

Extending the role of social networks to study social organization and interaction structure of animal groups

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Social network analysis is an increasingly popular method for analyzing relational data in animal social systems. The abstract nature of network metrics primes them for use in cross-comparisons of social systems, but more work is needed to determine how well such measures can approximate meaningful biological properties. Finding biological correlates of network metrics, and extending the existing network methods to include the analysis of ongoing dynamics of social processes, will bring us closer to standardization of the terminology used to describe animal social and interaction networks. This will allow us to use the social networks in simultaneously studying the individuals embedded in a social setting, the consequences of their interactions, and the global properties of the social system. We discuss how certain facets of the existing network methods need be further developed to fulfill this potential and provide a multi-scale systems approach to the studies of animal sociality.

Introduction

Social network analysis (SNA) is a powerful tool that allows for visualization and quantitative analysis of relational data in a wide variety of social systems and contexts. SNA has already been successfully applied to analyze interaction patterns in other disciplines, such as in sociology (Freeman 1979), and is gaining increased prominence in biology, primarily as a method to describe relational data in animal social groups (Croft *et al.* 2008, Wey *et al.* 2008, Sih *et al.* 2009). The different approaches used in SNA to analyze interaction structure rely on representing groups of individuals as nodes in a network with

different types of relationships as connections between those nodes (cf. Carrington *et al.* 2005). This basic architecture can be applied to a wide variety of situations, depending on the attributes of the individuals/nodes and the characteristics of the interactions/connections one wishes to investigate. The interaction pattern can then be quantified both at the level of an individual, defining its social position or network centrality within a group, or at the level of an entire network, looking at how the social structure affects individuals within the network (Hock *et al.* 2010). For biological systems, the process usually involves collecting data on animal social interactions of interest, translating these data

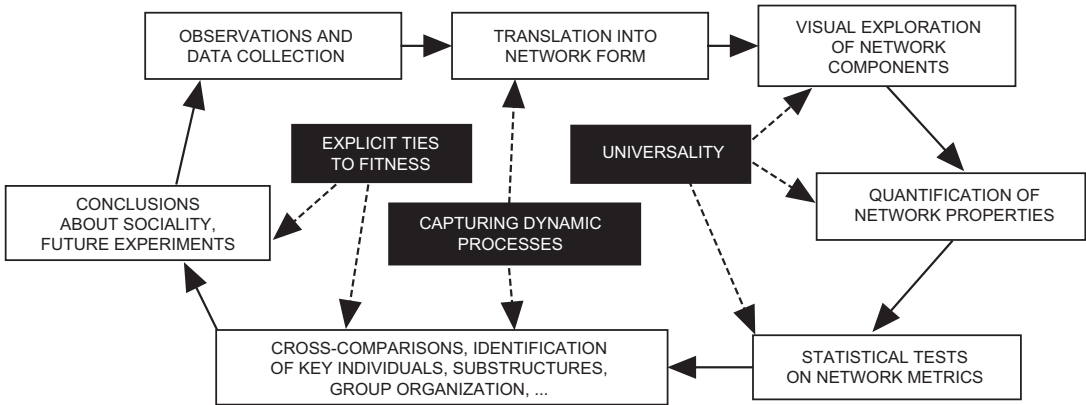


Fig. 1. A flowchart representing the commonly used sequence of steps involved in a social network analysis (based on methods proposed by Croft *et al.* 2008). Open frames represent common methodological steps and the solid arrows the sequence of those steps; closed frames represent the suggested areas of improvement while dashed arrows represent the expected impact of those improvements on specific methodological steps.

into a network form, defining the individual- or group-level metrics based on connectedness of the individuals, and performing a data analysis on those metrics, either in forms of statistical measures or direct comparisons among the networks (Croft *et al.* 2008; Fig. 1). Usually the easiest method to define social position of an individual, or the overall network connectedness, is to count the number of the direct social connections for each individual. However, it is also possible to characterize an individual's position within a group beyond its immediate social relations and define, for example, how important an individual is as a mediator that connects other elements of a group, which can then be expressed both for each individual and the level of network organization (Fig. 2).

