American Journal of Primatology 73:720–730 (2011)

REVIEW ARTICLE

Social Network Analysis in the Study of Nonhuman Primates: A Historical Perspective

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Advances over the last 15 years have made social network analysis (SNA) a powerful tool for the study of nonhuman primate social behavior. Although many SNA-based techniques have been only very recently adopted in primatological research, others have been commonly used by primatologists for decades. The roots of SNA also stem from some of the same conceptual frameworks as the majority of nonhuman primate behavioral research. The rapid development of SNA in recent years has led to questions within the primatological community of where and how SNA fits within this field. We aim to address these questions by providing an overview of the historical relationship between SNA and the study of nonhuman primates. We begin with a brief history of the development of SNA, followed by a detailed description of the network-based visualization techniques, analytical methods and conceptual frameworks which have been employed by primatologists since as early as the 1960s. We also introduce some of the latest advances to SNA, thereby demonstrating that this approach contains novel tools for the study of nonhuman primate social behavior which may be used to shed light on questions that cannot be addressed fully using more conventional methods. Am. J. Primatol. 73:720–730, 2011.

Key words: social network analysis; social behavior; social structure; history of primatology

INTRODUCTION

Social network analysis (SNA) is a framework used to study the structure of societies. A social network, in its simplest form, is a set of social units (nodes) and the ties (edges) between them [Wasserman & Faust, 1994]. On the whole, SNA is an umbrella term that encompasses a number of different graphical tools to visualize networks (e.g. sociograms), as well as tools for mathematical modeling (e.g. matrix algebra and permutation-based analyses) that allow the detection and quantification of patterns in social networks [Freeman, 2004].

With powerful analytical tools that address a range of commonly investigated aspects of animal social behavior, SNA has become increasingly popular in recent years and has been employed in studies of taxa ranging from insects and fish to birds and mammals [Croft et al., 2008; Krause et al., 2007; Sih et al., 2009; Wey et al., 2008; Whitehead, 2008], including many studies of nonhuman primates [e.g. Brent et al., 2011; Flack et al., 2006; Henzi et al., 2009; Lehmann & Boesch, 2009; Ramos-Fernández et al., 2009; Sueur & Petit, 2008]. The publication of this research has raised important questions within the primatological community pertaining to where and to how SNA fits into this field.

The application of SNA to the study of most animals groups has occurred largely in the last decade [Krause et al., 2009]. In contrast, some of the techniques and conceptual frameworks associated with SNA have been used in primatological research since as early as the 1960s. For example, some of the same techniques for visualizing and analyzing data that have been used commonly by primatologists are associated with SNA (e.g. sociograms). There are also similarities between the main conceptual framework underlying SNA and the framework which has formed the basis of many studies of nonhuman primate sociality [i.e. Hinde, 1976]. However, there exist many other SNA-based

Contract grant sponsor: NIH; Contract grant number: 1R01-MH-089484-01; Contract grant sponsor: CONACYT; Contract grant number: J51278; Contract grant sponsor: Instituto Politécnico Nacional.

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Received 3 December 2010; revised 12 February 2011; revision accepted 26 February 2011

DOI 10.1002/ajp.20949
Published online 23 March 2011 in Wiley Online Library (wiley onlinelibrary.com).

methods which are unfamiliar to primatologists or which have only very recently been adopted. In particular, the last 15 years have seen the culmination of an unprecedented number of advances in SNA, resulting in fresh perspectives on the structure of complex networks [e.g. Barabási, 2002; Watts & Strogatz, 1998], the development of new network metrics [e.g. Barrat et al., 2004; Newman, 2005, 2006; Opsahl, 2009], and the creation of numerous readily available software packages and scripts for the implementation of network analyses [e.g. Borgatti et al., 2002; Opsahl, 2009].

In order to bring these issues to the forefront, we felt an overview of the history of the relationship between SNA and the study of nonhuman primates would be helpful. The origins of the unique relationship between SNA and primatology are rooted in the fact that the history of the study of social behavior in nonhuman primates is extensive compared with that in other taxonomic groups. For many years, nonhuman primates were erroneously believed to be the most, if not only, socially complex animals other than humans. As a result, much of the detailed research regarding social behavior was until relatively recently (up until the 1980s and 1990s) conducted on this group [Silk, 2007; Whitehead, 2008]. Studies of nonhuman primates have also traditionally been influenced to a greater extent by human-based disciplines, such as sociology and anthropology, than studies of other taxa because of the close common ancestry between nonhuman primates and humans [Krause et al., 2007; Whitehead, 2008]. This, coupled with the ability to collect finely detailed behavioral data in many species has resulted in a rich and varied repertoire of analytical techniques within primatology, including some that are today associated with SNA.

