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REVIEW

Social network analysis of animal behaviour: a promising tool for the study of sociality

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Social animals live and interact together, forming complex relationships and social structure. These relationships can have important fitness consequences, but most studies do not explicitly measure those relationships. An approach that explicitly measures relationships will further our understanding of social complexity and the consequences of both direct and indirect interactions. Social network analysis is the study of social groups as networks of nodes connected by social ties. This approach examines individuals and groups in the context of relationships between group members. Application of social network analysis to animal behaviour can advance the field by identifying and quantifying specific attributes of social relationships, many of which are not captured by more common measures of sociality, such as group size. Sophisticated methods for network construction and analysis exist in other fields, but until recently, have seen relatively little application to animal systems. We present a brief history of social network analysis, a description of basic concepts and previous applications to animal behaviour. We then highlight relevance and constraints of some network measures, including results from an original study of the effect of sampling on network parameter estimates, and we end with promising directions for research. By doing so, we provide a prospective overview of social network analysis' general utility for the study of animal social behaviour.

Keywords: animal behaviour; quantifying sociality; social network analysis; social structure

Sociality implies a number of individuals living and/or interacting together, which can lead to complex social relationships and structure. Studying these aspects helps us understand the causes and consequences of sociality (Hinde 1976; Krause & Ruxton 2002; Whitehead 2008). Commonly used measures of social complexity (e.g. group size, mating system) have revealed many consequences of sociality (e.g. Côté & Poulin 1995; Hoogland 1995; Brown & Brown 1996; Dunbar 1998). Yet these measures only indirectly reflect the social relationships between individuals, and they assume homogeneity of effect on all individuals. We suggest that social network analysis will provide a deeper understanding of social complexity by measuring social relationships directly. Formal network analyses will complement relationship-based approaches previously applied to animal behaviour (Hinde 1976; Whitehead 1997; Pepper et al. 1999). We believe that social network analysis has general relevance to all social systems, and that by expanding its application in animal behaviour, we will gain novel insights about the evolution and maintenance of sociality. In this review, we suggest how social network analysis can be used for studying animal systems, we use socially transmittable pathogens as a concrete example to illustrate specific points, and we identify possible constraints of this approach. Our goal is to briefly introduce and advocate the further use of social network analysis in animal behaviour; for an extensive review of this topic, see Croft et al. (2007).

NETWORK THEORY

A network models a system composed of individual components (*nodes*) and their connections (*ties*; see Table 1

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Table 1. Terminology

Basic terms

Graph: a set of nodes and a set of relationships between the nodes, given by a matrix or visualized as a picture showing dots connected by lines

Node: a component of a network with known relationships to others in the graph model representing the network; in a social network, this can be an individual (person or animal) or group; also called a vertex or point

Path length: the shortest number of ties between two nodes

Sociomatrix: for a group with n members, an $n \times n$ matrix with each group member along the vertical and horizontal axes and each entry in the grid as the weight of the social relationship, if any, between the two intersecting individuals

Tie: a relationship between two components of a network, where the two related components are nodes in the graph model representing the network; in a social network, these can be any sort of social relationship, such as social interactions or information transfer; also called an edge or link

Individual (local) measures

Betweenness centrality: centrality based on the number of shortest paths between every pair of other group members on which the focal individual lies

Centrality: a measure of an individual's structural importance in a group based on its network position

Closeness centrality: centrality based on the shortest path length between a focal individual and all other members of the social group

Degree centrality: centrality based on the number of direct ties an individual has

Indegree (reception): the number of ties directed towards an animal, e.g. the number of social interactions it receives

Node degree: the number of ties a focal animal has; the number of other animals with which the focal individual interacts

Outdegree (emission): the number of ties originating from an animal, e.g. the number of social interactions it initiates

Intermediate measures

Clustering coefficient: the density of the subnetwork of a focal individual's neighbours; the number of ties between neighbours is divided by the maximal possible number of ties between them

Cliquishness: how much the network is divided into cohesive subgroups; a clique is a set of nodes where each node is directly tied to each other

Group measures

Average path length: the average of all path lengths between all pairs of nodes in the network

Density: the number of realized ties divided by the number of possible ties in the network

Diameter: the longest path length in the network

for definitions of italicized terms). The shortest number of ties between two nodes is the *path length* between that pair. This approach provides the best tools for understanding systems in which the most important characteristics are the connections between components. The social network approach addresses the structure of relationships and the mutual interplay between the individual and the group. While 'group' can be defined in many ways, here we use 'group' to mean the network as a whole, or the collection of potentially interacting individuals that are distinguished from other such collections of individuals. As with other definitions of 'group', this can theoretically range from two individuals to whole populations. For simplicity, here we generally refer to intermediately sized groups, such as a herd of horses or a colony of birds. Two major reasons to use formal network analysis are that it provides formal descriptors (definitions and measures) for characterizing social groups and that, by providing quantitative measures of relationships, it allows us to test statistical models about relationships and structure (Wasserman & Faust 1994).

In social networks, nodes are social entities, which can be individuals or units (e.g. corporations in a business network), and ties are social relationships between two nodes at a given time; these can be interactions or associations (e.g. business dealings or friendships). In animals, relationships can include well-studied social interactions (e.g. agonistic interactions that create dominance hierarchies or grooming relationships in primate affiliative networks), as well as transmission events (e.g. pathogens, signals or social learning), resource sharing (e.g. food, territories or even heat in socially thermoregulating animals) and kinship ties. Ties can also have weight, direction and sign (i.e. positive or negative) to provide additional details about interactions (Fig. 1). In an unweighted (binary) network, all ties have value of 1, reflecting presence of a relationship between two nodes, and absence of a relationship is denoted by a 0. In a weighted network, ties reflect the strength of the relationships and can have different values. In a nondirected network, ties simply show that two nodes are connected. However, in a directed network, there can be potential inequality in the relationship, and A—B may not be the same as B—A. In animal behaviour, an easy way to conceptualize directionality is as directed social interactions, where ties reflect the initiator and recipient of the relationship (but note that directed ties need not have an initiator or recipient, e.g. A is the boss of B). Positive and negative values of ties can denote the nature of interactions or their effects on individuals. A network is commonly depicted visually as a *graph* (Fig. 1), also called a sociogram for social networks. More useful for quantitative analysis is a *sociomatrix* (a matrix with each node along the vertical and horizontal axes and each entry in the grid as the weight of the social relationship, if any, between the two intersecting nodes), and this form is the basis for many network analysis programs.