While SNA proves to be a useful tool to visualize and represent relational data, the question is how the use of this attractive method can be extended beyond its current, largely descriptive, use in biology. While networks have been successfully applied in specific cases to complement the more traditional methods in social ecology, we anticipate that the three major obstacles need to be overcome before the role of SNA in evolutionary and behavioral biology can be expanded and its potential fulfilled: (1) the current methods of measurement lack sufficient universality: it will be necessary to create a standardized set of network metrics that could apply across con-

texts; (2) the current methods lack the capacity to describe or quantify dynamic network processes: it will be necessary to create measures that do not just record or summarize single, static states of a system but instead capture changing network structures; and (3) current methods fail to provide firm links between abstract network metrics and biological fitness of animals: it will be necessary to create methods that provide this explicit link before SNA can be used most effectively to quantitatively characterize effective benefits and costs of a social position. Efforts to extend the current methods to address these interdependent needs will greatly expand the types of accessible research questions in the area of animal sociality.

Universality

We anticipate that the standardization of the terminology pertaining to animal sociality will be a part of a larger effort to characterize the social position in a group in a context of utility of sociality. Much of the debate on the levels of biological organization, not just in social evolution but also in the evolution of multicellularity and other forms of biocomplexity, have concentrated on the costs and benefits of integration for the individual components of the system (Michod 1999, Camazine *et al.* 1999). However,

a precise quantification, or indeed nomenclature, to relay these results is often lacking. One of the illustrative examples of this kind is the ongoing debate on the definition of dominance within hierarchies (e.g. De Vries 1999). Numerous methods and measures have been proposed to determine the order of dominance in hierarchically structured groups, yet the debate on whether any metric is better than all others is still far from settled. The absence of a universal measure of social importance within what is defined as an ordered system hampers not only our efforts to understand the costs and benefits of social life, but also our ability to more easily understand and cross-compare the different studies of hierarchical dominance.

The diversity of the different metrics used to analyze social structure of a group is even more staggering (Croft *et al.* 2008). To name only a few examples of the metrics that have been used in a biological context, individuals' position in a group have been characterized according to (1) the number of connections with direct partners (Madden *et al.* 2009), (2) ability to "reach" other individuals in a group — as exemplified by the number of steps in which an individual could affect the indirect social partners (Flack *et al.* 2006), (3) the essentiality of individuals to act as intermediaries between other individuals (Lusseau 2007), (4) the tendency of individuals to form 'cliques' — distinct sets of frequently interacting individuals (Flack *et al.* 2006; Madden *et al.* 2009), and (5), tendency that the individuals with similar numbers of partners preferentially interact with each other (Flack *et al.* 2006; Wolf *et al.* 2007). With such a variety of attributes available to define both the individuals and their interactions, it is easy to see the potential and the allure of SNA for quantitative analysis of social systems. However, such an abundance of ways to define relative importance also begs the question whether SNA can be sufficiently universal as a tool by which to compare relevant insights across networks, or the positions of the individuals within each network. To conduct effective cross-comparisons, thereby broadening the types of accessible questions in the field, we need ways to compare results across systems. One such approach would be to compare interaction networks collected from different taxa,