We begin this review by briefly describing the history of SNA, thereby demonstrating that SNA is not a static entity but is instead the result of contributions from a variety of disciplines over the last century. Building on this, we describe the relationship between the study of nonhuman primate social behavior and SNA. We outline in detail the visualization techniques and analytical methods employed traditionally by primatologists that are associated with SNA. We also focus on two network-based conceptual frameworks, sociometry and role theory, that have formed the basis of SNA as well as the study of nonhuman primate behavior. Throughout, we include descriptions of some of the recent advances to SNA, focusing in particular on those which may prove most valuable to the study of nonhuman primates. We propose that many of these contemporary techniques are useful extensions to conventional methods, which could be used to shed light on questions that previously could not be addressed fully by primatologists.

Overall, we aim to bring to light the complex and perhaps understated historical relationship between SNA and the study of nonhuman primates. In doing so, we hope to foster an appreciation of some of the factors that have shaped primatology over the years. But, perhaps more importantly, we hope to provide primatologists the background required in order to fully evaluate current applications of SNA to the study of nonhuman primates (and other animals), as well as aid in the effective implementation of network-based approaches to the study of nonhuman primate social behavior in the future.

A BRIEF HISTORY OF SNA

From a historical perspective, it is difficult to name any one founder of SNA. In a general sense, the origins of many components of SNA can be traced to the 18th century with the development of graph theory [for a review see Biggs et al., 1986]. It was not until the 1930s, however, with the introduction of an approach to the quantitative analysis of human social data termed ‘‘sociometry’’ [Moreno, 1934; Scott, 2000; Wasserman & Faust, 1994], that the study of social interactions were formalized in a manner that somewhat resembles what today is considered SNA.

Sociometry is defined as the ‘‘...application of quantitative methods...which inquire into the evolution and organization of groups and the position of individuals within them’’ [Moreno, 1934]. According to sociometry, interactions between pairs of individuals are the basis upon which the structure of societies are built and can, as a result, affect society as a whole [Scott, 2000]. The notion that social structure emerges from pairwise interactions has formed the main conceptual framework underlying contemporary SNA [Scott, 2000] and modern network research has provided empirical evidence that the patterning of interactions between individuals can impact upon a range of emergent properties of groups, including information flow [Voelkl & Noë, 2008; Watts & Strogatz, 1998], individual well-being [Fowler & Christakis, 2008; Hill et al., 2010; Seeman, 1996], and cooperation [Voelkl & Kasper, 2009].

The overall performance of the group, e.g. group problem solving, was a particular concern of some of the early sociometric studies [e.g. Bavelas, 1950]. These studies developed many of the network metrics that are still commonly used in SNA today. These metrics include measures of overall network structure, such as *density*, a measure of the number of ties present in relation to all possible ties; and *network centralization*, a measure of the extent to which all interactions involve a single individual. Some of the earliest developed network metrics also included individual-based measures of *centrality*, or the position of individuals within the network. Early examples of individual-based centrality measures include *degree*, the number of direct connections a node has within the network; and *clustering* *coefficient*, a measure of the extent to which a node's neighbors are directly connected to one another [for overviews of network metrics see: Wasserman & Faust, 1994; Wey et al., 2008]. Measures of centrality allowed scientists to identify the so-called key-players within networks and also led to the influential concept of weak ties, i.e. acquaintances who are occasionally socially associated but not closely involved and whose ties keep the network together [Granovetter, 1973, 1983].

In addition to the influence of the social sciences, the development of SNA has also benefited from contributions from the fields of mathematics and physics. After the important methodological development of expressing sociometric data as matrices in the 1940s [Forsyth & Katz, 1946], mathematicians and physicists generated much needed computational models to analyze the patterning of links connecting nodes in a network [Freeman, 2004]. Mathematicians also continued to develop graph theory, resulting in the production of a number of random network models in the late 1950s [Erdős & Rényi, 1959; Gilbert, 1959]. These models, in which the edges between nodes result from random processes, have been hugely influential in SNA as they allow researchers to identify the processes that may cause observed networks to differ from randomly generated networks [Newman et al., 2002].