Hereafter, we use the term 'node' interchangeably with 'individual', and 'tie' with 'relationship'. While other terms have been used for these concepts, in animal social networks, we anticipate that nodes will most commonly represent individuals, and we choose 'relationship' rather than 'relation' (which is common in sociology) to avoid confusion with the term 'relatedness', which might limit the idea of social relationships. Here and elsewhere, we will illustrate the biological relevance of network concepts with the example of socially influenced transmission of a pathogen in a group of animals. Pathogen transmission can be influenced by social networks through rate of contact as well as overall social structure. While social influence can be general as in an airborne disease (e.g. a cold virus) that will be influenced by proximity and all types of social interactions, we will use the specific case of sexually transmitted diseases (STDs) and sexual networks. In this system, nodes are potentially sexually active individuals, and ties are sexual relationships along which an STD may be transmitted. Binary ties would simply reflect the presence or absence of a sexual relationship, while weighted ties might reflect different rates of sexual contact between two individuals. Directed ties may become important if only one individual in a pair is infected, and the flow of the transmission can only go from one direction to another. While we use the example of disease, in which it may be desirable to minimize transmission, it is important to realize that in other cases (e.g. communication) selection should act to maximize transmission.

Broadly, the scope of network measures ranges from describing individuals to groups, with intermediate ‘mesoscale’ measures in between. At an individual level, network measures can describe the neighbourhood of a focal individual, patterns of direct and short indirect ties, and effects of strong and weak relationships. An example of an individual measure is *node degree*, which is the number of direct ties an individual has, i.e. the number of other individuals with which it has relationships. Direct ties are a focal individual’s immediate connections; indirect ties are those with individuals more than one step away (see Fig. 2c). Although the relevance of indirect and weak interactions is not always obvious, their effects can be significant (see Granovetter 1973). For example, an individual’s chance of contracting an STD depends not only on its own sexual partners, but also on their sexual partners. An infected individual may ultimately pass the disease to someone several partners removed, so an individual may be affected by anyone to whom it is connected through a continuous chain of intermediates. Thus, in addition to disease characteristics such as virulence, the nature and structure of social relationships will also affect likelihood and paths of transmission. In this way, social network analysis should explain biological phenomena that are influenced by indirect relationships better than other measures, such as group size, which do not contain sufficient details about individual social relationships. Importantly, network measures are calculated from explicit mathematical formulae, offering objective measures of individual and group sociality, and many measures can be standardized by dividing by group size, facilitating comparisons between groups. Thus, they may be useful for comparative studies (Faust & Skvoretz 2002; but see also Faust 2006 for issues that arise when comparing networks with very different sizes and densities).

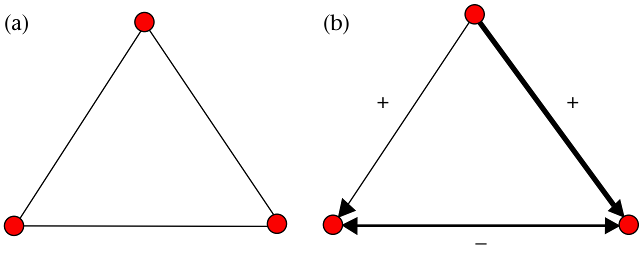

Figure 1. (a) A simple three-node network (triad) with ties that are unweighted, nondirected, and have no sign. (b) The same network with ties given weights, directions and signs, providing more information about the network; this triad also illustrates transitivity and a reciprocal negative relationship between the two bottom nodes.

At a group level, network measures can describe the overall structure and possible stability (or vulnerability) of groups. Examples of group measures include *average path length*, the average of all path length between all pairs of individuals in the network, and *diameter*, the longest path length in a network. In social networks, group-level stability has implications for the removal (death or emigration) or addition (birth or immigration) of individuals, and for the extent to which structure influences network function or efficiency. These properties can only be understood in a network context and at the level of the whole network, and thus modern network theory can be the basis for a more holistic understanding of how social interactions influence group structure and dynamics. In the case of an STD, some network structures may allow for faster or more pervasive spread of the disease, and some social groups may be more at risk than others (Klovdahl et al. 1994).

PREVIOUS NETWORK STUDIES

Network theory originated in mathematical graph theory and was soon applied to other fields (e.g. sociology: Cartwright & Harary 1956; business: Levine 1972; markets: Burt 1988; political science: Harary 1959, 1961a; ecology: Harary 1961b). Social network analysis has a long history of application in human sociology (Wasserman & Faust 1994; Degenne & Forsé 1999; Hanneman & Riddle 2005; also see the scientific journals *Social Networks*, *Journal of Mathematical Sociology* and *Connections*), and some network phrases describing sociological phenomena are even in general usage, e.g. the idea of ‘six degrees of separation’ based on a study by Milgram (1967) and popularized in a play (Guare 1990) and movie (Guare 1993). Network concepts have also been topics of recent popular literature (Gladwell 2000; Barabási 2002; Watts 2003). In various fields, social network analysis has contributed novel insights through the relationship-based approach. In epidemiology, for example traditional models of disease transmission assume random interactions between individuals (Anderson & May 1991), but social relationships are not random and can strongly affect the spread of disease. These effects can be subtle, but still change disease transmission dynamics (Watts 1999). The utility of network models to incorporate patterns of social relationships is ideally illustrated in the case of an STD, whose transmission can only occur through the network of sexual relations and cannot be accurately modelled without understanding social structure (reviewed in Liljeros et al. 2003). Yet while network analyses became important tools in many fields, there was a limited and delayed application in ecosystems ecology (Levine 1980), in which it was mostly restricted to economic input–output analyses (Hannon 1973). Remarkably, there was even less application to behavioural sciences; ethologists mostly restricted network analyses to describing dominance relationships from observed agonistic interactions (e.g. Appleby 1983; Archie et al. 2006). Note, however, that concepts of dominance developed quite independently of social network analysis (e.g. de Vries et al. 2006).

