

REVIEW ARTICLE

How Can Social Network Analysis Improve the Study of Primate Behavior?

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When living in a group, individuals have to make trade-offs, and compromise, in order to balance the advantages and disadvantages of group life. Strategies that enable individuals to achieve this typically affect inter-individual interactions resulting in nonrandom associations. Studying the patterns of this assortativity using social network analyses can allow us to explore how individual behavior influences what happens at the group, or population level. Understanding the consequences of these interactions at multiple scales may allow us to better understand the fitness implications for individuals. Social network analyses offer the tools to achieve this. This special issue aims to highlight the benefits of social network analysis for the study of primate behaviour, assessing its suitability for analyzing individual social characteristics as well as group/population patterns. In this introduction to the special issue, we first introduce social network theory, then demonstrate with examples how social networks can influence individual and collective behaviors, and finally conclude with some outstanding questions for future primatological research. *Am. J. Primatol.* 73:703–719, 2011. © 2011 Wiley-Liss, Inc.

Key words: interaction; association; social system; social structure; methodology; behavioral sampling

INTRODUCTION

Many animal species live in groups. Commonly cited benefits to sociality include decreased predation risk through better detection of predators or “selfish herd” effects, and increased foraging efficiency through better acquisition and defense of food resources [Alexander, 1974; Hamilton, 1971; Wrangham, 1980]. Conversely, living in group generates competition where resources are limited in space or time [Janson & Goldsmith, 1995] that can result in increased rates of disease transmission through closer/more frequent contact among individuals [Freeland, 1976, 1979; Huffman & Chapman, 2009; Nunn et al., 2006]. Moreover, living in group can be difficult to maintain where individuals differ in their morphological–physiological state [Krause & Ruxton, 2002]. Thus, individuals face a trade-off and have to balance both the advantages and disadvantages of group life [Conradt & Roper, 2005].

Trade-offs associated with group living can emerge at the individual, group, or population level, and the costs and benefits associated with these trade-offs can be understood by scrutinizing the associations and interactions between individuals at each of these levels. In this review, we use “association” to describe a situation where two or more individuals share the same space at the same time,

and “interaction” to describe behavior directed from one individual to another (e.g. grooming). We use relationship when we wish to refer to either association, interaction, or both. In almost all social species, individuals are known to associate in a nonrandom way [honeybees *Apis mellifera*: Naug, 2009; guppies *Poecilia reticulata*: Morrell et al., 2008; Colombian ground squirrel *Spermophilus colombianus*: Manno, 2008; African elephants *Loxodonta Africana*: Wittemyer et al., 2005; bottlenose dolphins *Tursiops truncatus*: Lusseau, 2003; Japanese macaques *Macaca fuscata*: Koyama, 2003; yellow baboons *Papio cynocephalus*: Silk et al., 2004], resulting in unevenly distributed social interaction. This can lead to distinct patterns of subgrouping, and these subgroups can be nested within larger collectives at the group or population level.

Contract grant sponsors: Franco-American Commission; The Fyssen Foundation; The Japan Society for the Promotion of Science.

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Received 26 July 2010; revised 19 November 2010; revision accepted 20 November 2010

DOI 10.1002/ajp.20915

Published online 22 December 2010 in Wiley Online Library (wileyonlinelibrary.com).

Primates—the subjects of this review and this special issue—are known to display nonrandom associations and interactions. Studies of these relationships can help us to understand how ecological factors shape social behavior [Crook & Gartlan, 1966; Gray, 1987; Thierry et al., 2004; Wrangham, 1987], and ultimately, the evolution of sociality [Hinde, 1976; Krause & Ruxton, 2002; Whitehead, 2008]. Patterns of association can emerge as a result of individuals sharing identical or similar motivations (levels of hunger, thirst, or response to threat). Such assortativity can reduce some of the costs of sociality [Ramos-Fernandez et al., 2006; Ward et al., 2008], since group cohesion can be “easier” to achieve where individuals have fewer conflicts of interest [Conradt & Roper, 2000; King & Cowlishaw, 2009a]. However, in cases in which sociality results in asymmetric payoffs for individuals (where individuals are required to group to reduce predation risks [Hill & Lee, 1998], but experience competition over resources [Janson & Goldsmith, 1995], for example), repeated interactions that result in stable social bonds may buffer the effects of competition [de Waal, 1986]. Indeed, social interaction can have a profound influence on patterns of association [Sterck et al., 1997; Thierry et al., 2004; Wrangham, 1987]. In this context, variability in social structure can be understood in terms of an individual adapting to its social and ecological environment.

The problem is that traditional primate research focuses on local dyadic associations and interactions, and we have little knowledge of how these dyadic relationships scale to a more global social structure. In order to understand the complexity of a social structure, and link the behavior of individuals with the functioning and efficiency of the dynamic group-level properties [Camazine et al., 2003; Couzin & Krause, 2003], we need to consider and analyze all relationships linking all group members [Croft et al., 2005; Flack et al., 2006; Wey et al., 2008; Whitehead, 2008]. Only then can we begin to explore variation in individual fitness in the context of social behavior.

Analyzing all relationships linking all group members is not a new concept. Hinde [1976] defined the social structure of a group as composed by the nature, quality, and patterning of relationships of its group members, where the relationship between two individuals captures their repeated interactions over time. Nevertheless, most of the studies focusing on animal groups—especially primates—concern only the analyses of dyadic relationships, even though the context of these relationships extends beyond the dyad of just two individuals [Arnold & Barton, 2001; Kutsukake & Castles, 2004; Silk, 1999], and specific individuals (or specific relationships) can be the mainstay of a social structure [Flack et al., 2006; Whitehead, 2008]. For instance, if an old and/or dominant female in a primate system characterized by matrilineal relationships dies, the relationships

among all the remaining individuals may change dramatically, and the group may even permanently split as a result [e.g. Beisner et al., 2010; Koyama, 2003; Lefebvre et al., 2003]. Thus, to reiterate, relationships need to be studied in the context in which they evolve, i.e. the social group, and Social Network Analysis (SNA) offers a framework to do this.

SNA methodology originated from mathematical graph theory and was soon applied in the social sciences [see Newman, 2010; Scott, 2000, for a review]. Early researchers envisaged studying human social groups in a physics framework, studying people as if they were “atoms” and relationships between people as “social gravitation” [see Borgatti et al., 2009 for details]. Although this representation did not persist, even metaphorically, SNA remained an important tool in the social sciences, and is the basis of some extremely important concepts. For instance, the concept of “small worlds”—networks whose structure allows a connection between two random individuals in the network via only a few key individuals—has resulted in the famous expression of “six degrees of separation” [Watts, 2004]. More recently, the availability of large data sets that describes the interactions between hundreds of thousands or millions of components (e.g. communication networks from mobile phones, or the World Wide Web, or transport networks of roads or airports) have allowed common signatures to be identified. Specifically, many of these networks correspond to a “scale-free network,” where the distribution of the relationships per individual follows a power-law, and we discuss the implication of the scale-free distribution in primate systems later in this review.

In biology, SNA has contributed to our understanding of gene, protein, and cell relationships [Barabasi & Oltvai, 2004; Laughlin & Sejnowski, 2003], and in the past 10 years, this methodology has been increasingly applied to the study of animal behavior [Borgatti et al., 2002; Flack et al., 2006; Krause et al., 2009; Lusseau, 2003; Whitehead, 2008]. Although this approach is being used more and more by primatologists [Chepko-Sade & Sade, 1979; Flack et al., 2006; Voelkl & Kasper, 2009; Table I], studies applying SNA to explain social relationships (see Table II for a list of methodological papers) are still surprisingly rare.

Our aim is to highlight the benefits that can be gained from using SNA to study primates, and specifically primate behavior [Brent et al., 2011, provide a more detailed historical perspective on the use of SNA in primatology]. We deliberately base the structure of our review on that of previously successful reviews and books that explore the use of network approaches to study animal behavior [Croft et al., 2008; Wey et al., 2008; Whitehead, 2008], updating the information and tailoring our examples for a primatology audience. We also hope to

TABLE I. Examples of Studies on Social Networks in Primates

Study	Topic	Species	Edge attribute	Measures
Chepko-Sade and Sade [1979]	Patterns of group splitting	<i>Macaca mulatta</i>	Fission	Fission events, individual “connector”
Dow and de Waal [1989]	Analyzing network subgroup interactions	<i>Macaca arctoides</i>	Grooming, aggression	Compactness, isolation
Chepko-Sade et al. [1989]	Analyzing network of pre-fission group	<i>M. mulatta</i>	Grooming	Cluster analysis
Sade [1989]	Analyzing centrality in networks	<i>M. mulatta</i>	Grooming	Path length
Watts [2000]	Grooming reciprocity	<i>Pan troglodytes</i>	Grooming	Matrices correlations
Flack et al. [2006]	Policing and network stability	<i>Macaca nemestrina</i>	Grooming, play	Degree, clustering
Sueur and Petit [2008]	Organization during collective movements	<i>M. mulatta</i> , <i>Macaca tonkeana</i>	Proximity, following	Eigenvector, modularity, density
McCowan et al. [2008]	Detecting group instability	<i>M. mulatta</i>	Grooming, aggression	Degree, reciprocity
Voelkl and Noë [2008]	Propagation of social information	<i>M. mulatta</i>	Grooming	Path length, diffusion analysis
Henzi et al. [2009]	Cyclicity in social network	<i>Papio cynocephalus</i>	Grooming, proximity	Clustering
Ramos-Fernandez et al. [2009]	Analyzing associations patterns	<i>Atteles geoffroyi</i>	Proximity	Strength, eigenvector
Franz and Nunn [2009]	Detecting social learning	<i>Macaca fuscata</i>	Co-feeding	Diffusion analysis
Voelkl and Kasper [2009]	Emergence of cooperation	30 species	Grooming, proximity	Probability to cooperate
Kasper and Voelkl [2009]	Global analysis	30 species	Grooming, proximity	Several group and individual measures
Sueur et al. [2010]	Sub-grouping patterns during fission	<i>M. mulatta</i> , <i>M. tonkeana</i>	Proximity, sub-groups	Matrix correlation, multidimensional scaling

TABLE II. Examples of Methodological Publications on Social Network Analysis

Study	Topics
Cairns and Schwager [1987]	Comparing associations indices
Whitehead [1997]	Analyzing animal social structure
Bejder et al. [1998]	Testing associations patterns
Girvan and Newman [2002]	Properties of community structure
Lusseau and Newman [2004]	Individual role in network
DeJordy et al. [2007]	Visualizing proximity data
Lusseau et al. [2009]	Incorporating uncertainty in social network analysis

emphasize how SNA methodology can be applied to analyze both individual social characteristics and group/population patterns.

