, and information integration will also influence receiver effects on the communication network (Schwartz et al. 2004; Akre and Ryan 2010). The information content of signals degrades with distance and over time, thus receivers may be affected by signals differently depending on their relative positions. For instance, individuals at close range to a signaling interaction between two other individuals may perceive and respond to the signal itself, while those further away might only perceive that an interaction is taking place (but not clearly perceive the signals). These secondary connections raise additional challenges for measuring communication networks.

Multimodal signals raise further challenges for characterizing communication networks because different components of the same display have different spatiotemporal propagation patterns (Uetz et al. 2013). The consequences of this differential propagation will depend on the function of the multiple signal components (Johnstone 1996). For instance, if the components are redundant (Uetz et al. 2009), then the communication network could reasonably be reconstructed based on the active space of the more distantly propagating modality. However, if the components provide separate messages, it may be necessary to calculate different network layers for each component (see the section Comparing network layers, below), due to the different propagation characteristics of each modality, and because there are essentially two different signals that just happen to be produced simultaneously. If the function of the signal depends on an interaction between the signal's components (Narins et al. 2003), then the network may instead be limited by the least distantly propagating modality, and there may be variation in the effect of the signal (i.e., the edge weight) depending on the distance to the receiver. In any of these cases, it is challenging to calculate associations between signalers and receivers because the response of receivers to each modality, and to their combination, must be understood. This difficulty is not limited to the study of communication networks but is a general challenge in the study of animal communication. However, the understanding of multimodal signal processing is rapidly advancing and may enable more accurate characterizations of connections between signalers and receivers in communication networks.

Feedback loops

Communication networks are of interest to the larger study of social structures in part because communication is fundamental in shaping that structure in the first place. Individual behavior in signaling interactions affects group-level phenomena such as the spacing, composition, and persistence of social groups. For instance: (1) Bouts of group signaling are often catalyzed by single individuals and can likewise be ended when specific individuals drop out (Brooke et al. 2000; Dapper et al. 2011). Finer temporal patterns can be generated by the coordination of signals between individuals, leading to whole groups signaling in synchrony or alternation (Greenfield 2005). (2) Spatial distributions are influenced by local levels of competition, with individuals adjusting their distance from one another according to the competitiveness of their neighbors' signals (Murphy and Floyd 2005; Nityananda and Balakrishnan 2008). (3) The presence of specific types of signalers or receivers in the network can have strong effects on network structure and function. For instance, unreliable signalers may destabilize both communication systems and social groups if they produce many dishonest signals (Popat et al. 2015). These effects may cascade across trophic levels in the broader communication network, as in the case of mimicry: if Batesian mimics become too prevalent, the effectiveness of aposematic signaling is reduced (Mallet and Joron 1999; Harper and Pfennig 2007), which could lead to changes in signaling strategies. Although eavesdroppers that use signals to locate prey are not considered in traditional social network studies, their presence can dramatically alter communication network structure (Zuk et al. 2006; Goodale et al. 2019). Meanwhile, the spatial structure also modulates the influence that individuals have on groups (Sosna et al. 2019). Many social network studies show that centrality in the network (Farine and Whitehead 2015) determines an individual's influence on the social group (Drewe 2010; Weber et al. 2013), although depending on how information spreads, peripheral individuals are sometimes more influential (Sosna et al. 2019; Firth 2020).

Individuals, via their communication behavior, therefore can affect their social group, but the opposite is also true: characteristics of the social group can affect individual communication behavior. For instance: (1) The density of individuals in the social group determines the intensity of competition, the level of noise (particularly noise produced by the signalers themselves), and the active space needed for effective signaling (Quick and Janik 2008; Fernandez et al. 2017), resulting in phenomena like the Lombard effect where signalers increase their signal amplitude in high noise levels (Brumm and

Zollinger 2011). (2) Network density (the number of actual edges out of all possible edges) and topology (distribution of edges) determine whether and how quickly information propagates to others, and thus whether these individuals' communication behavior is affected (Kashima et al. 2013; Romano et al. 2018). (3) The actual pattern of connections, for instance, the network assortativity (phenotypic correlations among connected individuals), shapes which individuals a signaler can reach (Croft et al. 2009), and therefore the costs and benefits of different signaling strategies (Bates et al. 2010). Thus, there are feedbacks between individual and group behavior. Individual-group feedbacks are emerging as an important phenomenon in animal social networks (Cantor et al. 2020), but have received little attention in the context of communication networks despite their likely prevalence.