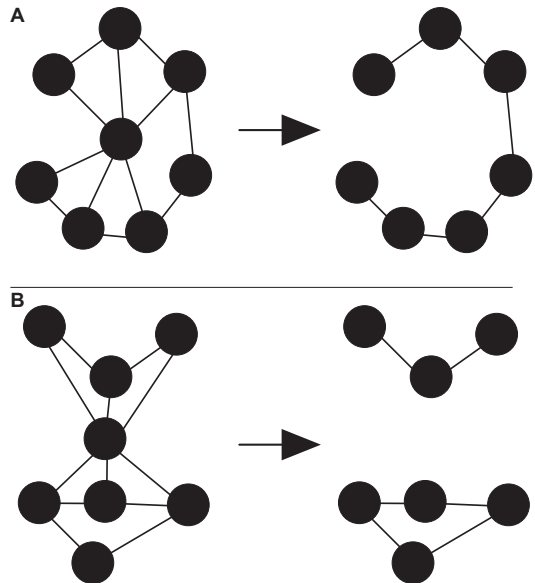


Fig. 2. An example illustrating the different ways which social position can be defined and quantified in a social network. Individuals in a network are represented as nodes, while their social interactions or affiliations are represented as connections between the nodes. While individuals in the middle of a group in both networks on the left side have six direct connections to social partners, removing those individuals from their respective networks yields different results: in case A, a single network component remains with all remaining nodes still connected to each other, albeit not as well as before; in case B, two disconnected components of a network remain with no direct links between them. The importance of the two remaining nodes was different in terms of the overall network structure and their impact on the rest of the group. Note also that the networks represent a pattern of social interactions, and not the spatial distribution of individuals.

but within the same social context, and to see if similarities in the network structure exist across social systems. The other would be to look whether the same network metric describes the social position of an individual in different systems, for example whether the number of social interactions always puts individual at greater risk of catching or transmitting an infection (e.g. Meyers *et al.* 2005, Godfrey *et al.* 2009). Social network analysis could then be employed to identify such individuals in animal groups and use them to assess the disease pressure in a population. The universal, system-independent measures used in SNA hold great potential for

studying the analogies and homologies of social systems, but require rigorous standardization with regard to their biological uses (*see* also ‘Explicit ties to fitness’ below) before they can be truly effective as tools for cross-comparisons across social systems.

Capturing dynamic processes

To understand how an individual attained a particular position within its group or how a specific pattern of group organization came to be, we need to understand the processes behind social organization: how individual behaviors give rise to social organization of a group, and particular social profiles of individuals that comprise it. However, the current biological applications of SNA often stop at using it only as a summary representation of interaction pattern: a freeze-frame snapshot of what is, in reality, an ongoing dynamic process of social organization. As such, static network representations often do not include the potentially interesting shifts and dynamics inherent in many social systems, and can only infer dynamics by inter- or extrapolation. Therefore, to explore the processes that give rise to social organization, a static network representation of the interactions is unlikely to be the most telling solution. While some representations include data on the frequencies or strength of interactions by weighting them (Croft *et al.* 2008), a more effective solution could be to employ models that can capture temporally explicit network dynamics to study such processes explicitly (Hock *et al.* 2010). Such models employ behavioral rules at the level of an individual, and are suitable to simulate dynamic exchanges and shifting allegiances often seen in animal social groups. A framework like this provides a controlled environment for studying social behavior in which each social decision can be manipulated and its effects on the system measured. A simple example is a model that consists of individuals that pick and choose their social partners based on the perceived social quality of each partner (Fefferman & Ng 2007, Hock *et al.* 2010). Each individual can then be given its own set of preferences for choosing partners, and as the time passes choose new partners while

dropping the existing ones. The paradigm of this kind provides a dynamic framework to study how individual’s immediate network of social partners, as well as the global network structure, shifts with time and in response to individual social decisions and changing social positions. Moreover, the models in which individuals obey the proposed or empirically observed rules of association could potentially allow us to assess how well we understand the processes of social organization in the system under study. As with other studies of biological complexity, the models can also generate predictions on how global social organization could arise from seemingly simple individual decisions at an individual level (Fefferman & Ng 2007). Such models provide not only insights into the ontogeny of the social structure in the observed group(s), but also a glimpse into the evolutionary history of a social system.

Explicit ties to fitness

While uniquely suited to identify and quantitatively characterize interaction patterns in animal groups, much foundational work is still needed before SNA can be used effectively to answer the ‘why’ questions in sociobiology. To study the function of social interaction patterns, a strong link between metrics used in social networks and biological fitness needs to be established. More specifically, we need more research to determine whether we can use SNA as an inductive reasoning tool instead of, or in addition to, the methods currently used to study fitness consequences of social life. This poses a substantial challenge as various measures of an individual’s position in a group can have different meanings in different systems (McDonald 2007; also *see* ‘Universality’ above). It is, therefore, hard to pinpoint whether some, or indeed any, of the metrics used to analyze network structure can be given a universally applicable meaning in terms of benefits arising from sociality. For example, an individual with the greatest number of social connections to other group members may be the one receiving the greatest number of beneficial interactions, as is the case with allogrooming or placatory behaviors (Madden *et al.* 2009), but also the

