

Chapter 18

Social Network Analysis: Applications to Primate and Cetacean Societies

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Abstract To better address questions concerning animal sociality, animal behaviorists and behavioral ecologists are increasingly turning to the suite of analytical techniques known as social network analysis (SNA). SNA allows for the quantification of multi-actor interactions, thereby providing a more realistic representation of social patterns and relationships. Here, we provide a brief introduction to SNA, consider some of the challenges in studying sociality, and discuss the application of SNA to studies of animal societies, with a focus on primates and cetaceans. Additionally, we present techniques for network comparison and dynamic network analysis developed in the social sciences with exciting potential applications to the study of animal behavior.

Keywords Animal societies • Dolphins • Metrics • Primates • Quantitative methods • Social network analysis

18.1 Introduction

A powerful quantitative tool with which to address the causes and consequences of sociality is social network analysis (SNA). Indeed, social network theory has potential in any discipline that requires the description of complex systems, including physics, psychology, sociology, ethology, neuroscience, cell and molecular biology, ecology, mathematics, military intelligence, and computer science (Wasserman and Faust 1994; Freeman 2004). A social network is defined as actors (or nodes, points, vertices) linked by relationships (edges, links, ties), and the visual representation of these nodes and edges is referred to as a graph (Fig. 18.1). This type of analysis was popularized in the 1970s after Stanley Milgram (1967) examined the social distance between individuals in the United States (U.S.), the results of which are commonly referred to as “Six Degrees of Separation.” Later, Watts and Strogatz (1998) formalized Milgram’s idea in their description of small-world phenomena, where tightly knit subgroups of individuals are closely connected to each other, but with at least one member maintaining a connection to a separate subgroup.

With recent advances in computing power, SNA has gained momentum in the field of animal behavior (Krause et al. 2007; Wey et al. 2008). Traditional studies of social relationships and structure focus on dyadic interactions, whereas network analysis applies graph theory to quantify multi-actor interactions, thereby providing more realistic representations of the complex societies typically observed in primates and cetaceans. Additionally, by providing more direct measurements of social relationships, rather than proxies such as group size, SNA allows for more in-depth investigations into complex sociality. By quantifying multi-actor interactions, SNA accounts for some of the unavoidable data dependency, which is problematic for traditional statistical analyses. Take, for example, an investigation into the relationship between dominance rank and relationship quality in a savanna baboon troop. With traditional methods, female rank and relationship quality are treated as independent, when in fact they are not. A female who grooms one female cannot simultaneously be grooming another. Rank is determined by who is above and below, so is by definition not

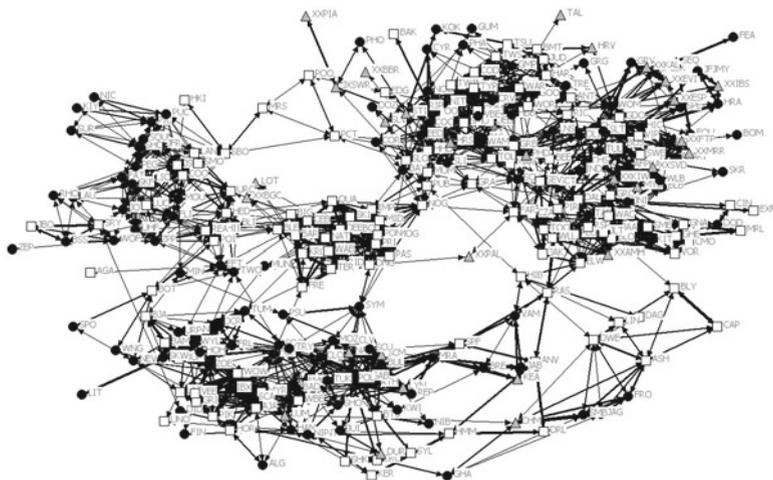


Fig. 18.1 Social network of Shark Bay adult and juvenile dolphins constructed from survey data from 1999 to 2007. Edges are weighted by half-weight coefficient and only those greater than the average (0.13) are included. *Circles*, females; *squares*, males; *triangles*, unknown