Measuring and constructing communication networks

A major challenge for characterizing communication networks is that while identifying signalers is straightforward, determining who both the intended and actual recipients are can be difficult. There are many ways to address this challenge, which we categorize here based on whether edges between signalers and receivers are defined by proximity, response, or timing (Fig. 2). There are advantages and disadvantages to each approach. Thus far, few studies have employed any of these approaches to characterizing communication networks but, given improvements in technology and analysis techniques, these should be considered in future studies.

1. Proximity approaches (Fig. 2A) assume that individuals within a given distance (millimeters to kilometers depending on signal characteristics) of the signaler are receivers, whether intended or otherwise. When constructing the network, edges are placed between the signaler and all individuals within the chosen distance (edge weights could be used to represent absolute distance, as many signals will have greater influence at close range; Snijders and Naguib 2017). This method applies well to broadcast signals (e.g., song, anti-predator signals) because these tend to be "intended" for many if not all individuals in proximity of the signal (Templeton and Carlson, 2019). This approach also works well for some signals that have a limited range because only individuals within a specific area can receive the signal (e.g., quiet calls; Reichard and Anderson, 2015). However, it can be difficult to determine signal range, for instance when signal propagation is directional and depends on the orientation of the signaler, or when environmental heterogeneity affects propagation patterns. Furthermore, the proximity approach assumes that all individuals in the area received the signal, but this may be incorrect because receivers vary in their sensory capabilities, attention, and threshold for response, both within species (Ronald et al. 2012) and between species (Stevens 2013). This is especially the case in instances of so-called "private" communication channels, in which signals have specific parameters (e.g., ultrasonic frequencies or ultraviolet light) that cannot be detected by unintended receivers such as eavesdropping predators (e.g., Cummings et al. 2003).

2. In response approaches (Fig. 2B), edges in the network are created between the signaler and all individuals that produce a specific behavioral response (e.g., fleeing, alertness, and direction changes; Suzuki 2012). An advantage of this approach over proximity approaches is that response behaviors are often straightforward to recognize and thus responding individuals can be confidently assigned as recipients of the signal. However, this requires monitoring all individuals in proximity to the signaler and a thorough understanding of their behavioral repertoire, which may be technically challenging. Furthermore, this approach ignores individuals that may have received, but not responded to, the signal with specific behaviors, and does not account for individuals that did not respond to the original signaler, but to another receiver of the initial signal instead.

3. Timing approaches (Fig. 2C) address some of the weaknesses of response approaches by placing edges between signalers and only those potential receivers that produce a behavioral response within a certain time window after the signal. These approaches are especially applicable to cases where the response is another signal, because many communication interactions require a specific timing to be effective. The major challenge for applying timing approaches to signaling interactions is to determine that a given signal was in fact a response to a previous signal. This may require knowledge of species-specific timing intervals (Heller and von Helversen 1986), but can also be tested statistically by examining whether response timing is non-random with respect to the signals of other individuals in the group. For instance, Anisimov et al. (2014) recorded vocalizations of all individuals in a group of zebra finches, and then used cross-correlation analyses of the timing of each individual's signals to determine which individuals responded to one another's calls.