BUILDING SOCIAL NETWORKS

The Social Network Framework

An adjacency matrix or *sociomatrix* (Table III) is classically the most suitable representation of social association or interaction data, long used by primatologists [for recent examples see: Silk et al., 2002a,b; Sueur & Petit, 2008; Thierry et al., 2004].

TABLE III. Binary Matrix of Relationships Between Individuals *a* to *s*

	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	<i>i</i>	<i>j</i>	<i>k</i>	<i>l</i>	<i>m</i>	<i>n</i>	<i>o</i>	<i>p</i>	<i>q</i>	<i>r</i>	<i>s</i>
<i>a</i>		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>b</i>	1		1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>c</i>	0	1		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>d</i>	0	1	0		1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>e</i>	0	0	1	1		1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>f</i>	0	0	1	1	1		1	1	0	0	0	0	0	0	0	0	0	0	0
<i>g</i>	0	0	0	0	1	1		1	0	1	0	0	0	0	0	0	0	0	0
<i>h</i>	0	0	0	0	0	1	1		1	0	0	0	0	0	0	0	0	0	0
<i>i</i>	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	0
<i>j</i>	0	0	0	0	0	0	1	0	0		1	0	1	1	0	0	0	0	0
<i>k</i>	0	0	0	0	0	0	0	0	0	1		0	0	1	1	0	0	0	0
<i>l</i>	0	0	0	0	0	0	0	0	0	0	0		0	0	1	0	0	0	0
<i>m</i>	0	0	0	0	0	0	0	0	0	1	0	0		1	0	0	0	0	0
<i>n</i>	0	0	0	0	0	0	0	0	0	1	1	0	1		1	1	1	1	0
<i>o</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	1		1	1	0	0
<i>p</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1		1	0	0
<i>q</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1		1	1
<i>r</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1		1
<i>s</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	

The network (graph shown in Fig. 1) is unweighted: either individuals are connected (value of relationships is 1), or they are not connected (value of relationships is 0).

The adjacency matrix is also the basis for SNA. A matrix contains rows and columns defining specific individuals, subgroups of individuals, groups of a

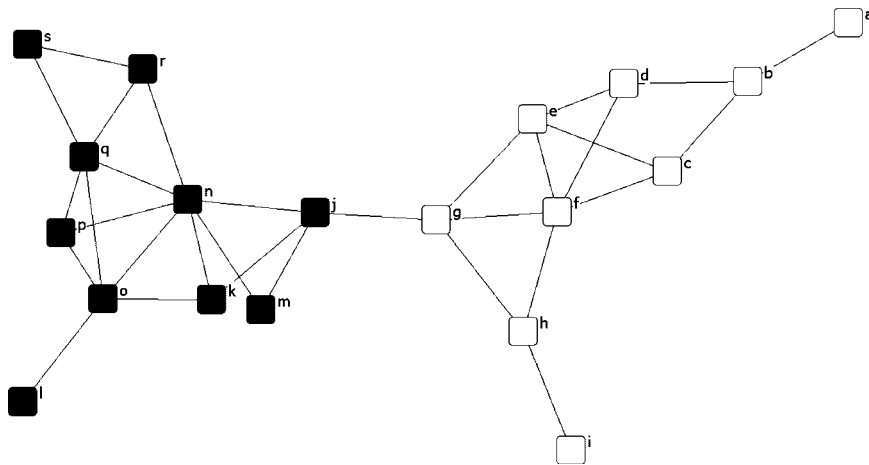


Fig. 1. Graphical representation of a theoretical social network. A node represents a group member. Nodes of same color belong to the same subgroup. An edge (line) represents the relationship between two individuals. This social network corresponds to the social structure of a group of 19 individuals (labeled from *a* to *s*: see Table III for the sociomatrix corresponding to this graph). Individual network measures are presented in Table IV.

same species or populations, or different species, which are commonly referred as actors. The data contained within the matrix describes relationships between these actors. Graph theory represents these actors (called *vertices* or *nodes*) and the relationships between them (called *edges*) and represents them as a network (Fig. 1). Attributes such as age, sex, size, hierarchical rank, species, or even categories such as “predator” or “prey” can also be assigned to the nodes in a network. For instance, black nodes in Figure 1 might represent males and white ones females, or nodes of the same color might belong to the same matriline, thus providing a visual representation of how sex or kinship influences social structure. The ties between the nodes—the edges—can be “positive,” “negative” (e.g. affiliative or aggressive behavior respectively in the case of individuals), or represent disease transmission or information flow. This framework is therefore extremely flexible, and can be used to address a variety of questions concerning sociality in primates (Tables I and II). We will now describe how networks can be constructed and analyzed from matrix data, and what software is available to do this.

Global Network Properties

In an “undirected network,” edges only show that two nodes are connected (Fig. 2A). Indeed, as shown in Table III and Figure 1, relationships between nodes of an undirected network are only represented by binary values, 1 for connected nodes, 0 for non connected nodes, and the network is therefore symmetrical. In a “directed network,” an edge is oriented from an emitter node to a receptor node, and the matrix is therefore unsymmetrical (Fig. 2B). Whether a network is directed or undirected, it is largely a consequence of the type of edges (associations or interactions) represented,

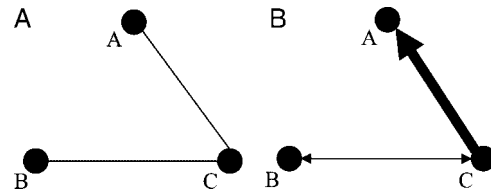


Fig. 2. Graphical representation of (A) an undirected and unweighted three-node network, and (B) a directed and weighted three-node network. (B) Gives information about the direction and the strength of interactions between individuals, while (A) does not.

and Figure 2B provides an example of both directed and undirected networks. The relationship between individuals B and C in Figure 2B is symmetrical since the frequency of behavior directed from B toward C is equivalent to those from C toward B. This is typical of association data where an observer will score the occasions individuals B and C were together at some defined spatial-temporal criterion. However, the relationship between A and C in Figure 2B is asymmetrical since only C emits behaviors toward A. This asymmetry is more typical of interaction data where one individual tends to direct behavior toward another (e.g. aggression).

Networks can also be “unweighted” or “weighted.” In an unweighted network (Figs. 1 and 3A), each edge is assigned a binary value: 0 if there is no relationship (and then no edge) and 1 when two nodes have a relationship (whatever the strength of relationship between these two individuals). However, where the frequency and/or duration of interactions can be recorded, the networks built from these interactions are weighted (Fig. 3B). When constructing weighted networks, a normalized value is often used, since this allows researchers to more easily compare the relative strength of interaction across nodes. Otherwise, a filter is applied to a

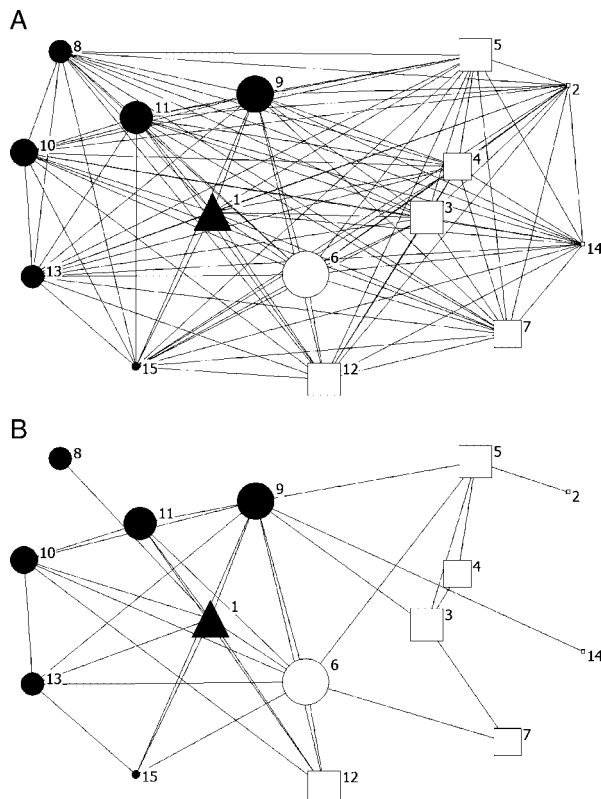


Fig. 3. Networks of leader-follower associations during collective movements for a group of rhesus macaques [see Sueur & Petit, 2008, for details]: (A) all relationships are represented (weighted networks); (B) only preferred relationships are represented (unweighted networks). Preferred relationships were obtained using the avoided/preferred associations test in SOCPROG [Whitehead, 2008, 2009]. Network graphs were drawn using Netdraw in UCINET 6.0 [Borgatti et al., 2002]. Nodes represent individuals. The number represents the hierarchical rank of the individual. Distance between individuals represents the Half Weight Index (HWI: the more closely associated two individuals are, the more frequently they associated they are during collective movements) and the graph was drawn using multi-dimensional scaling [Borgatti et al., 2002; Whitehead, 2008, 2009]. Similar shapes characterize individuals having the same matriline and identical colors define individuals belonging to the same subgroup during collective movements, which was defined by the modularity clustering method [Newman, 2004; Whitehead, 2008, 2009]. The size of a node is directly related to the individual eigenvector centrality coefficient (the higher the centrality coefficient is, the greater the influence of the individual in the joining of group members is, that is, central individuals are more often followed).

weighted network to categorize associations, which is especially useful when a network is “full mesh” i.e. all nodes are interconnected. This filter is most often applied to generate “above average” and “below average” relationships (but can be set at any level), and thus reduce the network to different clusters or (sub)groups of nodes of different relationship strength [Franks et al., 2010]. Presenting spatial information in this way can be extremely informative where researchers are interested in relational data for animal systems that display high fission–fusion dynamics [Aureli et al., 2008], and we discuss how to apply a filter in our next section.