one facing the greatest risk of catching an infectious disease (Godfrey *et al.* 2009), leading to conflicting fitness consequences. The question is then whether we can use the metric that defines this individual as central in its group as a proxy for its fitness. The answer, of course, is that it depends on the nature of the interactions, the tradeoffs that they contain, and the social context in which we observe this interaction pattern. In other words, additional biological analysis is still necessary before we can ascribe a fitness value to some measure of network centrality, and the end result will likely be a system-specific relationship between the network measure and its biological correlate. The logical next step would therefore be to compare network metrics with individual's fitness in a concrete biological system to determine to what extent the two coincide. In particular, SNA has the potential to provide insights into the aspects of social organization that are less dependent on direct interactions (e.g. Lusseau 2007; K. Hock & N. H. Fefferman unpubl. data). For example, direct interactions alone tell us little about how important an individual is as a component of a network that ties different subgroups into a complete system (Lusseau 2007; *see also* Fig. 2). Yet such information may be crucial in terms of fitness of the individual, who may be of an essential importance for the fitness of other members of the group in both negative and positive terms. For example, a particularly disruptive behavior of an individual may have long-term fitness consequences for the reproductive success of others in its group (Sih & Watters 2005), whereas a particularly well connected individual may be an effective leader of a herd or a family group in challenging times (Wittemyer *et al.* 2005). Therefore, once biological correlates specific to the system are defined, SNA may provide a tool to elegantly compare the utility of sociality for the different participants, at least within the social system under study. If such correlations can be reliably ascertained, SNA metrics stand to provide an elegant means to assess the costs and benefits of the individuals within a social environment. We therefore believe an area ripe for future research will be the investigation of the biological and methodological reasons why some metrics can be used across systems while others cannot.

Such studies will also lead to better understanding of the interplay between group structure and the position of individuals in the group. In social systems where the group structure and interaction patterns are not predetermined, the social organization arises from the interaction decisions made at the level of an individual. Thus, the rules that underlie such decision-making processes will also shape the overall social architecture, and consequently determine its functionality and effectiveness. As actions of the individuals change their social environment, we can establish a link between such actions and their impact on a focal individual, its partners, and the functioning of the group as a system (Williams & Lusseau 2006, Hock *et al.* 2010). The beauty of SNA lies in its ability to quantitatively characterize not only the interaction pattern of a focal individual, but also the effects each individual has on connection patterns of the others, and ultimately on the structure of the entire interacting group (*see also* Fig. 2). If particular structure of a social environment provides benefits to the individuals, such as by channeling information flow (Lusseau 2007), it will be particularly intriguing to investigate the links between individual actions and system-wide consequences of such actions. While the emergent social structure may not be characteristic of all animal social systems, the ability of SNA to independently quantify individual position and system-level properties shows great promise for future investigations into the utility of animal sociality, as well as other levels of biological organization.

Conclusions

Linking the social decisions of individuals, system-level group structure, and selection pressures that shape both of these properties promises to usher a new era of studies of animal sociality, one in which we will be able to answer how structure of animal groups is shaped by individual-level selection. Further advancements in biological applications of SNA hold great promise in discerning such social components of fitness. However, to effectively fulfill this potential, the use of SNA in evolutionary and behavioral ecol-

ogy needs to be expanded in several ways. Most notably, we need strong links between the quantitative descriptors used in SNA and their biological correlates before we can use such metrics to compare social importance across systems and advance our ability to characterize and analyze the ongoing social processes. Expanding SNA methods will allow us to analyze the emergence of social structure with time, link this emergence with decisions of individuals, and study the homologies or analogies of social structure in different social systems. Consequently, this will greatly increase our ability to characterize animal social systems at the individual and system-wide level, as well as our capacity to study the selection pressures in, and the evolution of, complex biological systems.

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