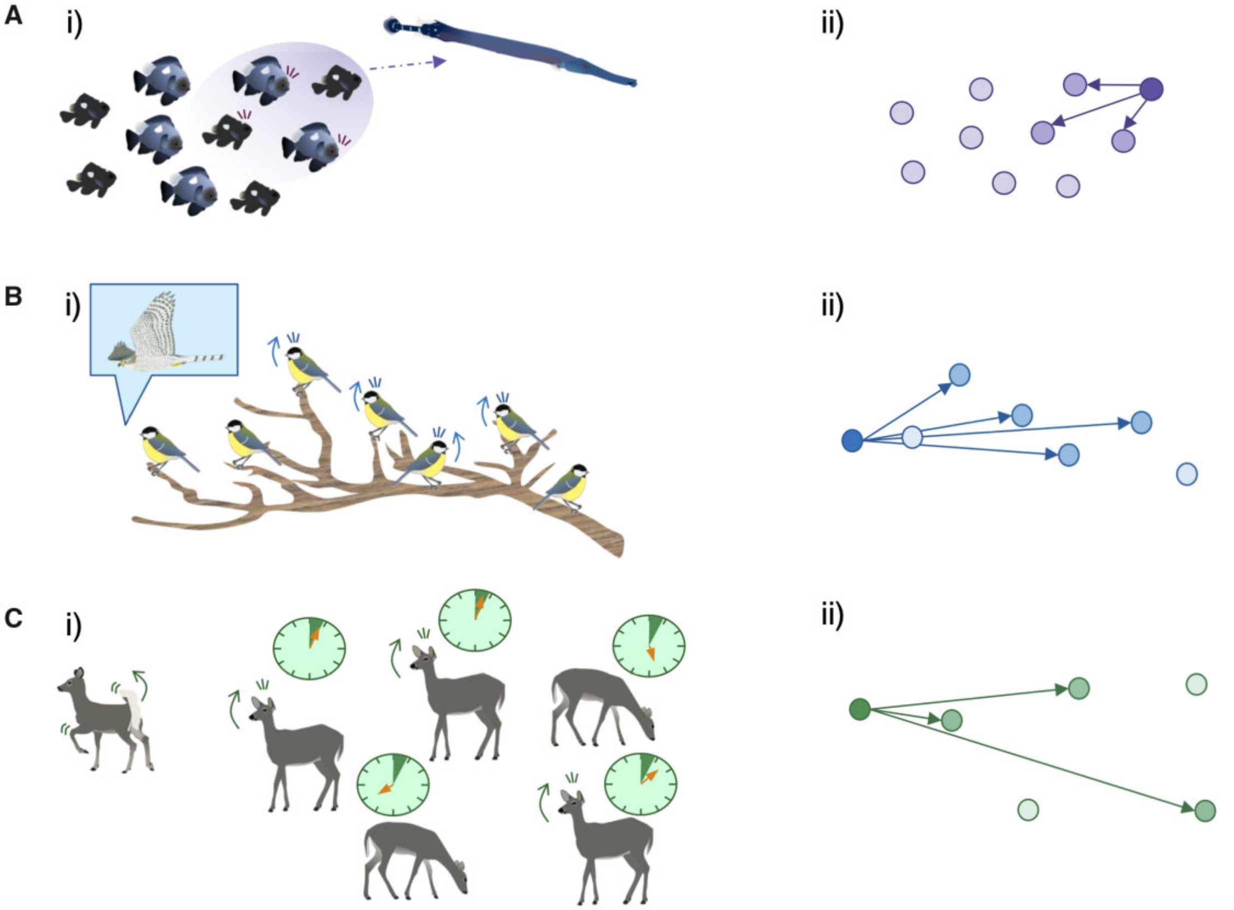

Fig. 2 Three approaches to determine edges in communication networks. Each example is based on alarm signaling. (**A**) Proximity approaches: a signal (produced by the individual spotting a predator, indicated by the arrow) has a specific area of influence (oval area) inside of which all individuals are assumed to receive the signal. (**B**) Response approaches: only individuals that exhibit a specific response (e.g., looking up after an alarm call) are considered to have received the signal. (**C**) Timing approaches: edges are made between the signaler and individuals that respond only within a specific period of time (timing represented by the clock above each potential receiver; assuming a signal produced at 12:00, individuals whose response timing (orange arrow) is within the specified time window (dark wedge) are considered to have responded to the signal), but no edges are created between the signaler and individuals that do not respond or that respond outside of that time window. For each approach, we illustrate (**i**) the signaler and individual responses and (**ii**) edges in the communication network for this instance of signaling, as arrows from signaler to receiver.

Similarly, Stowell et al. (2016) used methods based on neural network analyses to analyze temporal patterning of interactions among individual zebra finches to examine network stability and the influence of specific individuals. Another complication with both response and timing approaches is if multiple individuals signal simultaneously, in which case it may be impossible to tell whether a receiver was responding to one or both of the signalers.