Software to Build Networks

Software used to undertake SNA are SOCPROG [Whitehead, 2009] (<http://myweb.dal.ca/hwhitehe/social.htm>), Ucinet [Borgatti et al., 2002] (<http://www.analytictech.com/ucinet/>), or Pajek [De Nooy et al., 2005] (<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>). Each of these tools allows calculation of SNA statistics (discussed below) and visualization of networks. Matman [de Vries et al., 1993] (<http://www.noldus.com/animal-behavior-research/products/matman>) is also a useful piece of software for matrix analyses, and while it does not allow the calculation of individual network statistics, it is useful to compare matrices or to test reciprocity of interactions.

When presented with a weighted network, as described above, Whitehead’s SOCPROG [2008, 2009] makes it possible to test for preferred/avoided associations (i.e. relationships) between individuals and also the opportunity to apply a filter to the network to transform the weighted network (Fig. 3A) into unweighted (i.e. 0–1) network (Fig. 3B). The level of preferred relationships (i.e. the filter) can be set either at a normal significant value ($\alpha = 0.05$) or at a value where all individuals are directly or indirectly connected. In each case, SOCPROG generates random matrices and assesses whether the value of an association in the observed matrix is higher than the generated association in the random matrices (in 95% of cases, for instance if $\alpha = 0.05$). If the observed association is significant, it is named as preferred association.

NETWORK STATISTICS

Measuring Attributes and Roles of Individuals

Although primatologists have long been interested in the “roles” that certain individuals have in a social context, e.g. measuring agonistic interactions, and assessing dominance rank [Aureli & de Waal, 2000; Chepko-Sade et al., 1989; Schino, 2001], we are now in a position to rigorously quantify and describe these roles using SNA. Brent et al. [2011] provide a discussion of the similarities and differences between traditional and modern methods of SNA, and there are now multitudes of statistics that represent an individual “influence” upon a network. The simplest of these is the *node degree* [Newman, 2003]. The node degree is a statistic that describes the number of edges (relationships) that a node (an actor) is involved in whatever the edges’ values (see Table IV for degree of each node represented in Fig. 1). For directed networks representing asymmetrical relationships, one can distinguish between the *in-degree* (the number of edges for which the node is the receptor) and the *out-degree* (the number of edges for which the node is the emitter). This distinction may be important when studying the reciprocity of interactions such as grooming or aggression where

TABLE IV. Individual Measures of Nodes of Figure 1

Node/individual	Degree	Strength*	Betweenness	Eigenvector	Clustering coefficient
<i>a</i>	1	1	0	0	–
<i>b</i>	3	3	17.5	0.02	0
<i>c</i>	3	3	19.667	0.04	0.33
<i>d</i>	3	3	10.333	0.04	0.33
<i>e</i>	4	4	12.833	0.06	0.5
<i>f</i>	5	5	41.667	0.07	0.4
<i>g</i>	4	4	81	0.11	0.33
<i>h</i>	3	3	17	0.05	0.33
<i>i</i>	1	1	0	0.01	–
<i>j</i>	4	4	81.833	0.27	0.33
<i>k</i>	3	3	16.5	0.29	0.67
<i>l</i>	1	1	0	0.1	–
<i>m</i>	2	2	8.333	0.19	1
<i>n</i>	7	7	46.333	0.51	0.33
<i>o</i>	5	5	6.667	0.39	0.4
<i>p</i>	3	3	0	0.32	1
<i>q</i>	5	5	8	0.4	0.5
<i>r</i>	3	3	9.333	0.26	0.67
<i>s</i>	2	2	0	0.16	1

*Note that since the network shown in Figure 1 is unweighted, strength is equal to the node degree.

nodes represent individuals. Another simple measure taking into account the edges' values is the *strength*, which is the sum of a node's edges' values (see Table IV for strength of each node represented in Fig. 1). For unweighted networks, the number of edges a node possesses can be used as an indication of node strength.

Although node degree and strength take into account the relationships of a node with its direct neighbors, other indices allow computation of the impact of a single node on the overall network structure. For instance, the node *n* in Figure 1 might be considered as the most central one because it is linked to many other nodes (and thus has got high score for the *node degree* measure, see above). The most central node can also be considered to be *j*, or *g*, as a consequence of their relative importance in the global structure of the network: even though these nodes (*j* and *g*) have a smaller node degree than *n*, the network would split into two subgroups if either was removed.

“Centrality” is another concept of node importance. There are a number of different statistics that allow the calculation of individual centralities, which have different meanings and purpose. According to the kind of data collected and to the network structure, the different measures of centralities might be correlated or not. Thus, researchers should consider their choice of centrality coefficient carefully, and choose according to the scoring methods used and the questions in hand. Two common statistics are the *betweenness centrality coefficient*, defined as the number of shortest paths that pass through the considered individual (with the *shortest*

path being the shortest distance, i.e. number of edges, between two nodes), and the *eigenvector centrality coefficient* [Newman, 2004]. The eigenvector centrality coefficient represents the connectivity of an individual within its network according to the number and strength of connections and considering the centrality of the individuals it is connected to [see Whitehead, 2008 for details about the calculation of this index]. Both coefficients can be extremely informative, and we discuss them in turn with illustrative examples.

The *betweenness centrality coefficient*, or “betweenness,” can be important to measure whether the edges in the network represent some active transfer of information, or the transmission of a disease, thus identifying nodes that play a key role in diffusion process. Following this definition, the removal of the most central individuals, in term of the highest betweenness, quickly results in a disconnection of the network into several disconnected parts. However, the consequences of such a removal will depend on the inter-individual betweenness. Indeed, if the differences in *betweenness* are weak (low variance between individuals), the removal of central individuals will have little impact on network structure. In contrast, if the variance of betweenness is large (typical scale-free networks, where the distribution of betweenness coefficients follows a power-law, i.e. one or two individuals are very central compared to their conspecifics), then removing one individual can have a substantial impact on the network structure. For example, one might expect that the removal of the central individual in a tolerant, egalitarian species (such as

Tonkean macaques, *Macaca tonkeana* or other Sulawesi macaques) where all individuals are connected together will not have the same impact as the removal of the central individual in a despotic species (such as rhesus macaques, *M. mulatta* or Japanese macaques, *M. fuscata*) where kinship and dominance highly constrain relationships [Thierry et al., 2004]. We illustrate this point in Figure 1, where the shortest path between the individuals *a* and *s* is 8 while the shortest path between *j* and *g* is 1. Nodes (i.e. individuals) having the most important betweenness coefficient are *j* and *g* (see Table IV for betweenness coefficient of each node represented in Fig. 1).

Lusseau and Newman [2004] used the betweenness centrality coefficient to determine the centrality of individuals in a bottlenose dolphin population. They found that some individuals had significantly higher betweenness coefficients than others. These central individuals were suggested to be linking subgroups in this highly dynamic fission–fusion system, and acting as “brokers” who mediated fusion in the population. Centrality can then be linked to other individual traits. In the case of the dolphins, Lusseau and Conradt [2009] showed that central individuals appear to have a greater knowledge about their environment, and as a consequence precipitate shifts in behavior of their conspecifics. This study raises the intriguing possibility that for certain animal systems (like those that show high fission–fusion dynamics), greater knowledge, or innovation may be inferred from the centrality of an individual in its social network. Since individuals can improve their performance with experience, i.e. better information [Corning & Lahue, 1972; Schneirla, 1943; Thorpe, 1963], it will be interesting to explore the directionality of such correlation in future. That is, are individuals central because they possess knowledge, or they are knowledgeable because they are central in the network, a position which they may have acquired through some other process?

The *eigenvector centrality coefficient* is another measure of centrality. Individuals will score highly on the eigenvector centrality coefficient either if they are highly connected to other network members or if they are connected to individuals who are highly connected themselves (see Table IV for eigenvector coefficient of each node represented in Fig. 1). This coefficient ranges from 0 (least central) to 1 (most central), and unlike the betweenness coefficient takes into account edges' direction and value. Therefore, it is a useful index to determine an individual's centrality within weighted networks [Bonacich, 2007], and to provide a useful tool to assess an individual's “influence” in a network. We provide three examples here, concerning group coordination, group cohesion, and grooming interaction.

