Social network analysis

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Abstract

Network science has advanced the study of animal social behavior over the past few decades, generating novel insights about the causes and consequences of social behavior. Social network analysis is used to examine the social position of individual animals as well as the global social structure of animal societies. The study of network dynamics is used to uncover changes to social interactions over time and processes that are facilitated by interactions. Other types of networks, such as physical and trait networks, further advance our understanding of animal behavior. Practical considerations, software, and other resources for conducting network analysis in animal behavior are provided. Continued advances in network science will facilitate the study of novel questions about animal social behavior.

Keywords

Network science; Social behavior; Social network analysis

Key points

- The study of animal social behavior has benefited from utilizing network science.
- Social network analysis is widely used in animal behavior to examine the social position of individuals as well as the global social structure of animal societies.
- Studies of network dynamics address both changes to interactions as well as the processes that are facilitated by interactions.
- Network science can be used to examine other types of networks, other than social networks, to advance the study of animal behavior.
- Practical considerations, software, and other resources for conducting network analysis in animal behavior are provided.

Introduction

The study of biological systems requires analysis tools that capture the relationships among biological entities because most biological functions emerge from interactions among system components. The development of 'Network Science' has enabled such analysis across fields of study, from social sciences to physics (Proulx et al., 2005). In the early 2000s, the field of animal behavior started to embrace the use of networks to study animal social behavior (Croft et al., 2008; Webber and Vander Wal, 2019).

Networks are comprised of nodes and edges. Nodes, also referred to as vertices, are the shapes in a network (Fig. 1) and they can represent biological units such as genes, proteins, neurons, individual animals, and species. Edges, also referred to as links, are the lines connecting the shapes in a network (Fig. 1) and they can represent relationships between units, such as genetic regulation, neuronal activation, social encounters, and trophic interactions. Networks have been used to represent and study a wide array of biological questions at multiple levels of analysis. For example, genes and proteins interact with one another, regulating each other's activity (Alon, 2007). Neurons and brain regions are connected to one another and co-activation networks are used to uncover the physiological mechanisms that underlie behavior (Newman, 1999). In ecological networks, nodes often represent species that are linked through trophic interactions to study predator-prey interactions and mutualistic relationships (Bascompte et al., 2006;

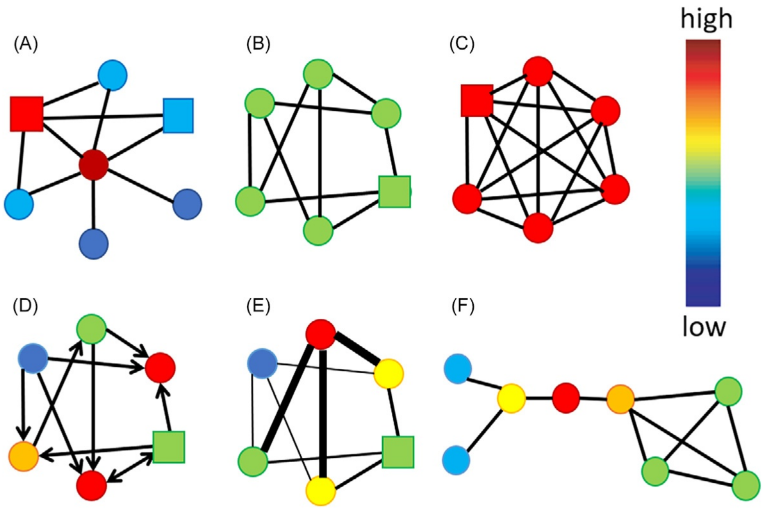

Fig. 1 This figure shows six networks with six nodes in the first five (A–E) and eight nodes in the last one (F). The nodes are shaped as circles and squares to denote different attributes (e.g., males and females). The color of the nodes in each panel reflects a different node attribute – degree in (A–C), in-degree in (D), strength in (E), and betweenness in (F). Network edges are denoted as lines connecting nodes in each network and they differ across panels to emphasize different types of social structures. In (A) the edges are distributed unevenly to make two nodes highly connected and the others weakly connected. In (B) all nodes have three edges connecting them with other nodes. In (C) all nodes have five edges connecting them with other nodes. In (D) there are directed edges that look like arrows pointing from one node to another. In (E) the edges are of different thicknesses to denote different strengths of social connection. In (F) there is one node in the center with just two edges that link it to two groups of nodes that are highly connected within them but not across the two groups. The center node that has only two connections is red to emphasize that it has high betweenness despite its low degree.