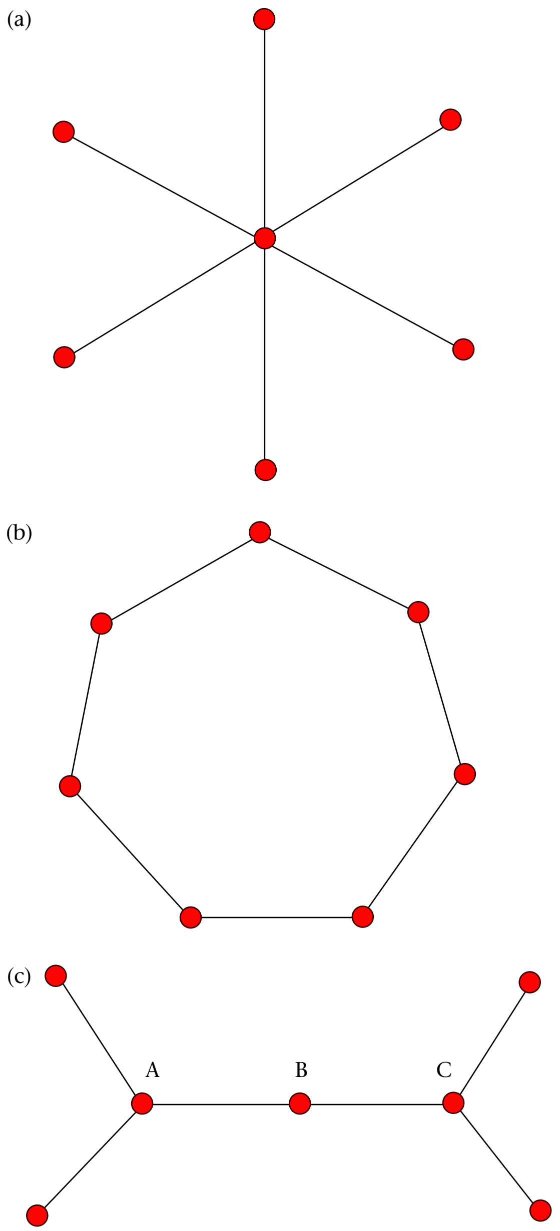

Figure 2. Three networks, each with seven nodes but different topologies: (a) a 'star' network where the individual in the middle has the highest degree, closeness and betweenness centrality and where the network has maximal centralization overall; (b) a 'closed' or 'circular' network where all individuals have equal degree, closeness and betweenness, while centralization is 0; and (c) a network where individuals A and C have highest degree, but individual B has highest closeness and betweenness. Note that A and C are indirectly tied to each other through their direct ties with B.

A recent explosion in computer processing power has created the ability to handle enormous databases and has revolutionized our understanding of larger and more complex networks describing real data (Strogatz 2001; Albert & Barabási 2002; Newman 2003b; Boccaletti et al. 2006). In general, we are no longer computationally limited by the number of nodes that can be studied, and researchers have begun to ask novel questions of phenomena as diverse as the Internet (Barabási et al. 2000), traffic patterns (Fekete et al. 2006), neural networks (Freeman 2005), food webs (Solé & Montoya 2001; Luczkovich et al. 2003), gene and protein networks (Milo et al. 2002), terrorist networks (Krebs 2002) and publication networks (Newman 2003a). There are both striking similarities and differences between diverse networks, and social networks may have some distinct properties of their own (Newman & Park 2003). In all of these cases, the study of networks fundamentally enhances our understanding of how parts are connected as a whole.

While some early sociometric analyses were applied to primates (Sade & Dow 1994), behavioural biologists have only more recently recognized the potential of modern network tools to broader contexts (McMahon et al. 2001; Fewell 2003; Proulx et al. 2005). In the last few years, there have been novel and diverse applications of current network theory to nonhuman taxa, demonstrating its potential for animal behaviour (Croft et al. 2007). Seminal work in bottle-nosed dolphins (*Tursiops* spp.) revealed many notable relational aspects of their social structure. Dolphin social groups showed a 'scale-free' pattern (meaning that the degree distribution of the network follows a power law: Barabási & Albert 1999), giving it similar properties (such as robustness to the random removal of individuals) of other scale-free networks, like the Internet or molecular networks. However, unlike previously studied scale-free networks, it was also robust to the removal of key individuals (Lusseau 2003). As in humans, affiliation by sex and age were important in group formation in these animals (but interestingly, unlike humans, dolphins did not affiliate by degree), and a few individuals held structurally important positions in the social network (Lusseau & Newman 2004). Furthermore, dolphin networks had 'small-world characteristics', a combination of highly clustered subgroups and short average path lengths, which exists in many human social networks and may be very efficient for communication (Watts & Strogatz 1998), and their ties were based mainly on short-term associations, suggesting a fission–fusion society (Lusseau et al. 2006). These studies and others (e.g. Connor et al. 1998; Nanayakkara & Blumstein 2003; Whitehead et al. 2005) used SOCPROG (Whitehead 2006), a valuable program for describing animal social structure from observed associations.

Social network analysis has also been used to describe complex social structure in fish. Guppies, *Poecilia reticulate*, had small-world networks, and the network structure predicted patterns of cooperation (Croft et al. 2004, 2006). A comparison of social networks in guppies and three-spine stickleback, *Gasterosteus aculeatus*, found significant structure with 'social cliquishness' (Croft et al. 2005). Mechanisms proposed to explain the observed structure included association of similar-sized individuals, shoaling tendencies and repeated interactions between individuals, traits that satisfy certain prerequisites for the evolution of reciprocity and cooperation.

Innovative network studies in pigtailed macaques, *Macaca nemestrina*, examined the effect on network structure of removing key individuals (Flack et al. 2005, 2006), using both simulated and experimental removals resembling genetic knock-outs used to identify gene function.

Results indicated that key individuals can have disproportionately large effects on network stability and that predictions based on simulations may not accurately approximate real-life consequences, a fact that often is not fully appreciated in network models of ecological food webs (Jordán & Scheuring 2002; Eklöf & Ebenman 2006).

Spatial association networks also have consequences for social animals. Rhodes et al. (2006) found a scale-free network in the pattern of roosting tree usage by white-striped freetail bats, *Tadarida australis*. A single habitat tree was the hub of the network, where nodes were roosting habitat trees, and ties were individual bats' roost-switching events. The topology of this spatial network could have consequences on the social life and epidemiology of these animals, since individuals using different roosting trees spread over a large area could meet with surprising frequency at the central communal roosting tree.

These studies in diverse taxa show how modern social network analysis can contribute novel insights to animal behaviour and how these findings may influence applications of behavioural studies. A common theme is the importance of relational data for understanding overall structure and the roles of individuals within that structure. While these studies have made important headway, modern social network analysis of animal systems is only in its earliest stages. Comprehensive network studies on more animal systems over longer time periods will enhance our understanding of sociality and will allow novel analyses and comparisons. Future studies must go beyond simple network description and begin to relate network structure to biological and evolutionary consequences.

NETWORK MEASURES

In this section we present some common network measures and discuss biological relevance to animal social behaviour in the specific context of a STD. This is not intended as a comprehensive description of all useful methods but rather as general suggestions to facilitate further research. We provide conceptual rather than formal definitions to highlight potential biological significance and to avoid confusion in some terms, for which exact definitions vary by source. For detailed definitions, formulae and methodology, see Wasserman & Faust (1994), Borgatti et al. (2006b) and Croft et al. (2007).

Individual Measures

Recall, individual measures are calculated from a focal individual's neighbours (those that are directly linked in the network). This individually based, or ego-centric, viewpoint describes a specific individual's position in the network, and the potential effect it has on (and receives from) others. An individual measure can reflect relationships with just those directly connected to the focal individual, or also individuals indirectly connected to the focal individual, up to a given number of steps. Specifications are set based on applicability to the study.