First, in the case of group coordination, Sueur and Petit [2008] and Sueur et al. [2009] studied

collective movement in rhesus macaques (Fig. 3) and Tonkean macaques. They created matrices describing the frequency with which individuals followed one another when moving after a resting period. Calculating an eigenvector centrality coefficient for the resulting networks, they found that in both species, some individuals were more central than others, and thus had a disproportionate influence on group coordination. Specifically, when these central individuals departed, whatever their position in the movement (i.e. first to leave, first to follow, second to follow, etc.), they were joined by a great number of individuals. Sueur and Petit [2008] labeled these “determinant individuals” and found that they were dominants or individuals linking different matrilineal lines in rhesus macaques (Fig. 3), and the most affiliated individuals in Tonkean macaques. These differences could be attributed to differences in each species' respective social systems [see Sueur and Petit, 2008; Sueur et al., 2009, for a discussion].

Second, in the case of group cohesion, Ramos-Fernandez et al. [2009] used the same eigenvector centrality coefficient to understand the spatial association of spider monkeys (*Ateles geoffroyi*). They not only showed that females had a higher eigenvector than males, but also reported that young adult males played the role of “brokers” between the female and the male clusters, similar to that seen in a dolphin population [Lusseau & Newman, 2004].

Finally, in the case of grooming, eigenvector centrality can also be informative, especially where two individuals have both the same number and strength of grooming relations. Two such individuals would not necessarily have the same eigenvector centrality, and Kanngiesser et al. in this issue provide an example of this in a captive chimpanzee (*Pan troglodytes*) community. They found that two subjects had the same number of grooming interactions, but found that one scored much higher in their eigenvector centrality. It turned out that the high scoring individual was the alpha male, who was connected to individuals who were themselves highly connected, unlike his lower ranked group-mate.

Between the Individual and the Group Level: Searching for Cliquishness

In our discussion of individual measures (above), we have presented several examples where an individual's centrality was related to their ability to “mediate” or “join” two subgroups, and where groups divide into subgroups of individuals sharing a similar characteristics [Aureli et al., 2008; Sueur et al., 2010]. In primates, it is well known that sex, age, or kinship influence subgrouping patterns of individuals (see Fig. 1). Individuals of same age or same sex, for instance, may interact more frequently and groups may show higher levels of synchrony of activity where individual interests converge as a

result of similar energetic or reproductive state [King & Cowlishaw, 2009b]. This specific clustering is expected to increase individual fitness [Conradt & Roper, 2000; Krause & Ruxton, 2002]. Nevertheless, while some individual/centrality measures allow us to identify subgrouping, more specific tools have been developed to assess how a group is clustered (i.e. the *cliquishness* of the group).

One such statistic is the clustering coefficient [Newman, 2003]. This measures the amount which a node tends to cluster with other nodes, and captures the level of cohesion of the network (see Table IV for clustering coefficient of nodes in Fig. 1). Specifically, if individuals connected to the focal subject of interest are fully connected to all other individuals, the clustering coefficient will be equal to 1; if no individual is connected with another, the clustering coefficient will equal to 0 [Whitehead, 2008]. This local clustering coefficient has the potential for broad application in primatology. For example, in a pioneering network study, Flack et al. [2006] studied the policing and group stability in pig-tailed macaques (*M. nemestrina*) using such an indicator. They identified specific individuals with a high clustering coefficient and, using experimental and theoretical knockout, removed these individuals from the group. As a consequence of the removal, the aggressive interactions between the remaining group members were more frequent and grooming interactions were less frequent, and less diverse, than before the removal. The authors therefore concluded that the individuals with a high clustering coefficient were important in conflict management and group stability. We can illustrate this with one of our example networks: if we remove individuals 9 and 6 from the network displayed in Figure 3B, the network divides into two subgroups. Thus, the higher the clustering coefficient of an individual, the higher the probability that the group splits after this individual is removed. This may be particularly important for the management of captive primate populations, where individuals and same age cohorts are moved between zoological collections.

Another method to identify subgroups within a network is to compare observed relationships of individuals to an expected or theoretical probability that these individuals would be connected. The *modularity method* developed by Newman [2004] for community detection on a network uses this type of calculation and can be found in SOCPROG [Whitehead, 2009]. Sueur and Petit [2008] used this modularity method to identify subgroups of rhesus macaques during collective movement, and found that rhesus macaques were associated according to kinship during collective movements (Fig. 3A).

We should also mention at this point that when producing network graphs or diagrams, it is also possible to infer something about patterns of subgrouping in a network, before calculating any

network statistics. In Figure 3A and B, individuals are positioned in the graph according to their associations using the *multidimensional scaling* method. This method plots individuals with strong relationships close to one another in the network space [see Whitehead, 2008, 2009 for details about calculation].

A more quantitative approach that allows visualization of sub-grouping is *Hierarchical cluster analysis*. Using this method, one can obtain a dendrogram with individuals on one axis and the degree of associations between these individuals on the other axis (Fig. 4A). Chepko-Sade et al. [1989] applied this methodology to study and visualize the distribution of grooming interactions in a group of rhesus macaques. Coupled with the modularity method (see Fig. 4B) and the knot diagram (see Fig. 4C), cluster analysis enables researchers to assess the amount of subdivision or “communities” that exist in a network. Subgrouping patterns of African elephants, known for their high degree of fission-fusion, offer a classic example. Wittemyer et al. [2005] were able to show that their elephant population was multitiered with different subgroups and different strength of relationship, and that these network properties were influenced by ecological constraints; with more frequent fission with increased ecological pressures.

Subgrouping patterns can also be identifiable at a much smaller scale (than population level). Chimpanzees, like elephants, show a fission–fusion structure and Clark [2011] showed distinct subgrouping in the affiliative network of captive chimpanzees, and these subgrouping patterns were aligned with maternal kinship. As default, clusters are defined at 95% (i.e. significance), but it may be appropriate to set two individuals as belonging to the same cluster when they spend at least 50% of their respective time together, or when they spend time together above the population mean, depending on the rationale for using cluster analyses. For example, the choice of cluster thresholds is particularly important where researchers are interested in the spread of disease or of information in a network, and Godfrey et al. [2009] found that higher levels of connectivity between individuals increased the risk of parasite infection in a lizard population (*Egernia stokesii*).

Another intermediate analysis using a social networking approach would be to assess whether the interactions between individuals are symmetrical or asymmetrical. We decided to introduce this symmetry measure in this section, because symmetry of relationships is not an attribute of individuals or of a group. Rather, it is a more specific measure of overall relationships. Symmetry of relationships can, by definition, only be carried out on directed networks (i.e. actor and receiver interactions, such as grooming, or unidirectional aggression) but not on undirected networks (e.g. simple associations defined

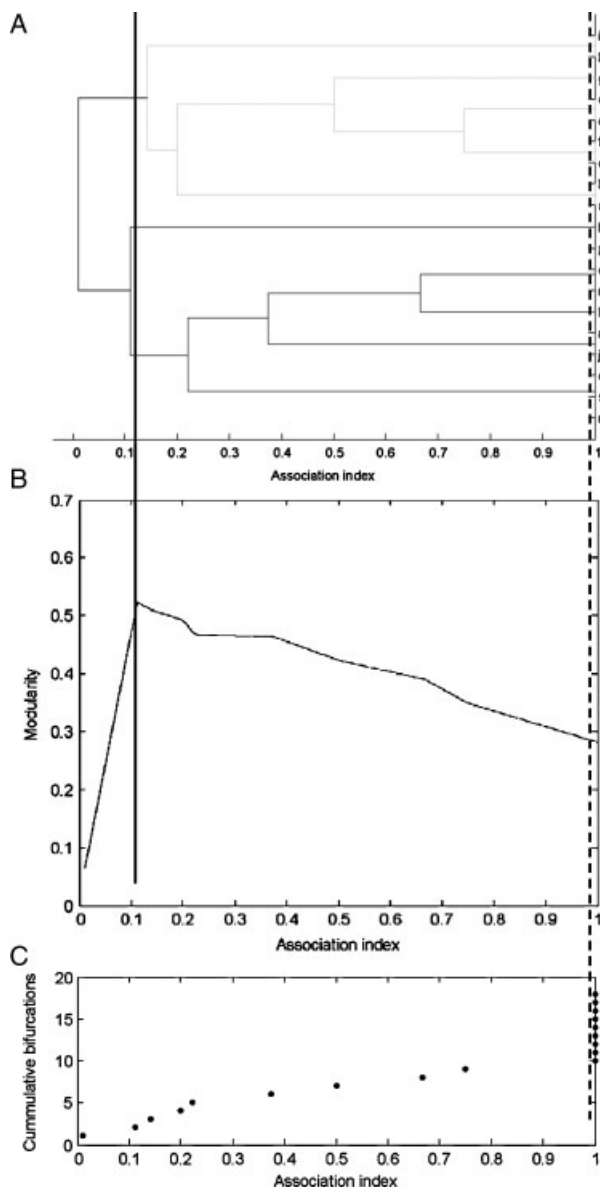


Fig. 4. Hierarchical cluster analysis of associations of the theoretical group in Figure 1. (A) Dendrogram of associations [average linkage, cophenetic correlation coefficient: 0.71, see Croft et al., 2008; Whitehead, 2008, 2009 for details about calculation]; gray lines suggest one subgroup, black lines suggest the other one. (B) Modularity of the dendrogram suggesting a division into clusters with an association index of 0.11 (solid line). (C) Knot diagram giving the cumulative number of bifurcations at different bifurcation distances and suggesting a knot at an association index at 1 (dashed line, direct associations for this case). A knot is a level of association such that the rate of cluster formation suddenly changes with the association index.

by contacts or proximities). Tests of symmetry will also advance the outstanding question of the function of grooming relationships, and whether individuals groom an individual in return for grooming, or for other commodities, e.g. tolerance at feeding sites or coalition support [Dufour et al., 2009; Fruteau et al., 2009; Kanngiesser et al., 2011; Pelé et al., 2010]. In this way, the term “symmetrical” can be replaced

by the term “reciprocal” [Hemelrijk, 1990; Whitehead, 2008]. Tests of symmetry normally compare one-half matrix (emitter to receptor for instance) to the other one (receptor to emitter) but can also compare data collected to random matrices. This comparison with random networks was introduced by Hemelrijk [1990] and are variants of the Mantel test (parametrical) or the Kendall test (nonparametrical). These tests use randomization and a predefined amount of permutations (e.g. 1,000) allowing the calculation of accurate and stable *P*-values [Hemelrijk, 1990; Lusseau et al., 2009; Vries et al., 1993; Whitehead, 2008].