Lafferty et al., 2006). In animal behavior, networks are predominantly used to examine social behavior, with nodes representing individual animals and edges representing social interactions (Croft et al., 2008; Wey et al., 2008).

When describing the relationships between individuals in a network, the edges can represent different types of social interactions, including aggressive and affiliative interactions, as well as other relationships, such as genetic relatedness. The type of interaction an edge represents will depend on the biological question being addressed. Edges in the network can be directed, if the direction of the interaction is known (e.g., if one individual aggressed another) (Fig. 1D). Network edges can further contain information about the strength of an interaction, for example, about how many times two individuals encountered each other (e.g., the number of aggressive interactions between two individuals) (Fig. 1E). Often, the strength of an interaction will account for observation intensity (i.e., how many times each individual was observed) to account for biases due to different sampling efforts of different individuals (Ginsberg and Young, 1992). Usually, the graphical representation for interaction direction is an arrow (Fig. 1D) and for interaction strength is the width of the edge (Fig. 1E). The type of biological questions that can be answered, and the network analysis that can be performed, depend on whether or not network edges have direction and weight information (i.e., whether networks are directed and/or weighted) because some network measures (as detailed below) are only appropriate for directed or weighted networks.

Because individuals differ from one another in many ways, it can be important to consider node attributes when constructing animal social networks. Node attributes can include information about the sex, age, behavioral type, physical state, and other features of each individual. Graphically, node attributes can be represented as node size for continuous attributes, such as age; node shape for categorical attributes, such as sex; and node color for both continuous and categorical attributes (Fig. 1). Information about node attributes can then be incorporated into the network analysis to ask if individual variation in a certain trait relates to variation in social position.

Social network analysis is used in animal behavior to address a wide variety of questions relating to the causes and consequences of social behavior. When addressing the causes, or drivers, of sociality, social networks have been used to determine how traits of individuals relate to their social position, how traits of individuals influence the formation of new relationships, and how the environment influences the ways in which animals interact, among other questions. Examinations of the consequences of social behavior using social network analysis include investigations of information and disease flow on social networks, as well as the effect of social connectivity on fitness outcomes (Pinter-Wollman et al., 2014). These biological questions are addressed by quantifying sociality using a variety of network measures, including node-level and global network level measures, and linking them with various individual traits and environmental conditions, and examining how they change over time.

Node-level network measures

Social network analysis is widely used in animal behavior to examine the social position of individuals. The position of an individual in a society can impact its ability to obtain information and its likelihood to contract a disease, which may impact its own fitness, as well as the success of all group members. Thus, understanding which individuals are central and what determines their social position has been investigated in a wide range of animals. To determine the social position of an individual, researchers use network measures that describe the connectivity of each individual in the network.

One of the most widely used measures of individual social centrality is ‘degree’: the number of unique individuals one is connected to in a network (Fig. 1A-C). The more individuals one encounters, the more social information it might receive, but also, the more exposure it might have to pathogens, depending on the type of interactions that are quantified. In larger networks, the degree of each individual can be greater than in smaller networks, therefore when comparing different networks, it is important to normalize this measure. Normalization of degree to account for network size is often accomplished by dividing degree by the number of individuals in the network minus one (to exclude the focal individual). Varieties of degree include ‘in-degree’ and ‘out-degree’, if information about the direction of edges is available (i.e., in directed networks). ‘In-degree’ quantifies the number of interactions received by the focal individual (arrows pointing at it, Fig. 1D) while ‘out-degree’ quantifies the number of interactions that the focal individual initiates (arrows pointing away from it). Distinguishing between in- and out-degree can be important for studies of dominance structures.

Another common individual-level network measure is ‘strength’: the number of interactions an individual experiences, regardless of the identity of who they interacted with (i.e., the sum of the edge weights for each individual (Fig. 1E)). This measure is only meaningful for weighted networks, in which edges have a weight, otherwise, it is identical to degree. The strength of an individual may impact how many resources it receives, for example, if interactions are used for resource exchange. As with degree, one might expect larger strength values in larger networks. Therefore, a normalization of strength is important when networks of different sizes are being compared. One normalization approach is to divide strength by the number of all interactions observed in the network (rather than the number of individuals). An individual might have high strength but low degree if all its interactions are focused on one or a few individuals. Likewise, an individual might have high degree but low strength if it interacts with many individuals but each interaction is very weak. Measures such as ′evenness′ can be used to examine the spread of interaction strength across partners, but such measures are surprisingly underutilized in the study of animal social networks.