SNA emerged formally as a field within the social sciences in the 1980s with the creation of the journal *Social Networks* and the establishment of a professional society, the *International Network for Social Network Analysis* [Borgatti et al., 2009]. Since this time, the number of different disciplines applying SNA has increased rapidly [Otte & Rousseau, 2002] and what started with the analysis of small groups of humans has since expanded to study phenomena in the fields of anthropology, mathematics, economics, political science, psychology, statistics, ethology, zoology, epidemiology, computer science, and physics [Freeman, 2004]. In the last 15 years in particular, SNA has grown steadily in popularity, a result almost certainly related to the production of readily available computer programs that allow researchers to calculate a large number of network metrics with relative ease [e.g. UCINET: Borgatti et al., 2002; TNet: Opsahl, 2009; Pajek: Batagelj & Mrvar, 2003 and SOCPROG: Whitehead, 2007]. Today, SNA continues to grow through the incorporation of advances from a wide range of disciplines and current social network-based research continues to increase our understanding of the functions and characteristics of networks [Barabási, 2002].

SOCIAL NETWORKS IN STUDIES OF NONHUMAN PRIMATE SOCIAL BEHAVIOR

While the idea of social networks in studies of human groups was thriving during the 1960s and 1970s, some primatologists were beginning to recognize the potential of this approach to explain social behavior and group dynamics in nonhuman primates [e.g. Fedigan, 1972; Hinde, 1976; Kummer, 1968; Sade, 1965]. Even though SNA has formally existed since the 1980s it was not until after the year 2000, following the aforementioned advances in computational power and the development of SNA-specific software programs, that primatologists began to use some of SNA's more computationally complex metrics in earnest and began to regularly use the term SNA to describe their research [e.g. Flack et al., 2006; McCowan et al., 2008; Voelkl & Noë, 2008].

We now turn to summarizing the relationship between SNA and the study of nonhuman primate behavior. This relationship includes: (i) the use of network-based graphs, (ii) the application of social network-derived measures of individual-based sociality, (iii) the application of social network-derived measures of social structure, (iv) the use of network-based inferential analysis tools, and (v) the application of the same conceptual frameworks that underlie SNA. Within each section, we begin by outlining the historical relationship between each approach and the study of nonhuman primate behavior. This is followed by a description of more recent applications of SNA within this field, as well as suggestions for directions of future research.

Network-Based Graphs

The first study to apply a social network-based technique to nonhuman primate data was published in 1965. Donald Stone Sade, arguably the most extensive applicant of a social network approach to the study of nonhuman primates prior to the turn of the century, used a network-based graphing technique (the sociogram, Fig. 1A) to visualize the patterning of grooming interactions between the members of a single group of rhesus macaques (*Macaca mulatta*) [Sade, 1965].

Sociograms are an attractive graphing technique for the study of animal social behavior because they provide visual representations of large amounts of information that would otherwise be difficult to depict. By summarizing the interactions among all members of a group in a single, compact diagram, sociograms put to paper what field researchers may envisage when they think of the relationships between their study subjects. Sociograms also highlight more subtle information that may not be obvious from looking at numbers on a spread-sheet alone. For instance, sociograms highlight the ties between pairs of individuals that do exist, but also make apparent the absence of ties (that is, the absence of interaction) between certain dyads. Commonalities and differences in social relationships are also made evident; for example, sociograms make readily visible a situation in which individuals