We defined *node degree* above as the number of direct ties a focal individual has. A related idea in a weighted network is relationship strength, which is the weight of the tie (Barthélemy et al. 2005). In our STD example, node degree might be the number of other animals with which the focal animal copulates, and relationship strength, the number of times the focal animals copulates with each. Total copulations (the sum of all the relationship strengths) might reflect differences in number of chances for an animal to be exposed to the STD. Although they reflect slightly different aspects of social relationships, both of these measures will affect an individual's risk of infection, but one may be more appropriate in a given context. For instance, node degree may be more relevant for spread of a highly infectious disease, while total relationship strength might be more relevant for a less virulent disease that requires repeated exposures for infection. In a directed network, *indegree* is the number of ties directed towards an animal (i.e. the number of relationships in which it is the receptor), and *outdegree* is the number of ties originating from an animal (i.e. the number of relationships in which it is the emitter). The difference between indegree and outdegree, which can be a positive or negative number, reflects the local component of sociometric 'net status' (sensu Harary 1959). Indegree might reflect how susceptible an uninfected animal is to infection, and outdegree might reflect how contagious an infected animal may be. These same ideas apply to other forms of transmission, such as the transmission of information contained in signals (McGregor 2005) and the spread of innovations (e.g. Swan et al. 1999; Perry & Manson 2003). One limitation of social network analysis in modelling dynamic processes such as transmission is that a network represents a structure at one point in time, while inferences about dynamics must be made over longer periods of time (see Issues In Applying Social Network Analysis).

Centrality is one way to quantify an individual's structural importance in a group (Freeman 1979; Friedkin 1991). There are three common ways to describe centrality. *Degree centrality* is based on the number of direct ties an animal has, i.e. the more others with which an animal has relationships, the more central it is. Therefore, an animal with more ties will have more influence on those around it and possibly on the whole network (cf. a network 'star', Fig. 2a). An animal with more sexual partners has more chance of catching an STD, and if infected, more importance in spreading it. *Closeness centrality* describes how well connected an animal is to all others in the network, based on the inverse of shortest path lengths between that animal and every other animal in the social network. This measure reflects both direct and indirect relationships. An animal that is not directly connected to every other group member could be indirectly connected through one, two, three or more others. Closeness centrality better reflects an individual's potential influence on the entire group and is particularly relevant if the number of transmission steps matters, e.g. in terms of time and how fast transmission can occur. High closeness centrality indicates an infected animal's potential to quickly spread a disease to the entire group, not just to immediate neighbours as with degree centrality. *Betweenness centrality* also incorporates indirect interactions, but it reflects the number of shortest paths between every other pair of animals in the network on which a focal animal lies. Betweenness thus indicates how important an animal is as a point of social connection and transfer. To contain disease transmission, it may be most effective to focus treatments on individuals with high betweenness. Besides being important in transfer, animals with high betweenness are likely to be important for group stability, and their removal (by death or dispersal) may fragment the group into smaller subgroups (McComb et al. 2001; Lusseau & Newman 2004; Flack et al. 2006). These three centrality concepts reflect different aspects of sociality, and are sometimes, but not always, correlated (Fig. 2). Another measure of centrality is 'eigenvector centrality' (Bonacich 1987), which factors in the importance of neighbours in determining centrality and may be more appropriate for weighted networks and association data (Newman 2004).

Intermediate Measures

Some network measures identify the presence of subgroups in the network, reflecting the distribution of the ties (Fig. 3). We call these 'intermediate' measures because they describe the relationships beyond a single individual (however, note that in very large networks, they will still be relatively local descriptors). *Clustering coefficient* quantifies the density of relationships among a focal node's neighbours (excluding the focal individual). The number of existing ties between neighbours is divided by the maximal possible number of such ties (e.g. if an individual has four neighbours, these neighbours may have $(4 \times 3)/2 = 6$ relationships among themselves). Clustering coefficient describes how densely (or sparsely) the network is clustered around the focal individual. *Cliquishness* describes to what extent the network is divided into cohesive subgroups. A clique is a set of nodes where each node is directly tied to each other (Fig. 3b), but less strict conditions can be defined as well. (A similar concept of 'compartment' has been used extensively in ecology, e.g. Krause et al. 2003.) The existence of subgroups may affect network robustness to fragmentation. With strong subgrouping, a network may be more quickly fragmented by removing a single or few animals or ties (e.g. by blocking a communication pathway). Higher clustering or cliquishness could also mean that transmission (e.g. of disease) would be very fast and complete within a subgroup, but slower throughout the entire network because transmission events would tend to stay within a subgroup. This could be beneficial or detrimental, for instance, by reducing disease or information transfer.

Group Measures

Group measures (calculated from the set of individual measures or defined only at the network level) describe aspects of overall network structure. Importantly, they go beyond simple measures of group size or composition, which are independent of the network of relationships. Diameter, mentioned previously, is the longest path length in the network (so if the diameter is n, no two individuals are more than n steps away from each other), and is a very basic measure of how well connected the network is. Generally, individuals in a group with a smaller diameter are connected to each other through fewer intermediates, and transfer between individuals is potentially faster than in a group with larger diameter. The average path length also gives a general idea of the network's overall connectedness, and a shorter average path length again suggests potential for quicker transfer among all group members.

Cohesion is defined in many ways, both colloquially and in the network literature, but generally, the term describes how well a group is connected based on more sophisticated calculations. One measure of cohesion is *density*, the number of ties present divided by the number of possible ties in the network. Density is generally calculated only for unweighted networks, and while some methods to measure density in weighted networks have been proposed (Wasserman & Faust 1994), they are not universally accepted, and we do not address them here. A group with higher density has more ties per individual than a group with lower density and therefore, is theoretically more cohesive. Another important concept is transitivity, which is the idea that if A has a relationship with B, and B has a relationship with C, then A has a relationship with C as well. Also important is the idea of reciprocity, which reflects how many of the relationships are mutual. Together, transitivity and reciprocity tell us more about how well balanced relationships are (Fig. 1b). For example, two groups could have the same density, but one could have higher reciprocity, indicating that the interactions are more balanced overall. Greater cohesion, transitivity and reciprocity might all suggest a greater potential for transmission within a network. With affiliative relationships, greater cohesion, transitivity and reciprocity might

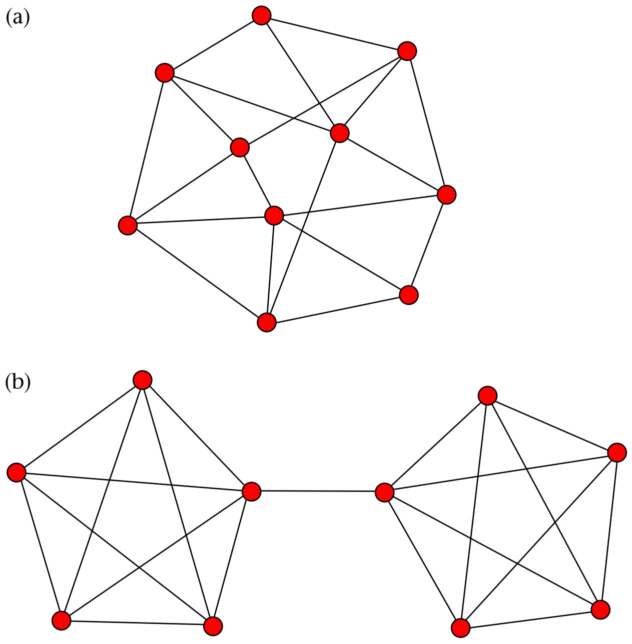

Figure 3. Two 10-node networks: (a) with no distinct subgroups, and (b) with two distinct subgroups (two cliques, i.e. groups of nodes with all possible ties among them, forming two complete subgraphs).

suggest a more tightly knit social group, in which positive interactions are consistent among triads and are mutual.