‘Betweenness’ centrality is a node-level measure that takes into account the global structure of the network, beyond the immediate connections of each individual. ‘Betweenness’ quantifies the number of shortest paths that pass through a node, with a shortest path being the sequences of fewest edges that connect any pair of nodes in the network (Fig. 1F). Taking into account all pairs of nodes into this measure, and not only the nodes that are immediately connected to the focal individual, provides information about the scale of influence an individual has on the entire network. Individuals with high betweenness are sometimes referred to as ‘brokers’ because their social position can link otherwise unconnected individuals. Note that an individual can have a high betweenness but low degree, for example when a network is comprised of two, or more, groups (clusters) in which individuals are highly connected with one another, but the connection between clusters is very low and occurs only through a single, or few, individuals. Those connecting individuals might interact with only one or two individuals in each cluster (having low degree) but because they sit on all the shortest paths that connect individuals in one cluster with individuals in another cluster, they will have high betweenness (Fig. 1F).

Degree, strength, and betweenness are just a few examples of node-level centrality measures. There are many other node-level centrality measures, such as closeness, farness, eigenvector centrality, including new ones that are developed regularly. Which centrality measure to use depends on the biological question addressed and the social position of interest. Once the social position of an individual is quantified, one can go on to ask what node attributes relate to the social position of individuals, what happens to the society when particular individuals with high or low centrality are removed, do individual differ in their impact on disease/ information flow, etc.

Global network measures

Studies of animal behavior that examine the social structure of animal societies have been greatly aided by global network measures. For example, when groups are compared to one another, global network measures, such as density, modularity, and degree distribution can be informative. Some global network measures, such as density (the number of observed edges divided by all possible edges), account for network size. Such measures are more appropriate for studies that compare different networks than measures that are impacted by network size and need to either be normalized to network size or used to compare groups of similar sizes. Using global network measures can help identify community structures, facilitate comparisons across systems, and aid in determining drivers of interactions.

Nodes in a network can form clusters, for example because certain individuals are more attracted to one another than others, or because there are physical barriers that prevent some individuals from interacting frequently with others (Wolf et al., 2007). Many different clustering algorithms have been developed for identifying network clusters, and each one optimizes different aspects of connectivity. After clusters are defined, one can quantify the ‘modularity’ of a network: the ratio between interactions within a cluster and interactions among clusters. In highly modular networks (Fig. 1F), nodes within a cluster are better connected with one another than they are with nodes in different clusters. Such segregation between clusters can facilitate system robustness to the spread of disease from one cluster to another, but it also creates isolated social communities that might not exchange information with other communities.

'Assortativity' is a global network measure used to describe potential drivers of interactions. It quantifies the tendency of similar (or different) individuals to interact with one another. For example, individuals that are healthy might interact more with one another than with diseased individuals, resulting in a network that is assorted by infectious state. Conversely, opposites might attract and individuals with opposite traits might be more likely to interact with one another. For example, if mating events are coded as edges in a network, those networks will be highly disassortative by sex because most connections would be between males and females.

Linking network structure to its global function can be accomplished by quantifying the types of relationships that structure the network. Each dyad (pair of nodes) in a network is either connected or not, and the frequency of such interactions is quantified as network density (Fig. 1B,C). Interaction patterns that relate three or more individuals with one another are referred to as 'motifs'. Because of computational limitations, most studies of network motifs focus on triads (three nodes). 'Global clustering coefficient' quantifies the proportion of closed triangles (i.e., three individuals that are all connected with one another) in a network, and can be applied to networks with or without directed interactions. Such a measure can be used to compare the social cohesion of different networks, similar to network density. When networks are directed, with edges that describe interactions with an initiator and a receiver, such as in communication networks and networks that describe agonistic encounters, there are 16 possible 3-node motifs – because individuals can be connected in one direction, both directions, or not at all (Fig. 2). The frequency of different motifs in a network can shed light on how social relationships are regulated. For example, a cyclic motif, in which individual A directs an interaction to individual B, who directs an interaction to individual C, who then directs and interaction back to individual A (like in a rock-paper-scissors game, Fig. 2), can lead to unstable social structures. However, transitive triads, in which individual A directs an interaction to both B and C, and B directs an interaction to C (Fig. 2), can facilitate stable dominance structures. Comparative work of such network motifs in networks of aggressive interactions across animal taxa has shown that transitive triads, and triads that can lead to transitive relationships, are much more prevalent in animal societies than cyclic motifs, or motifs that can result in a cyclic relationship (Shizuka and McDonald, 2015).