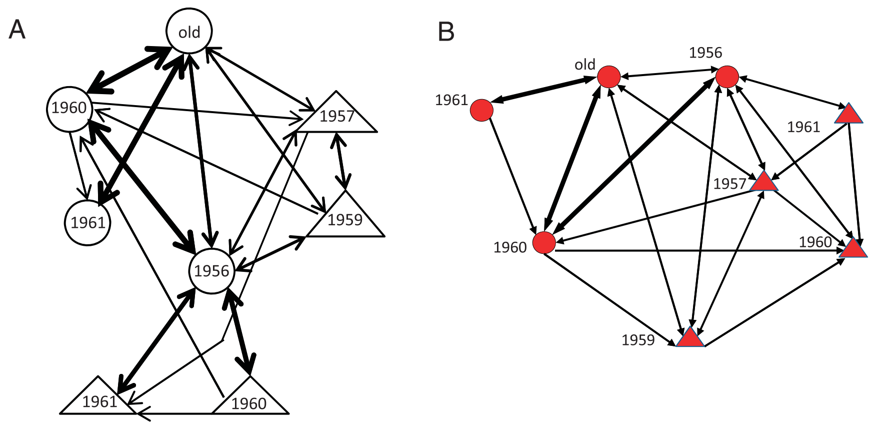

Fig. 1. (**A**) Sociogram of a rhesus macaque grooming network, reproduced following Sade [1965, Fig. 3], (**B**) Spring-embedded version of Sade's sociogram generated in Netdraw. The individual with the highest centrality (''1957'') is placed in the center of the spring-embedded graph. In both sociograms, circles represent females, triangles represent males. Lines between nodes represent the presence of a grooming tie. Arrows indicate the direction of grooming (i.e. given or received) and the thickness of lines indicates the relative frequency at which grooming occurred.

A, B, and C groom individual D, whereas only individuals B and C also groom individual E. Finally, sociograms provide researchers with a first glimpse at information about the network itself. For instance, sociograms offer insight into which individuals may be particularly important to the cohesion of the network (i.e. which individuals would cause the network to split into unconnected components if removed), as well as the overall pattern or ''structure'' of the network.

Since the publication of Sade's work, sociograms have proved popular with primatologists and have been used to visualize a variety of interactions including grooming [Chepko-Sade et al., 1989; Fairbanks, 1980; Mitani, 1986; Nakagawa, 1992; Pearl, 1983; Seyfarth, 1976, 1977; Soczka, 1974], proximity [Fairbanks, 1980; Hanby, 1980; Koenig & Rothe, 1991; Nakagawa, 1992; Seyfarth, 1980], vocalizations [Mitani, 1986; Nakagawa, 1992], copulations [Cheney, 1978a; Pearl & Schulman, 1983], agonism [Keverne, 1992; Pearl & Schulman, 1983], and play [Cheney, 1978b; Pearl & Schulman, 1983; Soczka, 1974].

In addition to sociograms, hierarchical clustering analysis and multidimensional scaling, both common visualization techniques in SNA, have been used in order to determine the division of nonhuman primate groups into subgroups based on the interactions between pairs of individuals and to graphically represent those divisions [Byrne et al., 1989; Chapman, 1990; Chepko-Sade et al., 1989; Corradino, 1990; Pearl, 1983; Pearl & Schulman, 1983; Schulman, 1980; Yeager, 1990], but their application has been less frequent.

Until very recently, however, primatologists have produced their network-based graphs by hand. This is highly labor intensive, even for groups containing a relatively small number of individuals. Hand-drawn sociograms also require researchers to decide for themselves on the physical positioning of nodes, which may result in graphs that are not optimized to provide information on the position of individuals in the network or the overall network structure (Fig. 1). Computer software programs [e.g. Netdraw: Borgatti, 2002] are now rapidly able to apply algorithms to interaction matrices in order to determine the placement of nodes based on specific criteria; for example, the spring-embedding algorithm places individuals with the highest centrality scores toward the center of the sociogram (individual ''1957'' in Fig. 1B). These programs also allow for the easy application of colors, sizes, and shapes to nodes based on attributes or centrality measures.

Measures of Individual-Based Sociality Using Networks

Primatologists tend to quantify sociality at the level of the individual (i.e. the extent to which an individual is involved in their social milieu) with one of two measures: an individual's number of social partners, and/or an individual's frequency of participation in a given type of interaction. For example, they may ask whether females with larger matrilines have a greater number of close social ties [Berman, 1982], or may examine the endocrine correlates of the frequency at which individuals engage in aggressive interactions [Gust et al., 1993; Sapolsky, 1982].

Number of social partners and frequency of interaction are also included as measures under the umbrella of SNA, referred to in network terminology as the centrality measures *degree* and *strength*, respectively [Croft et al., 2008]. Historically, primatologists have not made explicit links between their use of degree and strength and the use of these measures in human-based social network research.

Indeed, it is unclear whether the use of these measures in studies of nonhuman primates was derived from network research conducted on humans, or whether these straightforward means to quantify the extent to which an individual is connected to their social group arose independently in primatology due to their highly intuitive nature.