independent. SNA treats the relational nature of data as part of the analysis. A network's edges can be directed or undirected, weighted or unweighted. Undirected edges indicate that the relationship is symmetrical, as in the case of a mutual friendship. However, if one individual identifies another as a friend and the sentiment is not reciprocated, the relationship is directed. Additionally, an unweighted edge indicates the presence of a relationship, while a weighted edge can indicate the presence and the strength of a relationship. Edges can also be either positive or negative, as might be quantified when individuals preferentially approach or avoid each other (Wasserman and Faust 1994; Croft et al. 2008; Wey et al. 2008). Network theory is also useful and unique in that it is capable of analysis on multiple levels by characterizing individuals, their subgroups of neighbors, and the network as a whole. Some basic social network metrics including measures of centrality (a node's connection to the rest of the network) and clustering (the tightness of subgroups or cliques) are described in Box 1, but it is most important to note at this juncture that distinct social network metrics provide different information about the same individual, subgroup, or network and that this information is not necessarily accessible using more conventional methods.

18.2 Considerations and Caveats

Despite the usefulness of SNA and the increasing frequency with which these techniques are applied, a number of considerations and caveats are warranted before the initiation of a network study (see James et al. 2009; Croft et al. 2011 for review of

SNA potential pitfalls). One important consideration is how to define a relationship. According to Hinde's (1976) classic framework for the study of social structure, a relationship is defined as successive interactions between individuals. In the study of animal behavior, however, interactions are often difficult to observe and quantify; therefore, relationships are often assessed in terms of association defined by shared group membership with the assumption that associating individuals have the potential to interact. Whitehead and Dufault (1999) refer to this assumption as the "gambit of the group," and for the purposes of SNA, researchers should be aware that networks built from group-defined association data may appear highly clustered by this sampling method. These associations are also typically measured in terms of an association index, such as the half-weight index, that accounts for sampling effort (Cairns and Schwager 1987). Additionally, there is no universally accepted method for determining whether a biologically meaningful relationship exists and should be included in a social network for analysis or whether the observed association is random, erroneous, or biased by sampling method or effort. A common response to this uncertainty to date has been to filter and dichotomize data, thereby only including edges or nodes above a certain value when constructing the network. However, the thresholds at which networks are filtered and dichotomized are arbitrary, and the resulting binary networks are likely oversimplified (Franks et al. 2010). Recent methodological developments are providing researchers with exciting new variations on centrality and clustering metrics for analyzing weighted networks, which are exceedingly useful for investigating animal social networks (Box 1) (Newman 2004; Lusseau et al. 2008).

Weighting edges by association should be considered whenever possible, and algorithm development is ongoing to facilitate further substantive interpretation of weighted graphs. Following construction of the network and calculation of network metrics, weighted or unweighted, the subsequent statistical analysis of network data must proceed with caution. For reasons of their very nature, network data

Box 1 Social network analysis terms. Definitions from Wey et al. (2008), p. 334, and Whitehead (2008), pp. 172–175

Individual measures

<i>Centrality</i>	A measure of an individual's structural importance based on its network position
<i>Degree centrality</i>	Centrality based on the number of direct edges connected to a node
<i>Betweenness centrality</i>	Centrality based on the number of shortest paths between every pair of other nodes in the network that pass through the node of interest
<i>Reach</i>	A measure of indirect connectedness that is defined as the number of nodes two or fewer steps away

(continued)

Box 1 (continued)

Affinity Average degree of a node's neighbors; a node with high affinity is connected to other nodes of high degree

Intermediate measures

Clustering coefficient The density of a node's local network; the number of observed edges between a node's neighbors is divided by the number of possible edges between them

Cliquishness How much the network is divided into subgroups; a clique is a set of nodes that are all directly connected to each other

Group measures

Average path length The average of all path lengths, or number of edges, between all pairs of nodes in the network

Density The number of observed edges divided by the number of possible edges in the network

Diameter The longest path length in the network

Weighted measures

Strength A measure of weighted degree that is the sum of the weights of the edges connected to a node

Betweenness Sum of the inverses of the weights on each edge that equals the shortest path lengths that pass through the node

Eigenvector The corresponding element of the first eigenvector of an association matrix; accounts for both the number and weights of all directly connected edges, as well as indirect connections

Reach Overall strength of a node's neighbors

Affinity Average weighted strength of a node's neighbors

Clustering coefficient A measure of cliquishness or how well connected neighbors are to each other considering the weight on all three edges of each triangle linking the nodes

violate the assumption of independence of traditional statistical methods. Therefore, when analyzing network data the scope of inference is generally constrained, and the statistical significance of network metrics is typically assessed by carefully chosen randomized techniques or models that account for network autocorrelation (Croft et al. 2011). This particular caveat has important implications for network comparison and dynamic network analysis.