Another challenge for constructing networks, and one that has received little attention in the context of communication networks, is to choose the time period in which associations are sampled to build the network (Psorakis et al. 2015; Zhao et al. 2018). Sampling times that are too short may miss rare, but important, events, while sampling times that are too long may obscure faster changes taking place in the network (Blonder et al. 2012; Davis et al. 2018). For instance, in many chorusing species, most signaling takes place within a discrete time period (Greenfield 1994; Staicer et al. 1996), which may therefore be a convenient sampling unit. However, within chorusing events, there can be bouts of signaling, and times with higher and lower signaling rates within bouts (Greenfield 2005). Additionally, some social relationships may only be detectable by examining associations across longer time periods, for instance, whether certain individuals tend to signal in especially dense areas, or in proximity to other specific individuals across multiple chorusing events. Here again, the modality and context of signaling will play a role in setting the temporal parameters of the network. Long-lasting chemical deposits and physical structures will have a very different turnover rate than ephemeral acoustic and visual displays. Likewise, whether or not the network is stable over time is an important consideration because it will determine whether a single snapshot of the communication network suffices to describe its properties (Fisher and Pinter-Wollman 2020). For instance, display networks in species with long-term territories may be stable relative to those in species engaged in scramble competition. Regardless, it is likely that communication network stability (the time period over which individual communication associations are relatively repeatable) will differ from that of other social network layers, although this has not been tested. A related temporal issue is to define what constitutes an edge in the communication network. Our discussion so far largely implies edge creation on every instance of a signal reaching a receiver, but this may be impractical or misleading for, among others, relatively stationary species with high signal repetition rates. Aggregating over longer temporal periods, for instance by creating edges based on participation in a bout of signaling, may be useful but faces the same tradeoffs discussed above for the timescale over which the network is constructed. Essentially the same issues arise for spatial network dynamics: some decisions must be made about what constitutes a group in space (James et al. 2009), and the outcome of this decision may differ between communication networks and other social network layers.

Comparing network layers

Communication networks are inherently a part of the larger social network. It is often of interest to determine the relationships of different network layers to one another (Finn et al. 2019). All of these network layers can be measured using a variety of methods and with different input data, which raises a challenge for analysis because these will not all recover the same network structure (Greenfield 2010; Templeton and Carlson 2019). Association networks (which characterize the amount of time individuals spend near one another) are one of the more common social networks measured, but many other networks exist based on specific interactions (e.g., affiliative, dominance, or grooming networks; Croft et al. 2008). Similarly, many different communication networks can be created for signals with different functions (e.g., affiliative signals, agonistic signals, feeding signals). The behaviors and signals used to construct the network will necessarily determine whether communication networks are correlated with other network layers. Comparing networks built from similar behaviors will likely result in higher correlation (e.g., grooming social networks and affiliative signal communication networks; Kulahci et al. 2015). However, the factors that determine the congruence of different network layers remain poorly understood.

Recent advances in multilayer network analyses allow for combining communication networks with other network layers (e.g., proximity, aggression, or affiliation networks) to create more comprehensive social networks and to determine the degree of overlap between different network layers. There are a number of different formulations of multilayer networks including multiplex networks (where each node connects to itself in multiple networks) and interconnected networks (where each node does not necessarily represent the same entity in each network; Finn et al. 2019). For example, Smith-Aguilar et al. (2019) show how multilayer network analysis can be used to incorporate multiple types of related networks to determine if some network layers are correlated, and to describe a more comprehensive group network using multiple interaction types. However, many methodological challenges remain, largely because of the spatiotemporal characteristics of different network processes (Hobson et al. 2013). Comparisons between network layers that were constructed using very different methods due to differing scales in time and space may not be valid (Castles et al. 2014). Analyses that explicitly focus on spatial and temporal dynamics of different network layers are needed to address these issues (Pinter-Wollman et al. 2014; Farine 2018; Fisher and Pinter-Wollman 2020). These techniques will be especially crucial for integrating communication networks with other layers of the social network, because of the complex spatiotemporal dimensions of signaling.

Conclusions and future directions

We have emphasized throughout that the spatial and temporal characteristics of communication signals have interesting and often unexplored implications for the broader understanding of animal social networks, and that indeed communication likely plays a larger role in shaping social network structure than is currently appreciated. Although the spatiotemporal dynamics of communication raise many challenges for characterizing animal communication networks, new technologies and analysis methods are rapidly expanding what is possible, and we argue that the resulting improved understanding of animal communication and social behavior will be well worth the effort. We conclude by briefly describing two profitable next steps.