What drives social interactions?

A common question in animal behavior is what determines whether or not two individuals will interact or if individuals interact with one another more (or less) than expected by chance (or 'randomly')? Many approaches are used to tackle these questions with varying degrees of complexity (Hobson et al., 2021). Because network data has inherent correlations (interactions of one node are not independent from the interactions of another), traditional statistics are seldom used, and scientists construct biologically informed 'chance' or 'reference' networks to compare with their observed networks. A reference network is a hypothesis that can be compared with the observed social structure, and if the hypothetical and observed networks are different, with substantial certainty, the hypothesis can be rejected. Not all animals are equally likely to interact with one another, therefore the construction of reference

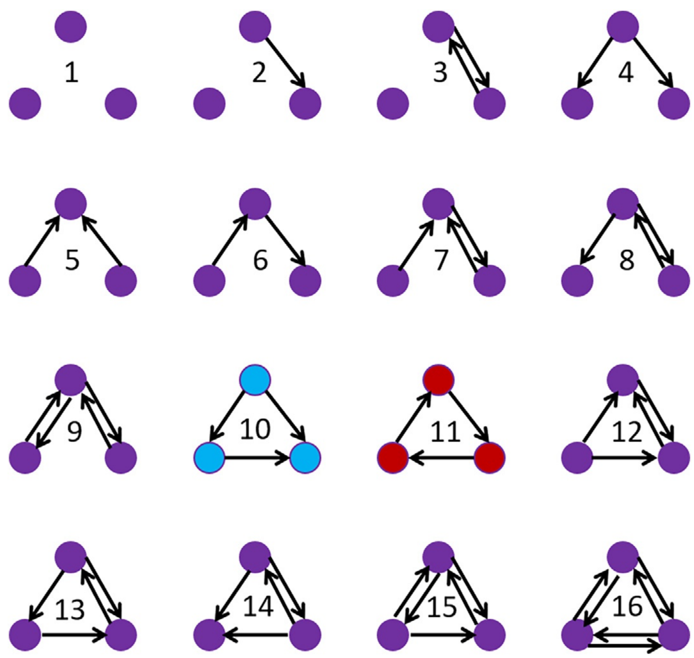

Fig. 2 This figure shows sixteen networks with three nodes in each network. All the nodes are purple circles but the nodes in the 10th and 11th networks are blue and red, respectively, to emphasize the transitive and cyclic structures discussed in the text. The nodes in the networks are connected with arrows to indicate that the interactions are directional. Each network has a different number of interactions, from no interactions in the first network to six arrows in the last one.

models should consider various constraints. For example, spatial barriers that prevent individuals from encountering one another, or different movement habits, can dictate which interactions are possible and which should (or should not) be included in a reference model. Incorporating restrictions on which interactions can occur in the reference network (e.g., Gahm et al., 2024), or using generative models that simulate specific drivers of interactions (e.g., Ilany and Akcay, 2016; Silk and Fisher, 2017), ensures that reference models are biologically appropriate and provide biologically meaningful conclusions.

Change over time – network dynamics

Social interactions, like all biological systems, change over time. The study of network dynamics addresses both changes to the interactions themselves (dynamics **of** networks), as well as the dynamic processes that are facilitated by interactions (dynamics **on** networks), such as the transmission of disease or information (Pinter-Wollman et al., 2014; Sih and Wey, 2014).

Examining what drives the formation of interactions, a question discussed in the previous section, can be used to address how and why networks change over time (i.e., the dynamics of networks). Changes to network structure can have important implications for the function of the society, for example, if central individuals are removed from society (e.g., because they die) the social structure can break down (Williams and Lusseau, 2006). The interactions that form a network occur at different time scales. Biologically important interactions can occur over a timescale of seconds or minutes (Pinter-Wollman et al., 2013), seasons (Holekamp et al., 2012), or years (McDonald, 2007), depending on the animal that is being studied and the biological question that is being investigated. The time scale over which interactions are recorded determines the types of changes that can be examined.