ISSUES WHEN APPLYING SOCIAL NETWORK ANALYSIS

Spatial and Temporal Limitations

Space constrains network structure, limiting the ways in which animals can construct their social networks and making some relationships and structures impossible or less likely than others. For example, locomotor ability, habitat topology and resource distribution will all influence the possible set of relationships. It is important to understand whether the observed social networks are distinct from relationships explained solely by shared space use (see Lusseau et al. 2006). Temporal limitations also arise because networks reflect the state of relationships in a group as if it were at one point in time, even if the data were collected over a longer period. Not all of the relationships represented may have existed at the same time, nor indeed may have all the individuals been together simultaneously. Network analysis assumes that the relationships included are relatively stable over time, and this assumption must be understood when using and interpreting networks. To examine network dynamics, one must look at how a network changes over time (e.g. by reconstructing and analysing the network at different points in time), or infer dynamics from the observed structure at only one point in time. One possible way to examine how temporal limitations may change network measures is to use permutation methods (Bejder et al. 1998; Whitehead 1999; Whitehead et al. 2005) to compare network measures calculated from permuted networks with measures calculated from the original networks.

Defining the Network

The decision about which individuals to include in a network analysis will affect the subsequent network structure and parameter estimates. Including too few individuals may give a truncated picture of the network, while including too many individuals may result in an unwieldy or highly fragmented network. In a fragmented network, the network is split into two or more unconnected subgroups, between which there are no interactions or communication. A number of network statistics cannot be defined and calculated for unconnected networks (e.g. diameter), while others generate misleading artefacts (Kossinets 2006). Thus, it is essential to carefully define a network in a way that reflects a biologically relevant level of resolution. For example, if the question is how social structure differs between populations of animals on isolated islands, it would be appropriate to define each island as a network, whether or not each is fragmented, in order to make comparisons between islands. However, if the question is how quickly information might be passed among connected individuals, then it would be inappropriate to look at a fragmented population (where, by definition, information cannot be transmitted). In this case, one might use connected components (sets of individuals that can all be tied to each other, whether directly or through intermediates) as the unit of analysis.

Robustness of Parameter Estimates

All descriptions of sociality are generated by sampling behaviour, and sampling might affect our ability to estimate network parameters. Missing data can significantly alter network measures (Kossinets 2006), although centrality measures calculated from subsets of the data may retain their relative relationships to each other despite sometimes large absolute differences (Costenbader & Valente 2003). Removal trials on simulated data showed predictable trends in the response of centrality measures, suggesting that confidence intervals can be established (Borgatti et al. 2006a).

To examine how sampling affects real networks, we conducted a series of removal trials on data collected by observing social interactions in yellow-bellied marmots, *Marmota flaviventris*, a facultatively social, ground-dwelling, sciurid rodent. Marmots in and around the Rocky Mountain Biological Laboratory, Colorado, were individually marked and systematically observed for the occurrence and nature of all social interactions (see Blumstein et al. 2004 for methods). We tested the robustness of several network measures by calculating the network measures with the complete data set of all observed social interactions (we defined relationships as social interactions), followed by random removal of 10%, 20%, 30%, etc., up to 90% of the observations. Each removal trial was replicated 10 times, and the measures were recalculated for each subset. Our data were directed and weighted. We used analysis of variance (ANOVA) to determine what percentage of data removal resulted in a significant change in the network measure of interest. While these data are technically nonindependent, ANOVA is useful in a boot-strapping study such as this. The results of these removal trials for individual and group measures are presented in Tables 2 and 3. The standard error within each trial was low, indicating that, for a given sample size, network parameters were measured precisely.

Overall, many network measures were relatively robust to reduced sampling effort, suggesting that, in this system, we were sampling sufficiently to obtain representative network measures. In general, measures calculated only from direct interactions (e.g. degree centrality) were more sensitive to data removal than were measures calculated from indirect interactions (e.g. closeness and betweenness). However, measures incorporating indirect interactions also showed less consistent trends. This suggests that degree will steadily decrease as more and more interactions are removed, but changes in indirect interactions will be less predictable. Diameter was extremely robust, probably because it provides little detail about the relationships in the network as a whole and was calculated based on redundant paths (i.e. if there are multiple relationships between two individuals, removing all but one of those interactions will still make no difference in the diameter). Cohesion (calculated based on reciprocity) was also robust, although asymmetries tended

Table 2. The effect of randomly removing observations on estimates of individual network parameters

ID number	Outdegree: weighted	Indegree: weighted	Node degree: unweighted	Node degree: weighted	Closeness centrality	Betweenness centrality
1382–1397	30	30	50	30	70	90
4016–4070	0	0	60	0	60	80
4026–4050	0	0	70	0	60	60
4079–4033	20	20	60	20	90	80
4682–4698	0	20	50	0	60	90
4703–4002	0	0	70	0	90	60
4711–4706	20	20	60	30	60	90
4715–4716	20	0	70	0	60	50
4844–4853	0	20	70	0	90	80
Average	10%	12%	62%	9%	71%	76%

Marmot social groups were defined based on spatial overlap (see Nanayakkara & Blumstein 2003). Data are the percentage of the original data that could be removed randomly with no significant ($P > 0.05$) difference in the value of the network measure.

to be exaggerated with less data. Density was less robust to data removal because as the number of interactions decreased, the potential number of interactions did not, so this measure necessarily changed quickly with data removal.

Other Considerations

Using network measures in combination will develop a more comprehensive understanding of social relationships. For example, using individual, intermediate and group measures together will provide a broader view of overall social behaviour. The type of relationship data used should depend on the questions being asked and the biology of the system under study. For instance, focusing on grooming bouts is an appropriate way to study affiliative associations in primates (Sade & Dow 1994; Silk et al. 2003), whereas agonistic interactions are used to examine dominance hierarchies (Appleby 1983; Archie et al. 2006).

Whether weighted, directed, and signed data are used will also affect the measures calculated (Vasas & Jordán 2006). While weighted and directed information should give a more detailed picture of group structure and dynamics (Newman 2004), it may be more difficult to collect such data, and more detailed information may also be more sensitive to reduced sampling. If questions can be answered just by the presence or absence of relationships, then binary data may be sufficient. However, weighted or directed information is indispensable if the question under study concerns the relative strength of relationships or the direction of transmission in the network.

Table 3. The effect of randomly removing observations on estimates of group-level network parameters

Group	Diameter	Density: unweighted	Density: weighted	Cohesion
BB	60	30	0	30
CC	80	0	0	20
GG	90	20	0	20
II	40	20	0	40
JJ	80	0	0	20
PP	80	20	0	30
Average	72%	15%	0%	27%

Marmot social groups were defined based on spatial overlap (see Nanayakkara & Blumstein 2003). Data are the percentage of the original data that could be removed randomly with no significant ($P > 0.05$) difference in the value of the network measure.