Better characterization of signal active spaces in networks

There have been many studies demonstrating how signals attenuate in different environmental conditions, but relatively few have considered how signal propagation relates to the spacing and detection capabilities of potential receivers. In some cases, active spaces, and therefore the potential to directly influence others in the network, are surprisingly small relative to typical interindividual distances (Deb and Balakrishnan 2014). There are many logistical challenges, but with increased ability to track the position of individuals, technology such as microphone arrays (Blumstein et al. 2011) and acoustic cameras (Stoeger et al. 2012), or even the use of neurophysiological presentations in the field (“biological microphones”; Gilbert and Elsner 2000), the true reach of signals in the network can be determined.

Anthropogenic effects

Human activities are dramatically altering populations and individual behavior (Palumbi 2001). These effects directly impinge on social associations and are therefore likely to affect network layers and the relationships between layers via feedback loops (Snijders et al. 2017). For instance, increases in anthropogenic noise and habitat fragmentation will reduce the number and strength of connections between individuals, slowing the spread of information (Laiolo and Tella 2005; Dunlop 2019; Grabarczyk et al. 2020), while reductions in population size or increased mortality of specific individuals may destabilize the network entirely (Williams and Lusseau 2006; Maldonado-Chaparro et al. 2018). Additionally, signaling by introduced species may disrupt communication networks in native species by adding noise and reducing signal active space, potentially also reducing the connections among individuals in the network (Medeiros et al. 2017). The severity of these effects will depend on their spatiotemporal extent and the resilience of networks to disturbance. Future studies examining the broader effects for networks of these disturbances and their mitigation will tell us a great deal about how populations respond to anthropogenic changes.

These are just a few of the many promising possibilities for research on communication as a social network. By more fully integrating these behaviors in realistic ecological contexts, we will come closer to understanding the complex social lives of animals.

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Conflicts of interest

We report no conflicts of interest.

Data availability statement

No new data were generated or analyzed in support of this research.

References

Akre KL, Ryan MJ. 2010. Complexity increases working memory for mating signals. Curr Biol 20:502–5.

Anisimov VN, Herbst JA, Abramchuk AN, Latanov AV, Hahnloser RHR, Vyssotski AL. 2014. Reconstruction of vocal interactions in a group of small songbirds. Nat Methods 11:1135–7.

Bates ME, Cropp BF, Gonchar M, Knowles J, Simmons JA, Simmons AM. 2010. Spatial location influences vocal interactions in bullfrog choruses. J Acoust Soc Am 127:2664–77.

Blonder B, Wey TW, Dornhaus A, James R, Sih A. 2012. Temporal dynamics and network analysis. Methods Ecol Evol 3:958–72.

Blumstein DT, Mennill DJ, Clemins P, Girod L, Yao K, Patricelli G, Deppe JL, Krakauer AH, Clark C, Cortopassi KA, et al. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. J Appl Ecol 48:758–67.

Brahmachary R, Poddar-Sarkar M. 2015. Fifty years of tiger pheromone research. Curr Sci 108:2178–85.

Brooke PN, Alford RA, Schwarzkopf L. 2000. Environmental and social factors influence chorusing behaviour in a tropical frog: examining various temporal and spatial scales. Behav Ecol Sociobiol 49:79–87.

Brumm H, Zollinger SA. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour 148:1173–98.

Cantor M, Maldonado-Chaparro AA, Beck KB, Brandl HB, Carter GG, He P, Hillemann F, Klarevas-Irby JA, Ogino M, Papageorgiou D, et al. 2020. The importance of individual-to-society feedbacks in animal ecology and evolution. J Anim Ecol 90:27–44.

Castles M, Heinsohn R, Marshall HH, Lee AEG, Cowlishaw G, Carter AJ. 2014. Social networks created with different techniques are not comparable. Anim Behav 96:59–67.

Christy JH, Backwell PRY, Goshima S. 2001. The design and production of a sexual signal: hoods and hood building by male fiddler crabs *Uca musica*. Behaviour 138:1065–83.

Čokl A, Virant-Doberlet M. 2003. Communication with substrate-borne signals in small plant-dwelling insects. Annu Rev Entomol 48:29–50.

Croft DP, James R, Krause J. 2008. Exploring animal social networks. Princeton (NJ): Princeton University Press.

Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R. 2009. Behavioural trait assortment in a social network: patterns and implications. Behav Ecol Sociobiol 63:1495–503.