Symmetry tests (or more precisely the intensity of asymmetry) are often a reflection of social system properties. We know for instance that in despotic species, agonistic interactions will be more asymmetric than in tolerant species [Thierry et al., 2004]. Asymmetry in a system is however not limited to agonistic interaction. Sueur and Petit [2008] assessed the symmetry of leader–follower interactions in rhesus and Tonkean macaques when studying the process of collective movements, as mentioned earlier. They found that in the egalitarian Tonkean macaque, leader–follower interactions (i.e. the frequency with which individual A followed individual B and vice versa) was symmetrical, whereas in the despotic and nepotistic rhesus macaque, these interactions were asymmetrical: among adults subordinate individuals more often followed dominant individuals, and juveniles followed their mothers.

Group Structure Properties

Group measures concern the overall group structure, and are especially useful for questions about group cohesion. Average, maximum, or variance values of individual measures also provide useful information on group-level properties, and we begin our group structure section with a discussion of these. For instance, we can calculate the *mean clustering coefficient* (i.e. a global clustering coefficient) or the *mean node degree*, that each give an indication of how individuals are connected and consequently a group’s cohesion or stability. For instance, if the mean clustering coefficient for a group network is high, then the group may be unstable because the removal or the death of specific individuals can lead to the group splitting. In contrast, low clustering coefficients (and then a high robustness of the social network because individuals are all similarly connected) can result in stability in the network, and facilitate the transmission of information of disease. For example, Naug [2009] showed that a low clustering coefficient was correlated to the transmission of disease in a honeybee colony.

The cumulative distribution of these group measures, and specifically the mean node degree,

also provide an indication of whether a network is random (linear distribution) or scale-free (power distribution). In bottlenose dolphins and in Columbian ground squirrels (*Spermophilus columbianus*), exploration of cumulative distributions suggested that both species have social structures more like scale-free than random networks [Lusseau, 2003; Manno, 2008, respectively]. Earlier in this review (*Measuring Attributes and Roles of Individuals*, above), we discussed how variance in betweenness may have implications for the stability of the network. In a scale-free network, if an individual with a high betweenness dies, then the network may be likely to split, because such individuals play the role of intermediary between other network members.

Two simpler and more commonly applied statistics to measure group cohesion are *group density* and *diameter*. The group density is defined as the number of observed edges divided by the number of possible edges in the network. For instance, the group density of the network in Figure 1 is 0.18 (31 observed edges divided by $(n^2 - n)/2$ possible ones). Thus, the higher the density, the more cohesive and stable the group. The *diameter* is defined as the longest path length in the network and is also a good measure of the group cohesion [Wasserman & Faust, 1994]. The lower the diameter is, the higher the group cohesion is and then the higher the transmission of information and/or of disease between two individuals would be. For instance, the diameter of the network in Figure 1 is 8 (i.e. the number of edges between the individual *a* and the individual *l* or between the individual *a* and the individual *s*). A low diameter—high cohesion—may be due to social structure constraints [Thierry et al., 2004] or because individuals that share similar characteristics (e.g. nutritional needs) tend to cluster together in time and space [Krause & Ruxton, 2002; Ramos-Fernandez et al., 2006]. The calculation of density and diameter is however currently suitable only for unweighted networks, and methods to calculate these two statistics for weighted networks are still under development [Wasserman & Faust, 1994; Whitehead, 2008]. One solution is to transform weighted networks to unweighted networks (using the preferential/avoided associations test in SOCPROG [Whitehead, 2008, 2009], Fig. 3).

COMPARING NETWORKS

An underdeveloped application of SNA is the comparison of a single network, different networks (groups) of a same species, or different species of a same genus through time. Comparing matrices in this way is not a new method, but the manner in which data are represented for network analyses lends itself to matrix correlations and thus comprise an important part of the modern SNA toolkit (see Brent et al. [2011] for a discussion on this point). These tests can be carried out in Matman software

[de Vries et al., 1993] or SOCPROG [Whitehead, 2008, 2009], and are used to correlate matrices within and across groups.

Comparing Different Relationship Matrices Within a Group

This special issue provides a number of examples of comparing different kinds of relationships or interactions within a group. The first concerns social foraging. King et al. [2011] compared co-feeding networks (i.e. occasions where individual A is seen foraging in a food patch with individual B), to grooming and kinship networks in wild chacma baboons (*Papio ursinus*), while controlling for dominance relationships. They found that co-feeding was significantly correlated to grooming relationships, but not to relatedness among individuals, and suggest that this may be a result of grooming relationships affording tolerance in competitive foraging situations. The other two examples in the special issue concern captive chimpanzees. Composite indices are often used as a proxy for the strength of social relationships in primates [Silk et al., 2006a,b], and Clark [2011] shows that the grooming network of a captive chimpanzee community was positively correlated with the association network, whereas Kanngiesser et al.'s [2011] study found that grooming networks were correlated to both age and kinship.

Comparing Individual Centralities of Different Relationships Within a Group

Individual measures (discussed above) for different interaction types can also be used to explore similarities in the properties of the network at a group level. For instance, the eigenvector centrality coefficient can be calculated for two types of interactions (e.g. grooming and third party support in aggressive interactions). Then, the different eigenvector coefficient for each type of interactions can be compared in order to assess whether the most central individual for grooming interactions is also the most central one for support during conflicts. This can provide insight into the selection pressures that individuals face, and Sih et al. [2009] used a correlation of “degrees” (see *Measuring attributes and roles of individuals*, above) between males and females for mating and found that males mating with many females tend not to mate with females who themselves mate with a lot of other males. Such a pattern would be extremely difficult to uncover by any other methodological approach.

Comparing Relationship Matrices Over Time

Individual relationships can also be explored over time: during seasons, over years, or before and after specific events, e.g. the death of an individual or the replacement of an alpha individual. Studies of

nonprimates again offer insight of how useful this approach can be for the study of primate behavior. Wittemyer et al. [2005] studied an African elephant population during a 4-year period and observed that the high-order social units (metagroup) changed over time, according to the ecological constraints. In the same way, Hansen et al. [2009] used SNA to study changes in social interaction of river otters (*Lontra canadensis*) captured and held in captivity for 10 months; they found that the strength of social interactions declined over time. However, such analyses are currently restricted to the comparison of two static networks at different “snapshots” in time and very few indicators currently exist to characterize the dynamics of social networks at multiple time points (or continuously) over a given period [Lahiri & Berger-Wolf, 2008; Tantipathananandh & Berger-Wolf, 2009].

Comparing Relationship Matrices of Different Groups

Comparing group networks from the same species in different environmental conditions, or for different group sizes can form the basis of comparative studies. For instance, Sueur et al. [2010] compared subgrouping patterns after short-term fissions between Tonkean and rhesus macaques and showed that rhesus macaques had higher fission–fusion dynamics [Aureli et al., 2008] than Tonkean macaques. Comparisons of the densities or the diameters of two different groups (see *Group structure properties*, above) would also provide an indication of both network cohesion and indication of individual network members level of tolerance or propensity to cooperate [Anderson, 2007; Aviles, 1999; de Waal & Luttrell, 1989; Thierry et al., 2004]. This approach would clearly be useful for researchers interested in cooperation (e.g. grooming, support during conflicts, vigilance). Networks of observed groups may also be compared with networks of artificial groups in which all parameters are fixed and known. This comparison can help to understand mechanisms underlying some social or collective phenomenon [Sueur et al., 2009; Voelkl & Noë, 2008]. Adopting this approach, Franz and Nunn [2009] studied how social learning opportunities can be affected by the group social structure.

Basic descriptive network measures, such as the average, variance, or distribution of interactions can also be compared in order to assess the importance and diversity of the interactions in one group relative to another. Even if the size or the sampling period differs between groups, indices of individuals (centrality statistics) or indices about the group (density, mean path length) can be comparable using SNA (to a certain extent). For instance, Faust and Skvoretz [2002] compared 42 networks from diverse species and contexts. When comparing

networks, however, we have to be careful to compare data on relationships collected/calculated in a similar manner [Cairns & Schwager, 1987; Whitehead, 2008, 2009]. Hopefully, as more and more SNA studies are carried out, a common methodology will emerge based on the success of previous investigations and early comparisons of these data [Franks et al., 2009; James et al., 2009; Whitehead, 2008].

PERSPECTIVES AND FUTURE RESEARCHES

We have outlined the SNA toolkit available to primatologists and presented some examples of how these can be applied at many levels (individual, group, and population) of social behavior. In this section, we identify five key research questions that we believe are ripe for exploitation and hope that our discussion of these issues will act as a springboard for future primate social network research.