SNA provides a number of measures of centrality besides degree and strength (e.g. clustering coefficient, eigenvector centrality). Rather than a summary of an individual's direct interactions with others, these measures represent different aspects of the nature of an individual's local network of relationships (see below for a discussion of the usefulness of these measures in recent studies of nonhuman primates). Although many of these measures were developed more than a decade ago, their use within the study of nonhuman primates (and in other fields) has been restricted by the impracticality of their implementation. Indeed, to our knowledge, there is only one research team that used a social network measure besides degree or strength in the study of nonhuman primates before the turn of the last century: Donald Sade et al. used the number of paths of length *n,* to study the grooming networks of rhesus macaques [Chepko-Sade et al., 1989; Sade, 1972, 1989; Sade et al., 1988] demonstrating that individuals who are higher in the dominance hierarchy have a greater number of grooming partners up to three path lengths away.

With recent advances in computational power and the development of accessible software, the ease of calculation of network-based measures of sociality besides degree and strength has increased dramatically. Although many of these measures may be correlated with one another, each provides information on a unique aspect of an individual's position in the network. As explained in detail by Sueur et al. (this issue), individuals who have, for example, the same degree (i.e. the same number of social ties) do not necessarily have the same eigenvector centrality; one individual may be partners with *n* individuals who themselves do not have many partners (low eigenvector centrality), while another may be partners with *n* individuals who themselves have a large number of partners (high eigenvector centrality).

This may be an important differentiation because while degree and strength reflect connections between pairs of individuals based on their direct interaction with one another, other social network metrics represent indirect connections within the network. Indirect connections are connections between pairs of individuals which result from their mutual direct connection to a third party, and may be important factors in the lives of social animals, influencing everything from dominance rank [McDonald, 2007] and stress-levels [Brent et al., 2011] to general well-being [Fowler & Christakis, 2008]. Indirect connections may be especially important to the many species of nonhuman primate who form highly differentiated relationships, recognize social bonds between pairs of third parties [Cheney & Seyfarth, 1999], and who may understand the perspectives of others [Flombaum & Santos, 2005; Hare et al., 2001; Lehmann & Dunbar, 2009].

Primatologists represent most of their data on social interactions as continuous variables in interaction matrices. In order to construct a network out of those matrices, and subsequently calculate individual measures of centrality, the choice has to be made whether to filter the network, considering a given dyad as bonded only when the value of their interaction is above a certain threshold, or whether to use the values of the interaction variables as the weights of bonds in the network. Although some studies advocate filtering as a way to remove spurious relationships that might not be significant [e.g. James et al., 2009], others have developed techniques that allow for the estimation of statistical significance of SNA metrics using weighted networks [Lusseau et al., 2008; Opsahl, 2009].

The use of weighted over binary network metrics may make particular sense in studies of small groups of nonhuman primates, in which all individuals may interact at least once with all others. For example, each individual may be found in spatial proximity to all other individuals at some point in the course of a study. In these cases, the amount of time spent with each potential partner may be where the meaningful variation lies and may be used to distinguish pairs of individuals who are ''bonded'' from those who are not. Thus, the use of weighted network metrics may somewhat circumvent the issue of filtering [Croft et al., 2008]. Nevertheless, primatologists should carefully consider which metrics are the most appropriate for their research questions, and should be aware of the fact that weighted versions of some network metrics do not yet exist. In their analysis of nonhuman primate social networks, Kasper and Voelkl [2009] used only weighted metrics, but acknowledged that using binary indices may be potentially very useful to determine which individuals are central in the network—not by virtue of their own direct relationships, but through their associates' relationships with others.

Network-Based Measures of Social Structure

Social structure, or the level of social organization that emerges from the patterning of relationships between all pairs of individuals [Hinde, 1976, and see Fig. 2], plays a critical role in shaping some of the emergent properties of groups, such as the rate at which information can spread [Watts & Strogatz, 1998]. Thus, studies of nonhuman primates have often examined sociality beyond the level of the individual to that of social structure. Primatologists interested in social structure may ask, for example,