Cummings ME, Rosenthal GG, Ryan MJ. 2003. A private ultraviolet channel in visual communication. Proc Biol Sci 270:897–904.

Dapper AL, Baugh AT, Ryan MJ. 2011. The sounds of silence as an alarm cue in túngara frogs, *Physalaemus pustulosus.* Biotropica 43:380–5.

Davis GH, Crofoot MC, Farine DR. 2018. Estimating the robustness and uncertainty of animal social networks using different observational methods. Anim Behav 141:29–44.

Deb R, Balakrishnan R. 2014. The opportunity for sampling: the ecological context of female mate choice. Behav Ecol 25:967–74.

Diamond J. 1986. Animal art: variation in bower decorating style among male bowerbirds *Amblyornis inornatus.* Proc Natl Acad Sci U S A 83:3042–6.

Drewe JA. 2010. Who infects whom? Social networks and tuberculosis transmission in wild meerkats. Proc Biol Sci 277:633–42.

Dunlop RA. 2019. The effects of vessel noise on the communication network of humpback whales. R Soc Open Sci 6:190967.

Dusenbery DB. 1989. Calculated effect of pulsed pheromone release on range of attraction. J Chem Ecol 15:971–7.

Farine DR. 2018. When to choose dynamic vs. static social network analysis. J Anim Ecol 87:128–38.

Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol 84:1144–63.

Fernandez MSA, Vignal C, Soula HA. 2017. Impact of group size and social composition on group vocal activity and acoustic network in a social songbird. Anim Behav 127:163–78.

Finn KR, Silk MJ, Porter MA, Pinter-Wollman N. 2019. The use of multilayer network analysis in animal behaviour. Anim Behav 149:7–22.

Firth J. 2020. Considering complexity: animal social networks and behavioural contagions. Trends Ecol Evol 35:100–4.

Firth JA, Voelkl B, Farine DR, Sheldon BC. 2015. Experimental evidence that social relationships determine individual foraging behavior. Curr Biol 25:3138–43.

Fisher DN, Pinter-Wollman N. 2020. Using multilayer network analysis to explore the temporal dynamics of collective behaviour. Curr Zool 67:71–80.

Gernat T, Rao VD, Middendorf M, Dankowicz H, Goldenfeld N, Robinson GE. 2018. Automated monitoring of behavior reveals bursty interaction patterns and rapid spreading dynamics in honeybee social networks. Proc Natl Acad Sci U S A 115:1433–8.

Gilbert F, Elsner N. 2000. Directional hearing of a grasshopper in the field. J Exp Biol 203:983–93.

Gill LF, D'Amelio PB, Adreani NM, Sagunsky H, Gahr MC, Maat A. 2016. A minimum-impact, flexible tool to study vocal communication of small animals with precise individual-level resolution. Methods Ecol Evol 7:1349–58.

Goodale E, Ruxton GD, Beauchamp G. 2019. Predator eavesdropping in a mixed-species environment: how prey species may use grouping, confusion, and the cocktail party effect to reduce predator detection. Front Ecol Evol 7:141.

Grabarczyk EE, Araya-salas M, Vonhof MJ, Gill SA. 2020. Anthropogenic noise affects female, not male house wren response to change in signaling network. Ethology 126:1069–78.

Greenfield M. 1994. Cooperation and conflict in the evolution of signal interactions. Annu Rev Ecol Syst 25:97–126.

Greenfield M. 2005. Mechanisms and evolution of communal sexual displays in arthropods and anurans. Adv Study Behav 35:1–62.

Greenfield M. 2010. Communication networks. In: Breed MD, Moore J, editors. Encyclopedia of animal behavior. Vol. 1. Oxford: Academic Press. p. 329–36.

Greenfield M, Snedden WA. 2003. Selective attention and the spatio-temporal structure of orthopteran choruses. Behaviour 140:1–26.

Halupka K. 2014. Spreading information in a network of interacting neighbours. PLoS One 9:e102801.

Hare JF, Campbell KL, Senkiw RW. 2014. Catch the wave: prairie dogs assess neighbours' awareness using contagious displays. Proc Biol Sci 281:20132153.

Harper GR, Pfennig DW. 2007. Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? Proc Biol Sci 274:1955–61.