18.3 Network Comparison and Dynamic Network Analysis

Two networks can be compared with permutation tests (Manly 2007), determining whether specific network metrics means differ more than random expectations. However, care must be taken to ensure that the networks under comparison are similar in size and density or that measures have been normalized based on the maximum value for a node in that network because most network metrics vary with the number of nodes and edges. An additional methodology for comparing networks regardless of differences in size, or even species, was suggested by Faust and Skvoretz (2002). This technique characterizes networks in terms of their structural properties and measures the similarity of networks based on the parameter estimates for models (exponential random graph models, or “ergms”) that predict the probability of network ties. Dynamic social data present additional methodological obstacles, and the techniques for analyzing such data using network theory are still in development or untested on real-life data. Intuitively, social networks are dynamic with relationships forming and fading over time; however, the vast majority of research has focused on static networks that are unable to capture information about changes in the network or the mechanisms related to observed dynamics. In the social sciences, Snijders (1996) and his colleagues (Steglich et al. 2010) developed some dynamic models used in the analysis of dynamic friendship networks. These dynamic models can identify what is likely driving change in social networks over time and could be particularly useful for studying animal social development. Research into dynamic network models is ongoing, and the availability of applied longitudinal datasets will facilitate the creation of exciting additional methodologies.

18.4 Analysis of Primate and Dolphin Social Networks

In the field of animal behavior, SNA is employed, generally on static graphs, to describe complex social structure and to provide insight into studies of cooperation, disease, and information transfer, the different roles of individuals in groups, and the consequences of anthropogenic disturbance on animal societies (see Krause et al. 2007; Wey et al. 2008 for excellent reviews). The specific applications of SNA to animal behavior are too numerous to enumerate in further detail here; however, it is worth noting some of the early and commonly cited animal SNA conducted on wild populations of bottlenose dolphins (*Tursiops* sp.) (Lusseau 2003; Lusseau and Newman 2004; Lusseau et al. 2006; Lusseau 2007). Bottlenose dolphins and some other odontocetes (toothed whales) are attractive candidates for SNA because of their dynamic and complex fission–fusion society. For example, Lusseau (2003) described the network of a relatively small population ($N=64$) of bottlenose dolphins in Doubtful Sound, New Zealand and investigated the theoretical removal of random individuals compared to specific individuals with a large number of associates. The dolphin network appeared robust to removal of random individuals whereas the removal of individuals with high degree increased the network diameter, defined as the average shortest path length between any two nodes, by 20–30 %.

In a separate study, Lusseau et al. (2006) described the network of bottlenose dolphins ($N=124$) in the inner Moray Firth in eastern Scotland. This study addressed the possible relationship between social structure and geographic preference by assigning dolphins to one of two categories, either (1) always sighted in inner Moray Firth or (2) sighted in inner Moray Firth and elsewhere, and determining whether dolphins in these two categories constitute cliques in the network. The researchers conclude that composition of the two communities identified in the social network matched well with the categories of geographic preference. More recent work in delphinids has continued to address spatial, as well as temporal and ecological, correlates of social network structure to better understand factors influencing social processes (Cantor et al. 2012; Foster et al. 2012).

We have recently published several detailed studies on bottlenose dolphin maternal and calf social networks (Stanton et al. 2011), the relationship between early calf networks and survival during the juvenile period (Stanton and Mann 2012), sex differences in social network metrics (Mann et al. 2012), and how SNA can help identify “culture” in dolphins (Mann et al. 2012). Most of the insights gained from these studies are attributable to the application of social network methods. For example, the likelihood of survival of male dolphins beyond weaning was positively related to eigenvector centrality as calves (Stanton and Mann 2012). This metric is an excellent measure of an individual’s importance in the network, and because this method accounts for both direct and indirect ties, we would not have detected this pattern without a SNA approach.