What is a Social Group?

Primates are commonly described as living in stable groups since many live all their lives in the same social group and maintain stable and long-term relationships with conspecifics [Kummer, 1971; Thierry et al., 2004; Wrangham, 1987]. This level of stability in sociality differs to that of many other gregarious species, such as shoals of fishes or flocks of birds. The composition of such ephemeral aggregations may change by the minute, hour, or day, and individuals may not have opportunity to develop and maintain stable relationships [Couzin & Krause, 2003]. Primatologists therefore define a group according to when individuals in proximity to one another tend to interact in a positive (e.g. affiliative) rather than negative (e.g. agonistic) manner, as well as their activities being somehow synchronized in time and space [Kummer, 1971]. We suggest how SNA can help in both cases.

Throughout this review, we have used the term relationship to describe both associations between individuals—which may be passive sharing of time and space—and interactions—which are more complex interactions that are typically directed—such as grooming behavior, reconciliation, or support during conflict. When defining a group, it could then be argued that one should use only interaction data, and not association data. Nevertheless, association data can be extremely informative, especially where these associations correlate to interaction data [Clark, 2011; Silk et al., 2002a,b], since association data are typically easier to collect. How can SNA of relationship data be used to define a group?

Instead of categorizing groups as “despotic” or “egalitarian” (with respect to agonistic interaction), or “cohesive” or “fission–fusion” (with respect to

patterns of spatial-temporal association) [Aureli et al., 2008; Thierry et al., 2004], SNA provides a suite of statistics for describing primate group structure [Kasper & Voelkl, 2009]. Sublevels of association/interaction can be defined within larger levels of organization [Aureli et al., 2008; Couzin, 2006; Wittemyer et al., 2005], and where groups split (in space and time) daughter groups may still have positive interactions during their next encounters, and even foraging on the same resources. We therefore have to understand the ecological and social drivers (or constraints) underlying formation and stability of social groups [Gero et al., 2008]. One way to do this is to calculate intermediate network measures such as the modularity method or hierarchical cluster analysis (*Between the individual and the group level: searching for cliquishness*, above). These approaches will identify different levels of associations, which can then be used to determine group composition. One can then consider what social and ecological factors may be influencing the composition of these subunits/groups. For example, Wolf et al. [2007] studied the social structure of a Galapagos sea lion (*Zalophus wollebaeki*) population. Analyses of their proximity network revealed that the population could be divided in different subgroups, defined both by the topography of the island on which they lived, and by male territoriality.

Who are the Most Important/Central Individuals in a Network?

Traditionally, the most central individual in a primate group was defined as the highest ranking individual, as defined by dominance hierarchy derived from agonistic interaction data, or the most affiliated individual defined by the frequency of affiliative interactions. This is a *kind* of centrality, but the most central or important individuals may also be considered the individuals facilitating group stability. These individuals are not necessarily the most affiliated (or those with higher node degrees), but rather those individuals with the highest clustering coefficients (i.e. the broker individuals, which can act as a bridge to two subunits, as already discussed). It is therefore important to understand that centrality can have different meanings: the central individual can be defined either as the individual allowing group cohesion by linking two subgroups, or as the individual allowing group stability by managing conflicts, or, it may represent the individual having the highest frequency of grooming interactions. The interpretation of the centrality will depend on your question and of the index used to calculate this centrality.

We also need to understand how behavioral traits or characteristics, such as sex, age, dominance, boldness, knowledge, or experience, may influence the network centrality of an individual. As already

mentioned, it has been suggested that individuals may develop relationships based on sharing similar needs and motivations [Couzin, 2006] and Ramos-Fernandez et al. [2006] proposed that nonrandom associations among group members can emerge solely as a consequence of the way in which individuals forage. How individual characteristics may confer an adaptive advantage and enhance the fitness of individuals via their network position (through the network centrality of individuals displaying this trait, for example) remains to be explored.

Can Network Properties Influence Individual Fitness?

Primates, but also all other animal groups, show an assortativity in the way group members associate and interact together, as we have already discussed. From a network perspective, these relationships define the structure of the group network, which in turn impact on the way an individual will behave with its partners. There is now growing support for the concept that the structure of a network is linked to its functioning, and is thus selected in order to increase the fitness of its members [Krause et al., 2007]. In baboons, Silk et al. [2009] showed that females having more relationships, i.e. a greater centrality, have more offspring than females with fewer relationships. In the wasp, *Ropalidia marginata*, the network structure of the colony changes dramatically, from tolerant to despotic after the removal of the queen. This change is a result of increases in aggressive interaction and competition for centrality and control of colony reproduction [Bhadra et al., 2009]. These examples not only emphasize how an individual behavior can influence a network, but also how the network influences individual behavior via a feedback loop [Krause et al., 2007; Naug, 2009].

King et al. [2011] provide a further example of how network structure may impact directly on individuals in the network. Their SNA of foraging associations in baboons showed that dominance interactions and affiliative patterns were crucial to shaping the co-feeding network. Examination of how the co-feeding network was structured suggested that individuals arranged themselves to increase foraging benefits and reduce aggression at the level of the individual. This arrangement was expected to reinforce the structure of grooming and dominance interactive networks. Traditional dyadic analyses of these patterns would not allow them to have come to such an interpretation.

The question of whether network structure can influence individual fitness can also be investigated at the population level. Animal population structure and dynamics have important implications for the transmission of genes, diseases, and information [Krause et al., 2007; Whitehead, 2008]. All these

transmissions will have an impact on the maintenance or the changes in genetic or cultural diversity, and where costs of sociality vary across individuals in a population. This can result in different behavioral strategies at the group level [Aureli et al., 2008; Conradt & Roper, 2005; Krause & Ruxton, 2002; Wrangham, 1987]. For example, varying inter-individual distances (dispersion of group members) and temporary or irreversible group fission events can allow individuals to temporarily or permanently reduce the costs they experience.

Some species of primates, fish, cetaceans, insects, and bats, all display a degree of fission–fusion dynamics [see Aureli et al., 2008 for a review]. SNA can allow researchers to characterize these dynamics at the population level. Relationships between groups can be measured not only by using direct interactions, such as dispersal of individuals or group encounters [Drewe et al., 2009], but also by using indirect interactions [Formica et al., 2010]. Indirect interaction can be important where disease or information can be transmitted among groups or individuals even if they do not share the same space at the same time. For several primate species, group home ranges are overlapping and scent marking behavior (for instance) can allow groups or individuals to exchange information. Analyzing intergroup relationships (direct or indirect) using SNA might improve our understanding of intergroup information exchange, group interactions, population structure, and disease transmission.

What Determines Network Stability?

One important question in primatology is why some groups are more stable than others with similar size, and in similar ecological conditions. SNA, once again, should be an important tool for understanding these differences. One way to understand network stability over time is to analyze how relationships are modified, or alter after the death of an individual, which can act as a kind of “natural experiment”. One can also study the effect of removal of individuals from a network theoretically, using an experimental knockout in SNA software such as in Ucinet. Results of such simulations should however be interpreted with caution since natural groups can have a great inertia to keep cohesion due to external or internal forces not taken into account in a simulated experiment. Experimental knockouts like that devised by Flack et al. [2006], are surely the way to go where this is practically possible. Comparisons of simulated and real knockouts will allow us to better understand the mechanisms underlying group cohesion, especially where simulations are not supported by data [James et al., 2009].

Most of the studies on the influence of social relationships upon group stability sum the

interactions of individuals over a defined observation period. Then, they attempt to understand how the interactions observed during this observation influence patterns of fission [e.g. van Horn et al., 2007]. This approach therefore considers relationships, and the network of these relationships as static. However, relationships between individuals change over time, and the group network is dynamic. King et al. [2011] suggest that to complement their analysis of static networks, data over a finer temporal scale may provide insight into variation in the value of grooming and food resources, and if these translate to changes in co-feeding networks. Other studies support this notion, since Henzi et al. [2009] showed cyclicity in the proximity and grooming networks of female baboons and suggest that this cyclicity can be attributed to changes in food availability (and thus value of grooming). However, it will be important for future studies on this topic to disentangle the influence of simple changes spatial distribution of individuals as a consequence of the configuration of food resources (e.g. when food is patchy, individuals will be spread out) that therefore may have nothing to do with the value of social relationships.

Although it is currently difficult to define communities and subgroups when a network changes over time, a number of new approaches makes this possible. For instance, Tantipathananandh and Berger-Wolf [2009] proposed two different algorithms for identifying communities in dynamic social networks. By applying these algorithms to several data sets of human and animal societies, they revealed novel patterns of associations, which were previously obscured by static network approaches. These approaches can allow researchers to tackle new questions. For example, two dyads might show the same cumulative frequency of interactions after a certain time period of observation. However, the two dyads interactions may differ markedly in their temporal distribution. For instance, each dyad may have interacted at the same low frequency each day, or one dyad may have had all their interactions in a single day. Thus, the frequency of interactions is the same across the two dyads, but this tells us nothing about the stability of social relationships. This requires a dynamic analysis and this kind of modeling approach and its impact on information or disease transmission is discussed in this issue by Jacobs and Petit [2011] and Hoppitt and Laland [2011].

Can SNA be Used to Manage and Conserve Primates?