Heller KG, von Helversen D. 1986. Acoustic communication in phaneropterid bushcrickets: species-specific delay of female stridulatory response and matching male sensory time window. Behav Ecol Sociobiol 18:189–98.

Hobson EA, Avery ML, Wright TF. 2013. An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. Anim Behav 85:83–96.

Hopkins CD. 1999. Design features for electric communication. J Exp Biol 202:1217–28.

James R, Croft DP, Krause J. 2009. Potential banana skins in animal social network analysis. Behav Ecol Sociobiol 63:989–97.

Johnstone RA. 1996. Multiple displays in animal communication: "backup signals" and "multiple messages". Philos Trans R Soc B Biol Sci 351:329–38.

Kashima K, Ohtsuki H, Satake A. 2013. Fission-fusion bat behavior as a strategy for balancing the conflicting needs of maximizing information accuracy and minimizing infection risk. J Theor Biol 318:101–9.

Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S, Rutz C. 2013. Reality mining of animal social systems. Trends Ecol Evol 28:541–51.

Kulahci IG, Rubenstein DI, Ghazanfar AA. 2015. Lemurs groom-at-a-distance through vocal networks. Anim Behav 110:179–86.

Laiolo P, Tella JL. 2005. Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's lark. J Appl Ecol 42:1183–93.

Levin II, Zonana DM, Burt JM, Safran RJ. 2015. Performance of Encounternet tags: field tests of miniaturized proximity loggers for use on small birds. PLoS One 10:e0137242.

Lohr B, Wright TF, Dooling RJ. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Anim Behav 65:763–77.

Maldonado-Chaparro AA, Alarcón-Nieto G, Klarevas-Irby JA, Farine DR. 2018. Experimental disturbances reveal group-level costs of social instability. Proc Biol Sci 285:20181577.

Mallet J, Joron M. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. Annu Rev Ecol Syst 30:201–33.

McComb K, Reby D, Baker L, Moss C, Sayialel S. 2003. Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav 65:317–29.

McDonald GC, Pizzari T. 2018. Structure of sexual networks determines the operation of sexual selection. Proc Natl Acad Sci 115:E53–61.

McGregor PK, Dabelsteen T. 1996. Communication networks. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds Ithaca. Ithaca (NY): Cornell University Press. p. 409–25.

Medeiros CI, Both C, Grant T, Hartz SM. 2017. Invasion of the acoustic niche: variable responses by native species to invasive American bullfrog calls. Biol Invasions 19:675–90.

Murphy CG, Floyd SB. 2005. The effect of call amplitude on male spacing in choruses of barking treefrogs, *Hyla gratiosa*. Anim Behav 69:419–26.

Narins PM, Hodl W, Grabul DS. 2003. Bimodal signal requisite for agonistic behavior in a dart-poison frog, *Epipedobates femoralis*. Proc Natl Acad Sci U S A 100:577–80.

Nityananda V, Balakrishnan R. 2008. Leaders and followers in katydid choruses in the field: call intensity, spacing and consistency. Anim Behav 76:723–35.

Palumbi SR. 2001. Humans as the world's greatest evolutionary force. Science 293:1786–90.

Payne R, Webb D. 1971. Orientation by means of long range acoustic signaling in baleen whales. Ann N Y Acad Sci 188:110–41.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, De Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, et al. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav Ecol 25:242–55.

Popat R, Pollitt EJG, Harrison F, Naghra H, Hong KW, Chan KG, Griffin AS, Williams P, Brown SP, West SA, et al. 2015. Conflict of interest and signal interference lead to the breakdown of honest signaling. Evolution 69:2371–83.

Psorakis I, Voelkl B, Garroway CJ, Radersma R, Aplin LM, Crates RA, Culina A, Farine DR, Firth JA, Hinde CA, et al. 2015. Inferring social structure from temporal data. Behav Ecol Sociobiol 69:857–66.

Quick NJ, Janik VM. 2008. Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): influences of group size and behavior. J Comp Psychol 122:305–11.

Reichard DG, Anderson RC. 2015. Why signal softly? The structure, function and evolutionary significance of low-amplitude signals. Anim Behav 105:253–65.

Richards DG, Wiley RH. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest - implications for animal communication. Am Nat 115:381–99.

Romano V, Shen M, Pansanel J, MacIntosh AJJ, Sueur C. 2018. Social transmission in networks: global efficiency peaks with intermediate levels of modularity. Behav Ecol Sociobiol 72:154.