The processes that are facilitated by interactions (i.e., dynamics on networks) are a central focus in the study of social networks because they convey the functional importance of social interactions. Social interactions can facilitate the spread of pathogens, which have negative implications; however, social information, which usually provides benefits, also spreads on interaction networks. Interactions will differ in their impact on these processes based on what is being transmitted and the modes of transmission. For example, sexually transmitted diseases spread only through sexual interactions, while more fleeting interactions can facilitate the spread through fomites of viruses that cause respiratory diseases. Thus, it is important to match the type of interactions that are being studied, and the time scale over which they occur, to the functional processes that are facilitated by those interactions. For example, information about food can be transmitted through interactions that occur on a time scale of seconds (Pinter-Wollman et al., 2013) while the transmission of ectoparasites can be facilitated by indirect interactions of shared space use over nights (Leu et al., 2010). One methodological approach to uncover the importance of social interactions in diffusion processes (e.g., of information or disease) is to compare acquisition rates through social interactions or via asocial means, using Network-Based Diffusion Analysis (NBDA) (Franz and Nunn, 2009; Hasenjager et al., 2021).

Other types of networks and interactions

Multilayer networks

Because the interactions that link individuals can take many forms, there has been recent interest in combining multiple types of interactions (or behaviors) into a single framework. Multilayer networks can depict different types of interactions that occur at various times, and social interactions can be linked with other types of networks, such as spatial networks (Barrett et al., 2012; Finn et al., 2019; Silk et al., 2018). For example, if animals groom one another as one type of interaction and are aggressive to one another in a different social situation, these can each be described as a network, and the two networks can be connected through the same individuals participating in both types of interactions. Furthermore, temporal changes in these interactions can be tracked and added to the multilayer network as a temporal aspect (Finn et al., 2019). Combining different types of interactions that occur over time in a single framework opens up opportunities for examining what types of interactions are important for long term relationships and for uncovering whether individuals that are central in one situation are also important in other situations (Sharma et al., 2022). Measures to quantify node position, detect communities, or quantify network structure in multilayer networks are still being developed. However, even though studies of animal behavior are only starting to utilize multilayer network measures, they have already provided novel insights in some systems and they are a promising tool for uncovering complex relationships.

Higher order interactions

Networks describe dyadic interactions; however, many interactions are performed by more than just two individuals. Some examples include alarm calls that are an interaction between one individual and many listeners; a pheromone trail that is laid by a single ant and communicates information to many other individuals; and food sharing and grooming interactions that often have multiple simultaneous participants. Interactions in which more than two individuals participate simultaneously are referred to as 'higher order interactions.' When information, food, or disease are transmitted via higher order interactions, efficiency can increase. For example, relaying information about a predator by emitting an alarm call that reaches many individuals simultaneously is more efficient than a quiet whisper to each individual separately. However, this increased efficiency can also come with a cost to participating individuals. For example, when food is shared in a higher order interaction, each individual receives less food than if it participated in a one-on-one interaction, because they have to share the food with more mouths. Traditional network analysis does not have the tools to distinguish between higher order interactions and many dyadic interactions that did not occur simultaneously. Simplicial sets (Greening et al., 2015; Silk et al., 2022) and hypergraphs (Silk, 2023) can distinguish between higher order interactions and groups of dyadic interactions. The integration of these tools into studies of animal behavior is only starting and it promises to uncover consequences of interactions that have alluded researchers of animal behavior thus far.

Non-social interactions

While the focus here has been on networks in which nodes are individuals connected by social interactions, networks that describe other types of connections have also been important for the study of animal behavior. Physical connections between locations can be described as networks, which can shape social networks because animal interactions emerge from the ways in which they move in their environment (Webber et al., 2023). The spatial connectivity of important environmental features, such as food patches or water sources, can affect the movements of animals, impacting who they encounter. For example, harvester ants live in subterranean nests comprised of chambers connected by tunnels, which can be quantified as spatial networks. Features of the nest network, such as average chamber degree and network meshedness, shape the collective foraging of the ant colony (Pinter-Wollman, 2015) because colony foraging is regulated through interactions among the ants that live in the nest (Gordon, 2010; Pinter-Wollman et al., 2013) and these interactions are shaped by the structure of the nest (Pinter-Wollman et al., 2011).