SNA can be useful in several ways for the management and conservation of wild and captive primates. Sometimes, both in the wild and in captivity, group size may increase so that it has

serious consequences for the well-being of animals; increasing within-group food competition and aggression which may cause injury. In the wild, this may result in permanent fission, and under these conditions in captivity, it may be necessary to divide the group into two or more subgroups. Similarly, where opportunity for immigration in wild populations is limited due to physical barriers created by human populations, natural fission events may be prevented, potentially escalating human-primate conflicts. Using cluster analysis on grooming interactions, researchers could predict the best group division that would result in preservation of the most affiliated individuals (see Clark [2011] for use of cluster analysis on captive chimpanzees). Using centrality measures on aggressive interactions, one can also identify the individual most disruptive to the network and then remove it in order to potentially decrease aggression rates and enhance group stability.

Clark [2011] provides an informative discussion of how SNA can be used from a captive management perspective, and two empirical examples are presented in this special issue. Dufour et al. [2011] used SNA to study the effect of relocation on stress and proximities in a captive capuchin and squirrel monkeys, and Beisner et al. [2011] used SNA to demonstrate the degree of integration of high-ranking natal adult males into social network of rhesus macaques. Beisner et al. find that the presence of adult natal males facilitates high levels of intense aggression and fragmentation of captive macaque social networks. Although we have known for a long time that the presence of natal males in captive social groups is associated with high risks of aggression, this analysis adds insight into the social dynamics involved. Thus, understanding interactions between group members in such situations can enable managers to monitor and respond to network changes in captive groups by removing some individuals. Individuals, subgroups, and whole groups are also frequently moved in captive and wild situations. SNA can inform institutions not only on the stability of networks pre- and post-relocation, but also about the predictors of group instabilities [McCowan et al., 2008].

Principles of individual centrality in a network might also facilitate management practices. Specifically, if there is a requirement for a new training technique/behavior to be introduced, a group for sanitary reasons or for medical, or behavioral research [Laule et al., 2003; Savastano et al., 2003; Schapiro et al., 2003], informing the most central individual first should allow a faster diffusion of the information inside the group than informing another individual. Concerning disease transmission, we might also expect that, in case of infection, isolating or first treating central individuals would limit the transmission of the disease.

CONCLUSIONS

Despite primate social interactions and resulting relationships typically involving more than two individuals, most previous studies focus only on dyadic interactions. SNA broadens our perspective, allowing researchers to quantify and explore not only the overall social structure of primate groups or populations, but also to examine the relationships a specific individual has with all other group members [Whitehead, 2008], i.e. the “social niche” [Flack et al., 2006].

The examples that are contained within this special issue showcase the potential of social network analyses to the study of primatology. Taking these works alongside books by Whitehead [2008] and Croft et al. [2008], and other review articles by Krause et al. [2007] and Wey et al. [2008], we hope that this special issue will help to stimulate other researchers to explore the questions we have identified and more, in a variety of primate species and study populations; we eagerly anticipate their findings.

ACKNOWLEDGMENTS

The authors are grateful to Lauren Brent, Bernhard Voelkl, and Claudia Kasper for their helpful comments. C.S. was supported by the Franco-American commission, the Fyssen foundation, and the Japan Society for the Promotion of Science. A.J. was supported by a grant from the French Ministry of Education and Research. This research adheres to the American Society of Primatologists principles for the ethical treatment of primates.

REFERENCES

- Alexander R. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Anderson JR. 2007. Animal behavior: tolerant primates cooperate best. *Current Biology* 17:R242–R244.
- Arnold K, Barton RA. 2001. Postconflict behavior of spectacled leaf monkeys (*Trachypitecus obscurus*). II. Contact with third parties. *International Journal of Primatology* 22: 267–286.
- Aureli F, de Waal FBM. 2000. *Natural conflict resolution*. Berkeley, CA: University of California Press.
- Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Fiore AD, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AM, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP. 2008. Fission–fusion dynamics: new research frameworks. *Current Anthropology* 49:627–654.
- Avilés L. 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evolutionary Ecology Research* 1:459–477.
- Barabasi A, Oltvai ZN. 2004. Network biology: understanding the cell's functional organization. *Nature Reviews. Genetics* 5:101–113.
- Beisner B, Jackson M, Cameron A, McCowan B. 2010. Detecting instability in animal social networks: genetic fragmentation is associated with social instability in rhesus macaques. *PLoS One*.
- Beisner BA, Jackson ME, Cameron A, McCowan B. 2011. Effects of natal male alliances on aggression and power

- dynamics in Rhesus Macaques. *American Journal of Primatology* 73:790–801.
- Bejder L, Fletcher D, Bräger S. 1998. A method for testing association patterns of social animals. *Animal Behaviour* 56: 719–725.
- Bhadra A, Jordan F, Sumana A, Deshpande SA, Gadagkar R. 2009. A comparative social network analysis of wasp colonies and classrooms: linking network structure to functioning. *Ecological Complexity* 6:48–55.
- Bonacich P. 2007. Some unique properties of eigenvector centrality. *Social Networks* 29:555–564.
- Borgatti S, Everett M, Freeman L. 2002. UCINET 6 For Windows. Software for Social Network Analysis.
- Borgatti SP, Mehra A, Brass DJ, Labianca G. 2009. Network analysis in the social sciences. *Science* 323:892–895.
- Brent LJN, Lehmann J, Ramos-Fernández G. 2011. Social network analysis in the study of nonhuman primates: a historical perspective. *American Journal of Primatology* 73: 720–730.
- Cairns SJ, Schwager SJ. 1987. A comparison of association indices. *Animal Behaviour* 35:1454–1469.
- Camazine S, Deneubourg J, Franks NR, Sneyd J, Theraula G, Bonabeau E. 2003. Self-organization in biological systems. Princeton, NJ: Princeton University Press.
- Chepko-Sade BD, Sade DS. 1979. Patterns of group splitting within matrilineal kinship groups. *Behavioral Ecology and Sociobiology* 5:67–86.
- Chepko-Sade BD, Reitz KP, Sade DS. 1989. Sociometrics of *Macaca Mulatta* IV: network analysis of social structure of a pre-fission group. *Social Networks* 11:293–314.
- Clark FE. 2011. Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology* 73:748–757.
- Conradt L, Roper T. 2005. Consensus decision making in animals. *Trends in Ecology and Evolution* 20:449–456.
- Conradt L, Roper TJ. 2000. Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society B: Biological Sciences* 267:2213–2218.
- Corning WC, Lahue R. 1972. Invertebrate strategies in comparative learning studies. *American Zoologist* 12:455–469.
- Couzin ID. 2006. Behavioral ecology: social organization in fission-fusion societies. *Current Biology* 16:R169–R171.
- Couzin ID, Krause J. 2003. Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior* 32:1–75.
- Croft DP, James R, Ward AJW, Botham MS, Mawdsley D, Krause J. 2005. Assortative interactions and social networks in fish. *Oecologia* 143:211–219.
- Croft DP, James R, Krause DJ. 2008. Exploring animal social networks. Princeton, NJ: Princeton University Press.
- Crook JH, Gartlan JS. 1966. Evolution of primate societies. *Nature* 210:1200–1203.
- DeJordy R, Borgatti SP, Roussin C, Halgin DS. 2007. Visualizing proximity data. *Field Methods* 19:239–263.
- de Waal FBM. 1986. The integration of dominance and social bonding in primates. *The Quarterly Review of Biology* 61: 459–479.
- de Waal FBM, Luttrell LM. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stump-tail monkeys. *American Journal of Primatology* 19:83–109.
- Dow MM, de Waal FBM. 1989. Assignment methods for the analysis of network subgroup interactions. *Social Networks* 11:237–255.
- Drewe JA, Madden JR, Pearce GP. 2009. The social network structure of a wild meerkat population: 1. Inter-group interactions. *Behavioral Ecology and Sociobiology* 63: 1295–1306.
- Dufour V, Sueur C, Whiten A, Buchanan-Smith HM. 2011. The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology* 73:802–811.
- Dufour V, Pelé M, Neumann M, Thierry B, Call J. 2009. Calculated reciprocity after all: computation behind token transfers in orang-utans. *Biology Letters* 5:172–175.
- Faust K, Skvoretz J. 2002. Comparing networks across space and time, size and species. *Sociological Methodology* 32: 267–299.
- Flack JC, Girvan M, de Waal FBM, Krakauer DC. 2006. Policing stabilizes construction of social niches in primates. *Nature* 439:426–429.
- Formica VA, Augat ME, Barnard ME, Butterfield RE, Wood CW, Brodie ED. 2010. Using home range estimates to construct social networks for species with indirect behavioral interactions. *Behavioral Ecology and Sociobiology* 64:1199–1208.
- Franks D, James R, Noble J, Ruxton G. 2009. A foundation for developing a methodology for social network sampling. *Behavioral Ecology and Sociobiology* 63:1079–1088.
- Franks DW, Ruxton GD, James R. 2010. Sampling animal association networks with the gambit of the group. *Behavioral Ecology and Sociobiology* 64:493–503.
- Franz M, Nunn CL. 2009. Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences* 276:1829–1836.
- Freeland WJ. 1976. Pathogens and the evolution of primate sociality. *Biotropica* 8:12–24.
- Freeland WJ. 1979. Primate social groups as biological islands. *Ecology* 60:719–728.
- Fruteau C, Voelkl B, van Damme E, Noë R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences of the United States of America* 106: 12007–12012.
- Gero S, Engelhaupt D, Whitehead H. 2008. Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology* 63:143–151.
- Girvan M, Newman MEJ. 2002. Community structure in social and biological networks. *Proceedings of the National Academy of Sciences of the United States of America* 99: 7821–7826.
- Godfrey S, Bull C, James R, Murray K. 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behavioral Ecology and Sociobiology* 63:1045–1056.
- Gray JA. 1987. The psychology of fear and stress. Cambridge, England: Cambridge University Press [Archive].
- Hamilton WD. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- Hansen H, McDonald DB, Groves P, Maier JAK, Ben-David M. 2009. Social networks and the formation and maintenance of river otter groups. *Ethology* 115:384–396.
- Hemelrijk CK. 1990. Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour* 39:1013–1029.
- Henzi S, Lusseau D, Weingrill T, van Schaik C, Barrett L. 2009. Cyclicity in the structure of female baboon social networks. *Behavioral Ecology and Sociobiology* 63: 1015–1021.
- Hill RA, Lee PC. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology* 245:447–456.
- Hinde RA. 1976. Interactions, relationships and social structure. *Man* 11:1–17.
- Hoppitt W, Laland KN. 2011. Detecting social learning using networks: a users guide. *American Journal of Primatology* 73:834–844.
- Huffman MA, Chapman CA. 2009. Primate parasite ecology: the dynamics and study of host-parasite relationships. Cambridge: Cambridge University Press.