Some network measures are calculated from shortest theoretical path lengths, but real transmission might not occur along these paths. Whether individuals perceive only their local neighbourhood or the entire network, along with the extent of an individual's control over transmission, can drastically change network dynamics. Given more knowledge about network structure, an individual might choose (or avoid) certain paths. In some animal groups, contact and transmission events may depend largely on chance. In these cases, it is unlikely for transmission to be along the most efficient path, and transmission may be more like diffusion. Additionally, the empirical effects of removing an important individual from a social group could be different from that predicted by simulated removals (Flack et al. 2006).

AREAS FOR FURTHER RESEARCH

Here we highlight some areas in which we feel social network analysis will bring immediate benefits (see also Croft et al. 2007).

Defining Social Groups

A nontrivial question is how to define a social group, and this will vary depending on the question. Social network analysis offers an alternate way to define animal social groups based on social relationships, rather than on spatial distribution or proximity. In nonhuman animals, especially those that are less social, it is also often difficult to distinguish between simple spatial and active social associations. Lusseau et al. (2006) showed that social relationships can be used to differentiate between the two, and groups defined by social relationships may be different from those based only on spatial proximity. Some recently developed methods are effective for picking out natural divisions or subgroups in networks (Newman & Girvan 2004; Newman 2006).

Identifying the Fitness Consequences of Sociality

Much is still not well understood about the fitness consequences of social relationships, and direct fitness correlates are rarely shown (but see Silk et al. 2003). In humans, the structure of an individual's social network can affect measures of health (Berkman 1984; Uchino et al. 1996; Cattell 2001; Friedman & Aral 2001). Quantitative network measures can be correlated with fitness measures (e.g. reproductive success or parasites) to identify possible selective pressures acting on specific aspects of sociality. For example, if more socially central animals have significantly higher reproductive success, this would suggest a role of sociality in increasing fitness. Alternatively, an animal that has relationships with more different individuals could also have increased exposure to pathogens and might suffer higher risk of disease or parasites as a fitness cost. Social network analysis offers a way to re-examine fitness consequences and should contribute novel insights into the evolution and maintenance of sociality. Studying facultatively social species will be particularly important because they can illustrate how variable social traits are correlated with fitness trade-offs.

Identifying Important Individuals and Their Structural Roles

Group members may have different social roles or importance to the group (McComb et al. 2001; Lusseau & Newman 2004; Flack et al. 2005, 2006). Social network analysis offers quantitative measures of sociality that can be standardized for group size and possibly used to describe and compare social complexity of individuals and groups across different taxa. While there are issues with comparing networks of very different sizes (Faust 2006), we feel that this is still a useful starting point for comparison. Sociometric analysis can provide an objective, systematic way to determine dominance roles (Archie et al. 2006), and centrality measures can be used to identify important individuals in animal social groups (Lusseau 2003). In the case of wasp colonies, several centrality indexes have been tested for usefulness as predictors of queen choice, and results suggest that a directed mesoscale index is the best (A. Bhadra, R. Gadagkar & F. Jordán, unpublished data). These measures provide different ways to define importance, and different measures may produce different rankings (Jordán et al. 2006). The most appropriate measure will likely depend on the question, but importantly, network measures provide a way to describe a continuum of social complexity that captures the social relationships within the group.

Developing a Comprehensive Understanding of Social Network Structure

Describing social networks in more species is essential for developing a comparative understanding of sociality and how it functions in different taxa, which will in turn allow us to better understand the evolution of sociality. This requires more detailed and long-term data on social relationships, which may be difficult to obtain. However, some relational data exist (e.g. in many detailed studies of nonhuman primates) but have not been analysed in a network context, and it would be relatively easy to analyse already collected data sets. Types of relational data appropriate for network analysis include social interactions or associations.

Social insects are an ideal system in which to apply social network analysis (Fewell 2003), and some work on them is now underway. While classic studies showed that ant colonies may design their activity performance charts according to reliability theoretical principles (Oster & Wilson 1978), recent results show that network analysis is a more efficient approach to characterize and quantify the social behaviour (e.g. queen choice) of primitively eusocial tropical paper wasps and to better understand differences between closely related species (A. Bhadra, R. Gadagkar & F. Jordán, unpublished data).

Other preliminary comparative results are also intriguing. Faust & Skvoretz (2002) found similarities in networks across very different species, while Lusseau & Newman (2004) found a distinct difference in assortativity between dolphin and human networks. There are also descriptions of the similarities and differences between social networks of two wasp species and students in classrooms (A. Bhadra, R. Gadagkar & F. Jordán, unpublished data). These initial comparative studies show the wide applicability and promise of social network analysis for animal studies.

Identifying Key Characteristics of Stable Groups

Trait group selection models of social evolution focus on traits that are expressed at the group level (Wilson 1975; Wilson & Dugatkin 1997). Social network analysis offers tools to identify group social traits, and so offers a way to gain novel insights into higher-level selection processes by identifying which network characteristics are important for group success. For instance, if groups with higher cohesion tended to out-produce or persist longer than groups with lower cohesion, it would suggest an important role for group cohesion in shaping the evolution of sociality. Used in conjunction with lagged association rates (Whitehead 1995) or other autoregressive methods to address temporal patterning (Whitehead 1997), social network analysis can be used to model group stability, but because models may not always accurately reflect empirical results, real tests of what group characteristics best promote stability will only come with more detailed longitudinal data.

Quantifying Anthropogenic Effects on Animals

Social network analysis could be helpful in wildlife conservation because it offers novel methods to document anthropogenic effects on animal social groups

(Tarlow & Blumstein 2007), and because it helps us better understand the mechanisms of disease transmission. Comparing animal social networks in disturbed and undisturbed areas could highlight changes in network structure that could have important fitness consequences. For some animals, disruptions in social structure may have negative effects in and of themselves (Flack et al. 2006) or lead to consequences for communication or mating, which can be better understood through social network analysis.

Understanding Disease Transmission in Natural Populations

There is an extensive literature on the application of networks to understand human epidemiology, making it a natural application to wildlife populations. The spread of different diseases may depend differentially on network structure because of varied modes of transmission (e.g. STDs versus nonsexually transmitted diseases: Altizer et al. 2003). As described above, social network analysis could help clarify to what degree the spread of various pathogens depends on social relationships in animals. Furthermore, identifying socially central animals could suggest which group members might be most influential in disease transfer. Some studies have already begun to apply network theory to better understand disease transmission in natural populations (Corner et al. 2003; Cross et al. 2004), and further research in this direction will be highly beneficial.

CONCLUSIONS

With this review, we hope to have illustrated the great potential that social network analysis has for the study of animal social behaviour. We expect that in the next decade there will be a fundamental increase in our understanding of social relationships and behaviour resulting from the wide-spread adoption of social network analyses, and we look forward to these insights.