Animal communication relies on elaborate signals that involve multiple components (e.g., vocal and visual traits). One creative use of network science in animal behavior quantified traits that are used in communication as phenotypic networks, in which nodes were traits (such as morphological measurement, plumage color, and song components), and edges connected traits according to their co-occurrence (Wilkins et al., 2015). These phenotypic networks were then used to determine the function of various traits, showing that some phenotypic components affect reproductive success while others shape the spatial structure of the population.

Practical considerations

The use of network science in the study of animal social behavior has been aided by the rapid development of animal tracking tools and the increased use of the R software in the study of animal behavior (Webber and Vander Wal, 2019). Many review articles (as well as many empirical studies) provide detailed supplementary information with analysis code that can be adjusted to other study systems (e.g., Farine and Whitehead, 2015; Franz and Nunn, 2009; Hobson et al., 2021; Silk and Fisher, 2017). Furthermore, helpful tutorials on how to analyze animal social networks are available online (e.g., https://dshizuka.github.io/networkanalysis/index.html).

Some practical considerations for researchers of animal social networks include the ways in which interaction data are obtained and recorded. Information about which animals interact can come from direct observations of animals, as well as from animal-borne tags that can provide remote-sensed information about the co-localization of tagged individuals (Smith and Pinter-Wollman, 2021). The format in which data are recorded will often be determined by the collection method. Generally, network data has two important components: information about nodes (e.g., a node attribute table) and information about edges. Node attribute tables contain information about all the nodes in the network and include various node attributes, such as unique identifiers, sex, age, etc. There are different ways to code network edges, with 'edge-lists' being less error-prone than 'adjacency matrices' for manually recorded interactions. In edge-lists, each row describes a social encounter and the first and second columns list the identities of the interacting individuals. If a network is directed then the first column can list the initiator and the second column can be the receiver of an interaction. Further information about each interaction can be provided in additional columns, such as the duration of the interaction (which can be used as an edge weight), its time, location, type of behavior etc. In an adjacency matrix, all individuals are listed in both the rows and the columns of the matrix, and information about the strength of interactions populates the matrix. Directionality can be inferred if the top and bottom triangles of the matrix are different (e.g., if rows list initiators and columns list receivers of an interaction). However, further information about the timing of each encounter and the type of encounters are only entered at the entire network-level rather than for each interaction, reducing flexibility in examining interaction dynamics. Furthermore, when many individuals are being tracked, it can be challenging, and error-prone, to enter data into large matrices.

The lack of independence within network data was mentioned above and should be considered carefully when performing statistical analysis on network data. Because reference networks are often utilized to compare with observed networks, and because of the many biological and conceptual considerations that need to be accounted for when constructing reference networks, it is important to think carefully about the questions that are being studied when comparing observed network to simulated ones (Hobson et al., 2021).

Conclusion

Network science has substantially advanced the study of animal social behavior over the past few decades. Novel insights about both the causes and consequences of social behavior have emerged from the use of social network analysis to study animal societies. As network measures continue to be developed and the acquisition of interaction data becomes easier (e.g., through automated animal tracking devices), new research avenues may open up. For example, comparative work that aims to find general principles in animal social behavior can be facilitated by the ubiquity of network data across taxa (Sah et al., 2019; Shizuka and McDonald, 2015). Investigations into synergies among multiple types of interactions (Finn et al., 2019) and incorporating ecological and spatial considerations into the study of animal social behavior (Silk et al., 2018) can be aided by emerging multilayer network tools. The study of temporal dynamics in animal behavior is constantly growing and is becoming more accessible with a variety of tools that are being developed (Blonder and Dornhaus, 2011; Tantipathananandh et al., 2007). Finally, new research directions that examine the formation and importance of higher order interactions may uncover processes that have been hidden thus far.

As researchers continue to use network science and develop new tools and measures to examine complex systems in biology and other fields, the types of questions that can be answered in animal behavior using networks will continue to grow. Animal behavior researchers not only benefit from the development of methods in other fields, they also have the potential to inform other disciplines. Animal societies are often tractable research systems that can provide inspiring solutions to questions in other domains. For example, the study of animal social behavior can inspire engineering efficient robot swarms and transportation networks. Studies of animal social interactions can provide a better understanding of processes that underlie the emergence of pandemics or disruptions to supply chains. Thus, continued interdisciplinary conversations that enable the exchange of research ideas and analysis tools can broadly advance science and society.

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