In primates, network theory has been applied to the analysis of grooming interaction networks as well as association networks (Flack et al. 2006; Lehmann and Boesch 2009). An interesting SNA study investigated the roles and structural positions of captive pigtailed macaques (*Macaca nemestrina*) in their social networks. In this case, dominant males perform a policing function by impartially intervening in conflicts between other members of the group. Both the simulated and empirical removal of just a few of these policing individuals altered the macaque social network, in some cases significantly decreasing in the mean degree and increasing clustering coefficients, which the authors conclude destabilizes the group (Flack et al. 2006). Such investigations can be utilized as a means of predicting anthropogenic effects on free-ranging animal social networks. Although many wildlife conservation management plans assume all animals are equal, research such as the macaque study just described, as well as an analysis of a killer whale (*Orcinus orca*) social network, indicates that certain individuals have a disproportionately large impact on their networks and should be differentially accounted for in conservation plans (Williams and Lusseau 2006).

Historically, some primate studies used the term social network when referring to associating individuals and grooming interactions, but do not actually apply network theory when analyzing data. However, as the utility of SNA becomes increasingly apparent, network theory is being applied to datasets from primate field sites to identify differences in association patterns between both individuals and age-sex classes, describe association trends over time, and provide new approaches and perspectives for measuring dominance and other hierarchical structures (Lehmann and Ross 2011; Henzi et al. 2009; Ramos-Fernández et al. 2009; Shizuka

and McDonald 2012). In recent years, studies have begun comparing social networks across closely related primate species. For example, in a study of four macaque species that vary in degree of social tolerance, SNA metrics revealed novel dimensions of these otherwise well-characterized societies (Sueur et al. 2011).

18.5 Additional Social Network Applications

The use of SNA in animal behavior is by no means confined to research in cetaceans and primates. Indeed, the use of these methods now ranges from studies of insects (Fewell 2003), rodents (Wey and Blumstein 2010), ungulates (Sundaresan et al. 2007), and social carnivores (Smith et al. 2010). An exceedingly useful social network technique is quadratic assignment procedure (QAP) regression, which allows for the regression of explanatory matrices on a response sociomatrix representing associations or interactions (Krackhardt 1988; Dekker et al. 2007). QAP regression first calculates coefficients by performing an ordinary least squares (OLS) regression, then randomly permutes the response matrix and reruns the OLS regression x number of times to obtain a matrix-specific distribution of coefficients against which the observed matrix coefficients can be compared and statistical significance evaluated. This permutation-based approach avoids the inflation of type I errors caused by the correlational nature of network data (Krackhardt 1988). As with traditional multiple regression, the multiple regression quadratic assignment procedure (MRQAP) allows for the inclusion of multiple factors that may account for variation in a sociomatrix, including factors that are not necessarily of interest that need to be controlled for. Animal behavior researchers are beginning to recognize the usefulness of this analysis (Croft et al. 2011) and have thus far employed QAP regression to investigate factors influencing network structure in yellow-bellied marmots (*Marmota flaviventris*) (Wey and Blumstein 2010) and ring-tailed coatis (*Nasua nasua*) (Hirsch et al. 2012). We have also recently applied this method to our own investigation of the social function of tool use in Shark Bay bottlenose dolphins (*Tursiops* sp.) (Mann et al. 2012). In that study, the MRQAP was used to control for sex as well as geographic distance and maternal relatedness between individuals while investigating whether similarity based on the use of marine sponges as tools is a significant predictor of association and indicative of culture. This was the first study to examine whether tool use or foraging similarity influences social preference. Such an examination is not possible with traditional non-network approaches.

18.6 Conclusion

As indicated here, we have applied SNA in our own work on bottlenose dolphins. Chapter 6 in this volume provides example measures from the networks of two calves, based on different measures of sociality including networks created from

association and petting/grooming interactions. As networks may differ based on the types of data used to define relationships between individuals, one exciting new direction for the field involves combining different behaviors (e.g., grooming, aggression, and proximity) into one multidimensional object (Barrett et al. 2012). As evidenced by the pioneering animal network studies described here, SNA of cetacean and primate populations is exceedingly applicable to free-ranging primate and cetacean populations, and the potential inquiries are plentiful.

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