Römer H. 2001. Ecological constraints for sound communication: from grasshoppers to elephants. In: Barth FG, Schmid A, editors. Ecology of sensing. Berlin: Springer. p. 59–77.

Ronald KL, Fernández-Juricic E, Lucas JR. 2012. Taking the sensory approach: how individual differences in sensory perception can influence mate choice. Anim Behav 84:1283–94.

Sah P, Mann J, Bansal S. 2018. Disease implications of animal social network structure: a synthesis across social systems. J Anim Ecol 87:546–58.

Schaedelin FC, Taborsky M. 2009. Extended phenotypes as signals. Biol Rev 84:293–313.

Schwartz JJ, Huth K, Hutchin T. 2004. How long do females really listen? Assessment time for female mate choice in the grey treefrog, *Hyla versicolor*. Anim Behav 68:533–40.

Smith-Aguilar SE, Aureli F, Busia L, Schaffner C, Ramos-Fernández G. 2019. Using multiplex networks to capture the multidimensional nature of social structure. Primates 60:277–95.

Smith JE, Pinter-Wollman N. 2021. Observing the unwatchable: integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data. J Anim Ecol 90:62–75.

Snijders L, Blumstein DT, Stanley CR, Franks DW. 2017. Animal social network theory can help wildlife conservation. Trends Ecol Evol 32:567–77.

Snijders L, Naguib M. 2017. Communication in animal social networks: a missing link? Adv Study Behav 49:297–359.

Soso SB, Koziel JA, Johnson A, Lee YG, Fairbanks WS. 2014. Analytical methods for chemical and sensory characterization of scent-markings in large wild mammals: a review. Sensors 14:4428–65.

Sosna MMG, Twomey CR, Bak-Coleman J, Poel W, Daniels BC, Romanczuk P, Couzin ID. 2019. Individual and collective encoding of risk in animal groups. Proc Natl Acad Sci U S A 116:20556–61.

Staicer CA, Spector DA, Horn AI, Kroodsma DE, Miller EH. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 426–53.

Stevens M. 2013. Sensory ecology, behaviour, and evolution. Oxford: Oxford University Press.

Stoeger AS, Heilmann G, Zeppelzauer M, Ganswindt A, Hensman S, Charlton BD. 2012. Visualizing sound emission of elephant vocalizations: evidence for two rumble production types. PLoS One 7:e48907.

Stowell D, Gill L, Clayton D. 2016. Detailed temporal structure of communication networks in groups of songbirds. bioRxiv 13:20160296.

Suzuki TN. 2012. Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. Anim Behav 84:53–7.

Templeton CN, Carlson NV. 2019. Communication networks. In: Choe JC, editor. Encyclopedia of Animal Behavior. 2nd Ed. Amsterdam: Elsevier. p. 568–80.

Uetz GW, Roberts JA, Clark DL, Gibson JS, Gordon SD. 2013. Multimodal signals increase active space of communication by wolf spiders in a complex litter environment. Behav Ecol Sociobiol 67:1471–82.

Uetz GW, Roberts JA, Taylor PW. 2009. Multimodal communication and mate choice in wolf spiders: female response to multimodal versus unimodal signals. Anim Behav 78:299–305.

Weber N, Carter SP, Dall SRX, Delahay RJ, McDonald JL, Bearhop S, McDonald RA. 2013. Badger social networks correlate with tuberculosis infection. Curr Biol 23:R915–16.

Whitehead H, Dufault S. 1999. Techniques for analyzing vertebrate social structure using identified individuals. Adv Study Behav 28:33–74.

Williams R, Lusseau D. 2006. A killer whale social network is vulnerable to targeted removals. Biol Lett 2:497–500.

Wong BBM, Candolin U, Lindström K. 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. Am Nat 170:184–9.

Yorzinski JL, Patricelli GL, Babcock JS, Pearson JM, Platt ML. 2013. Through their eyes: selective attention in peahens during courtship. J Exp Biol 216:3035–46.

Zhao MJ, Driscoll AR, Sengupta S, Stevens NT, Fricker RD, Woodall WH. 2018. The effect of temporal aggregation level in social network monitoring. PLoS One 13:e0209075.

Zuk M, Rotenberry JT, Tinghitella RM. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. Biol Lett 2:521–4.