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References

Albert, R. & Barabási, A. L. 2002. Statistical mechanics of complex networks. *Reviews of Modern Physics*, **74**, 47–97.

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M. & Pulliam, J. R. C. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 517–547.

Anderson, R. & May, R. M. 1991. *Infectious Disease of Humans*. Oxford: Oxford University Press.

Appleby, M. C. 1983. The probability of linearity in hierarchies. *Animal Behaviour*, **31**, 600–608.

Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J. & Alberts, S. C. 2006. Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, **71**, 117–127.

Barabási, A. L. 2002. *Linked: the New Science of Networks*. Cambridge: Perseus.

Barabási, A. L. & Albert, R. 1999. Emergence of scaling in random networks. *Science*, **286**, 509–512.

Barabási, A. L., Albert, R. & Jeong, H. 2000. Scale-free characteristics of random networks: the topology of the world-wide web. *Physica A: Statistical Mechanics and Its Applications*, **281**, 69–77.

Barthélemy, M., Barrat, A., Pastor-Satorras, R. & Vespignani, A. 2005. Characterization and modeling of weighted networks. *Physica A: Statistical Mechanics and Its Applications*, **346**, 34–43.

Bejder, L., Fletcher, D. & Bräger, S. 1998. A method for testing association patterns of social animals. *Animal Behaviour*, **56**, 719–725.

Berkman, L. F. 1984. Assessing the physical health effects of social networks and social support. *Annual Review of Public Health*, **5**, 413–432.

Blumstein, D. T., Im, S., Nicodemus, A. & Zugmeyer, C. 2004. Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. *Journal of Mammalogy*, **85**, 25–29.

Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. & Hwang, D. U. 2006. Complex networks: structure and dynamics. *Physics Reports*, **424**, 175–308.

Bonacich, P. 1987. Power and centrality: a family of measures. *American Journal of Sociology*, **92**, 1170–1182.

Borgatti, S. P., Carley, K. M. & Krackhardt, D. 2006a. On the robustness of centrality measures under conditions of imperfect data. *Social Networks*, **28**, 124–136.

Borgatti, S. P., Everett, M. G. & Freeman, L. C. 2006b. *Ucinet for Windows: Software for Social Network Analysis*. Harvard, Massachusetts: Analytic Technologies.

Brown, C. R. & Brown, M. B. 1996. *Coloniality in the Cliff Swallow: the Effect of Group Size on Social Behavior*. Chicago: University of Chicago Press.

Burt, R. S. 1988. The stability of American markets. *American Journal of Sociology*, **94**, 356–395.

Cartwright, D. & Harary, F. 1956. Structural balance: a generalization of Heider theory. *Psychological Review*, **63**, 277–293.

Cattell, V. 2001. Poor people, poor places, and poor health: the mediating role of social networks and social capital. *Social Science and Medicine*, **52**, 1501–1516.

Connor, R. C., Mann, J., Tyack, P. L. & Whitehead, H. 1998. Social evolution in toothed whales. *Trends in Ecology and Evolution*, **13**, 228–232.

Corner, L. A. L., Pfeiffer, D. U. & Morris, R. S. 2003. Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). *Preventive Veterinary Medicine*, **59**, 147–167.

Costenbader, E. & Valente, T. W. 2003. The stability of centrality measures when networks are sampled. *Social Networks*, **25**, 283–307.

Côté, I. M. & Poulin, R. 1995. Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology*, **6**, 159–165.

Croft, D. P., Krause, J. & James, R. 2004. Social networks in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B*, **271**, S516–S519.

Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D. & Krause, J. 2005. Assortative interactions and social networks in fish. *Oecologia*, **143**, 211–219.

Croft, D. P., James, R., Thomas, P. O. R., Hathaway, C., Mawdsley, D., Laland, K. N. & Krause, J. 2006. Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, **59**, 644–650.

Croft, D. P., James, R. & Krause, J. 2007. *Exploring Animal Social Networks*. Princeton, New Jersey: Princeton University Press.

Cross, P. C., Lloyd-Smith, J. O., Bowers, J. A., Hay, C. T., Hofmeyr, M. & Getz, W. M. 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Annales Zoologici Fennici*, **41**, 879–892.

Degenne, A. & Forsé, M. 1999. *Introducing Social Networks*. Thousand Oaks, California: Sage.

Dunbar, R. I. M. 1998. The social brain hypothesis. *Evolutionary Anthropology*, **6**, 178–190.

Eklöf, A. & Ebenman, B. 2006. Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, **75**, 239–246.

Faust, K. 2006. Comparing social networks: size, density, and local structure. *Metodološki zvezki*, **3**, 185–216.

Faust, K. & Skvoretz, J. 2002. Comparing networks across space and time, size and species. *Sociological Methodology*, **32**, 267–299.

Fekete, A., Vattay, G. & Kocarev, L. 2006. Traffic dynamics in scale-free networks. *Complexus*, **3**, 97–107.

Fewell, J. H. 2003. Social insect networks. *Science*, **301**, 1867–1870.

Flack, J. C., Krakauer, D. C. & de Waal, F. B. M. 2005. Robustness mechanisms in primate societies: a perturbation study. *Proceedings of the Royal Society of London, Series B*, **272**, 1091–1099.

Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. 2006. Policing stabilizes construction of social niches in primates. *Nature*, **439**, 426–429.

Freeman, L. C. 1979. Centrality in social networks: conceptual clarification. *Social Networks*, **1**, 215–239.

Freeman, W. J. 2005. A field-theoretic approach to understanding scale-free neocortical dynamics. *Biological Cybernetics*, **92**, 350–359.

Friedkin, N. E. 1991. Theoretical foundations for centrality measures. *American Journal of Sociology*, **96**, 1478–1504.

Friedman, S. R. & Aral, S. 2001. Social networks, risk-potential networks, health, and disease. *Journal of Urban Health: Bulletin of the New York Academy of Medicine*, **78**, 411–418.

Gladwell, M. 2000. *The Tipping Point: How Little Things Can Make a Big Difference*. New York: Little, Brown.

Granovetter, M. S. 1973. The strength of weak ties. *American Journal of Sociology*, **78**, 1360–1380.

Guare, J. 1990. *Six Degrees of Separation*. New York: Random House.

Guare, J. 1993. *Six Degrees of Separation*. Los Angeles: MGM/UA Home Entertainment.

Hanneman, R. & Riddle, M. 2005. *Introduction to Social Network Methods*. Riverside: University of California.

Hannon, B. 1973. Structure of ecosystems. *Journal of Theoretical Biology*, **41**, 535–546.

Harary, F. 1959. Status and contrastatus. *Sociometry*, **22**, 23–43.

Harary, F. 1961a. A structural analysis of the situation in the Middle East in 1956. *Journal of Conflict Resolution*, **5**, 167–178.

Harary, F. 1961b. Who eats whom? *General Systems*, **6**, 41–44.

Hinde, R. A. 1976. Interactions, relationships and social structure. *Man*, **11**, 1–17.