- Jacobs A, Petit O. 2011. Social network modeling: a powerful tool for the study of group scale phenomena in primates. *American Journal of Primatology* 73:741–747.
- James R, Croft D, Krause J. 2009. Potential banana skins in animal social network analysis. *Behavioral Ecology and Sociobiology* 63:989–997.
- Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology* 6:326–336.
- Kanngiesser P, Sueur C, Riedl K, Grossmann J, Call J. 2011. Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology* 73:758–767.
- Kasper C, Voelkl B. 2009. A social network analysis of primate groups. *Primates* 50:343–356.
- King AJ, Cowlshaw G. 2009a. Leaders, followers and group decision-making. *Communicative and Integrative Biology* 2: 147–150.
- King AJ, Clark FE, Cowlshaw G. 2011. The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology* 73:768–774.
- King AJ, Cowlshaw G. 2009b. All together now: behavioural synchrony in baboons. *Animal Behaviour* 78:1381–1387.
- Koyama NF. 2003. Matrilineal cohesion and social networks in *Macaca fuscata*. *International Journal of Primatology* 24: 797–811.
- Krause J, Ruxton GD. 2002. *Living in groups*. Oxford, UK: Oxford University Press.
- Krause J, Croft D, James R. 2007. Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology* 62:15–27.
- Krause J, Lusseau D, James R. 2009. Animal social networks: an introduction. *Behavioral Ecology and Sociobiology* 63: 967–973.
- Kummer H. 1971. *Primate societies: group techniques of ecological adaptation*. Aldine Transaction.
- Kutsukake N, Castles DL. 2004. Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 45:157–165.
- Lahiri M, Berger-Wolf TY. 2008. Proceedings of the 2008 Eighth IEEE International Conference on Data Mining. Washington, DC: IEEE Computer Society. p 373–382.
- Laughlin SB, Sejnowski TJ. 2003. Communication in neuronal networks. *Science* 301:1870–1874.
- Laule GE, Bloomsmith MA, Schapiro SJ. 2003. The use of positive reinforcement training techniques to enhance the care, management, and welfare of primates in the laboratory. *Journal of Applied Animal Welfare Science* 6:163.
- Lefebvre D, Ménard N, Pierre JS. 2003. Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. *Behavioral Ecology and Sociobiology* 53:402–410.
- Lehmann J, Ross C. 2011. Baboon (*Papio anubis*) social complexity—a network approach. *American Journal of Primatology* 73:775–789.
- Lusseau D. 2003. The emergent properties of a dolphin social network. *Proceedings of the Royal Society B: Biological Sciences* 270:S186–S188.
- Lusseau D, Conradt L. 2009. The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology* 63:1067–1077.
- Lusseau D, Newman MEJ. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B: Biological Sciences* 271:S477–S481.
- Lusseau D, Whitehead H, Gero S. 2009. Incorporating uncertainty into the study of animal social networks. *Animal Behaviour* 75:1809–1815.
- Manno TG. 2008. Social networking in the Columbian ground squirrel, *Spermophilus columbianus*. *Animal Behaviour* 75: 1221–1228.
- McCowan B, Anderson K, Heagarty A, Cameron A. 2008. Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behaviour Science* 109:396–405.
- Morrell LJ, Croft DP, Dyer JR, Chapman BB, Kelley JL, Laland KN, Krause J. 2008. Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour* 76:855–864.
- Naug D. 2009. Structure and resilience of the social network in an insect colony as a function of colony size. *Behavioral Ecology and Sociobiology* 63:1023–1028.
- Newman MEJ. 2003. Mixing patterns in networks. *Physical Review E* 67:026126.
- Newman MEJ. 2004. Analysis of weighted networks. *Physical Review E* 70:056131.
- Newman MEJ. 2010. *Networks. An introduction*. Oxford: Oxford University Press.
- Nooy WD, Mrvar A, Batagelj V. 2005. *Exploratory social network analysis with Pajek*. Cambridge: Cambridge University Press.
- Nunn CL, Altizer S, Altizer SM. 2006. Infectious diseases in primates: behavior, ecology and evolution. Oxford: Oxford University Press.
- Pelé M, Thierry B, Call J, Dufour V. 2010. Monkeys fail to reciprocate in an exchange task. *Animal Cognition* 13:745–751.
- Ramos-Fernández G, Boyer D, Gómez V. 2006. A complex social structure with fission–fusion properties can emerge from a simple foraging model. *Behavioral Ecology and Sociobiology* 60:536–549.
- Ramos-Fernández G, Boyer D, Aureli F, Vick L. 2009. Association networks in spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology* 63:999–1013.
- Sade DS. 1989. Sociometrics of *Macaca Mulatta* III: n-path centrality in grooming networks. *Social Networks* 11: 273–292.
- Savastano G, Hanson A, McCann C. 2003. The development of an operant conditioning training program for new world primates at the Bronx Zoo. *Journal of Applied Animal Welfare Science* 6:247.
- Schapiro SJ, Bloomsmith MA, Laule GE. 2003. Positive reinforcement training as a technique to alter nonhuman primate behavior: quantitative assessments of effectiveness. *Journal of Applied Animal Welfare Science* 6:175.
- Schino G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour* 62: 265–271.
- Schneirla T. 1943. The nature of ant learning. II. The intermediate stage of segmental maze adjustment. *Journal of Comparative Psychology* 35:149–176.
- Scott J. 2000. *Social network analysis: a handbook*. Beverley Hills, CA: SAGE.
- Sih A, Hanser S, McHugh K. 2009. Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology* 63:975–988.
- Silk JB. 1999. Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour* 58:45–51.
- Silk JB. 2002a. Females, food, family, and friendship. *Evolutionary Anthropology: Issues, News, and Reviews* 11:85–87.
- Silk JB. 2002b. The form and function of reconciliation in primates. *Annual Review of Anthropology* 31:21–44.
- Silk JB, Alberts SC, Altmann J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour* 67:573–582.
- Silk J, Alberts S, Altmann J. 2006a. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology* 61:197–204.
- Silk J, Altmann J, Alberts S. 2006b. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology* 61:183–195.

- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences* 276:3099–3104.
- Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* 41:291–309.
- Sueur C, Petit O. 2008. Organization of group members at departure is driven by social structure in *Macaca*. *International Journal of Primatology* 29:1085–1098.
- Sueur C, Petit O, Deneubourg J. 2009. Selective mimetism at departure in collective movements of *Macaca tonkeana*: an experimental and theoretical approach. *Animal Behaviour* 78:1087–1095.
- Sueur C, Petit O, Deneubourg J. 2010. Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology* 213:1338–1346.
- Tantipathananandh C, Berger-Wolf T. 2009. Constant-factor approximation algorithms for identifying dynamic communities. *Fifteenth ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*. Paris, France. p 827.
- Thierry B, Singh M, Kaumanns W. 2004. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press.
- Thorpe W. 1963. *Learning and instinct in animals*. Cambridge, EUA: Harvard University.
- Van Horn R, Buchan J, Altmann J, Alberts S. 2007. Divided destinies: group choice by female savannah baboons during social group fission. *Behavioral Ecology and Sociobiology* 61:1823–1837.
- Voelkl B, Kasper C. 2009. Social structure of primate interaction networks facilitates the emergence of cooperation. *Biology Letters* 5:462–464.
- Voelkl B, Noë R. 2008. The influence of social structure on the propagation of social information in artificial primate groups: a graph-based simulation approach. *Journal of Theoretical Biology* 252:77–86.
- Vries HD, Netto WJ, Hanegraaf PLH. 1993. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* 125:157–175.
- Ward AJW, Sumpter DJT, Couzin ID, Hart PJB, Krause J. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America* 105:6948–6953.
- Wasserman S, Faust K. 1994. *Social network analysis: methods and applications*. Cambridge: Cambridge University Press.
- Watts D. 2000. Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology* 21:189–210.
- Watts DJ. 2004. *Six degrees: the science of a connected age*. New York, NY: W. W. Norton & Company.
- Wey T, Blumstein DT, Shen W, Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* 75:333–344.
- Whitehead H. 1997. Analysing animal social structure. *Animal Behaviour* 53:1053–1067.
- Whitehead H. 2008. *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago: University of Chicago Press.
- Whitehead H. 2009. SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology* 63:765–778.
- Wittemyer G, Douglas-Hamilton I, Getz W. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* 69:1357–1371.
- Wolf JB, Mawdsley D, Trillmich F, James R. 2007. Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour* 74:1293–1302.
- Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.
- Wrangham RW. 1987. Evolution of social structure. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: Chicago University Press. p 227–239.