Hoogland, J. L. 1995. *The Black-tailed Prairie Dog: Social Life of a Burrowing Mammal*. Chicago: University of Chicago Press.

Jordán, F. & Scheuring, I. 2002. Searching for keystones in ecological networks. *Oikos*, **99**, 607–612.

Jordán, F., Liu, W.-C. & Davis, A. J. 2006. Topological keystone species: measures of positional importance in food webs. *Oikos*, **112**, 535–546.

Klovdahl, A. S., Potterat, J. J., Woodhouse, D. E., Muth, J. B., Muth, S. Q. & Darrow, W. W. 1994. Social networks and infectious disease: the Colorado Springs study. *Social Science and Medicine*, **38**, 79–88.

Kossinets, G. 2006. Effects of missing data in social networks. *Social Networks*, **28**, 247–268.

Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. New York: Oxford University Press.

Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E. & Taylor, W. W. 2003. Compartments revealed in food-web structure. *Nature*, **426**, 282–285.

Krebs, V. E. 2002. Mapping terrorist networks. *Connections*, **24**, 43–52.

Levine, J. H. 1972. The sphere of influence. *American Sociological Review*, **37**, 14–27.

Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology*, **83**, 195–207.

Liljeros, F., Edling, C. R. & Amaral, L. A. N. 2003. Sexual networks: implications for the transmission of sexually transmitted infections. *Microbes and Infection*, **5**, 189–196.

Luczkovich, J. J., Borgatti, S. P., Johnson, J. C. & Everett, M. G. 2003. Defining and measuring trophic role similarity in food webs using regular equivalence. *Journal of Theoretical Biology*, **220**, 303–321.

Lusseau, D. 2003. The emergent properties of a dolphin social network. *Proceedings of the Royal Society of London, Series B*, **270**, S186–S188.

Lusseau, D. & Newman, M. E. J. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London, Series B*, **271**, S477–S481.

Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., Barton, T. R. & Thompson, P. M. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, **75**, 14–24.

McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science*, **292**, 491–494.

McGregor, P. K. 2005. *Animal Communication Networks*. New York: Cambridge University Press.

McMahon, S. M., Miller, K. H. & Drake, J. 2001. Social science and ecology: networking tips for social scientists and ecologists. *Science*, **293**, 1604–1605.

Milgram, S. 1967. The small-world problem. *Psychology Today*, **1**, 61–67.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. 2002. Network motifs: simple building blocks of complex networks. *Science*, **298**, 824–827.

Nanayakkara, D. D. & Blumstein, D. T. 2003. Defining yellow-bellied marmot social groups using association indices. *Oecologia Montana*, **12**, 7–11.

Newman, M. E. J. 2003a. Ego-centered networks and the ripple effect. *Social Networks*, **25**, 83–95.

Newman, M. E. J. 2003b. The structure and function of complex networks. *SIAM Review*, **45**, 167–256.

Newman, M. E. J. 2004. Analysis of weighted networks. *Physical Review E*, **70**, article number 056131.

Newman, M. E. J. 2006. Modularity and community structure in networks. *Proceedings of the Indian National Academy of Sciences*, **103**, 8577–8582.

Newman, M. E. J. & Girvan, M. 2004. Finding and evaluating community structure in networks. *Physical Review E*, **69**, 026113.

Newman, M. E. J. & Park, J. 2003. Why social networks are different from other types of networks. *Physical Review E*, **68**, 036122.

Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology of Social Insects*. Princeton, New Jersey: Princeton University Press.

Pepper, J. W., Mitani, J. C. & Watts, D. P. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, **20**, 613.

Perry, S. & Manson, J. H. 2003. Traditions in monkeys. *Evolutionary Anthropology: Issues, News, and Reviews*, **12**, 71–81.

Proulx, S. R., Promislow, D. E. L. & Phillips, P. C. 2005. Network thinking in ecology and evolution. *Trends in Ecology and Evolution*, **20**, 345–353.

Rhodes, M., Wardell-Johnson, G. W., Rhodes, M. P. & Raymond, B. 2006. Applying network analysis to the conservation of habitat trees in urban environments: a case study from Brisbane, Australia. *Conservation Biology*, **20**, 861–870.

Sade, D. S. & Dow, M. 1994. Primate social networks. In: *Advances in Social Network Analysis: Research in the Social and Behavioral Sciences* (Ed. by S. Wasserman & J. Galaskiewicz), pp. 152–166. Thousand Oaks, California: Sage.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231–1234.

Solé, R. V. & Montoya, J. M. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London, Series B*, **268**, 2039–2045.

Strogatz, S. H. 2001. Exploring complex networks. *Nature*, **410**, 268–276.

Swan, J., Newell, S., Scarbrough, H. & Hislop, D. 1999. Knowledge management and innovation: networks and networking. *Journal of Knowledge Management*, **3**, 262–275.

Tarlow, E. & Blumstein, D. T. 2007. Evaluating methods to quantify anthropogenic stressors on animals. *Applied Animal Behaviour Science*, **102**, 429–451.

Uchino, B. N., Cacioppo, J. T. & Kiecolt-Glaser, J. K. 1996. The relationship between social support and physiological processes: a review with emphasis on underlying mechanisms and implications for health. *Psychological Bulletin*, **119**, 488–531.

Vasas, V. & Jordán, F. 2006. Topological keystone species in ecological interaction networks: considering link quality and non-trophic effects. *Ecological Modelling*, **196**, 365–378.

de Vries, H., Stevens, J. M. G. & Vervaecke, H. 2006. Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, **71**, 585–592.

Wasserman, S. & Faust, K. 1994. *Social Network Analysis: Methods and Applications*. New York: Cambridge University Press.

Watts, D. J. 1999. Networks, dynamics, and the small-world phenomenon. *American Journal of Sociology*, **105**, 493–527.

Watts, D. J. 2003. *Six Degrees: the Science of a Connected Age*. New York: W.W. Norton.

Watts, D. J. & Strogatz, S. H. 1998. Collective dynamics of ‘small-world’ networks. *Nature*, **393**, 440–442.

Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology*, **6**, 199–208.

Whitehead, H. 1997. Analysing animal social structure. *Animal Behaviour*, **53**, 1053–1067.

Whitehead, H. 1999. Testing association patterns of social animals. *Animal Behaviour*, **57**, F26–F29.

Whitehead, H. 2006. *Programs for the Analysis of Animal Social Structure (SOCPROG)*. Halifax, Nova Scotia: Dalhousie University. <http://myweb.dal.ca/hwhitehe/social.htm>.

Whitehead, H. 2008. *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago: University of Chicago Press.

Whitehead, H., Bejder, L. & Ottensmeyer, C. A. 2005. Testing association patterns; issues arising and extensions. *Animal Behaviour*, **69**, e1–e6.

Wilson, D. S. 1975. A theory of group selection. *Proceedings of the National Academy of Sciences, U.S.A.*, **72**, 143–146.

Wilson, D. S. & Dugatkin, L. A. 1997. Group selection and assortative interactions. *American Naturalist*, **149**, 336–351.