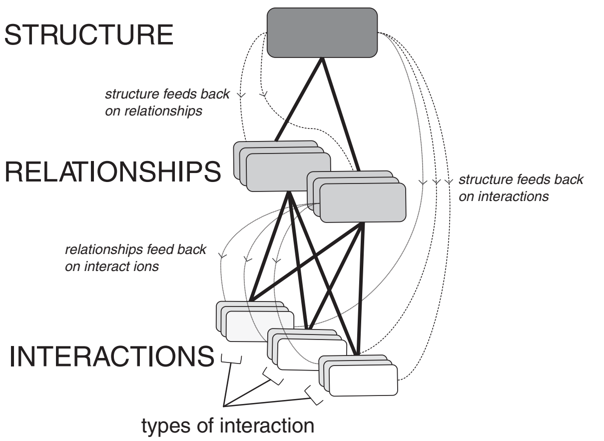

Fig. 2. Schematic representation of Hinde's conceptual framework for the study of nonhuman primate social behavior, reproduced following Hinde [1976, Fig. 1]. Relationships between individuals emerge from the patterning of their interactions, and social structure emerges from the patterning of relationships. Social structure consequently feeds back to influence relationships and interactions, and relationships feedback to influence interactions. In this schematic, interactions are grouped according to type; for example, affiliative, agonistic, and sexual interactions, whereas relationships are grouped according to the types of individuals involved; for example, mother–infant, male–female, and kin-based relationships.

whether the average number of grooming partners of individuals within their group changes along with changes to group size [Henzi et al., 1997], or whether the average rate at which group members groom one another changes along with reproductive season [Cheney & Seyfarth, 1990]. Average number of partners and average frequency of interaction are group-level extensions of the individual-based measures degree and strength. However, as with individual-based measures, SNA offers other measures of social structure that contain information extending beyond a summary of the average tendencies of interactions between pairs of dyads.

One example of how a network-based approach can serve to study nonhuman primate social behavior at a level beyond the dyadic is provided by Maryanski [1987]. In a study of African apes, Maryanski used Granovetter's concept of weak ties (see above) to demonstrate that gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) exhibit very similar underlying social network structures, despite obvious differences demonstrated using traditional, dyadic-based methods [Maryanski, 1987]. In particular, Maryanski used the frequency of social interaction between individuals to create a gradient of weak to strong social ties. Using the distribution of tie strengths in the two species, she was able to compare how individuals from different age-sex classes are bonded to one another and thereby draw conclusions regarding social structure.

More recently, a small number of studies of nonhuman primates have taken advantage of the technical advances which facilitate the application of social network-based measures of social structure: Flack et al. [2006] examined the impact of removing individual males with ''policing'' roles on the social structure derived from socio-positive interactions for captive pigtailed macaques (*Macaca nemestrina*). They found that policing resulted in networks that were less clustered, had a greater number of indirect connections, and a larger average number of social partners per individual, which suggests that policing may control conflict and may have important implications for the emergence of cooperative behavior in this species [Flack et al., 2006]. Similarly, Lehmann et al. [2010] found that simulated removal of individuals identified as brokers in 11 species of female-bonded Old World monkey resulted in networks that were less well connected. Their results led these authors to suggest that brokers have a considerable impact on the social structure of female-bonded monkey groups.

By allowing researchers to describe social structure in a fully quantitative manner based on a series of continuous, rather than discrete, measures, SNA has opened the door to the study of a wide range of research questions in nonhuman primates that cannot be addressed fully using traditional methods. For example, Kasper and Voelkl [2009] analyzed 70 nonhuman primate groups from 30 species using SNA metrics of social structure and argued that studying the variability of social systems in this way allows for a more objective quantification of the differences and similarities between species, thus avoiding the problems of classifying primate social systems into categories [e.g. Thierry, 2008]. As such, SNA has the potential to provide considerable new insight into the patterning and expression of social structure in group-living nonhuman primates.

One SNA measure of social structure that may prove particularly useful in the study of nonhuman primates and which to date has not received much attention is assortativity. Assortativity refers to the tendency of nodes of a given class to connect preferentially to others of the same class. In a random network, where every node has the same probability of being linked to any other, assortativity is null. In nonhuman primate societies, age and sex classes are clear determinants of the quality and frequency of interactions, so in that sense, nonhuman primate social networks are assortative.

Assortative mixing has at least three important consequences for nonhuman primate social structure. First, several studies of evolutionary dynamics of cooperation have shown that cooperative behavior can spread if the assumption of a well-mixed population normally made in game theoretical models is changed to a sparsely connected network [Ohtsuki et al., 2006], or to a heterogeneous network with some degree of assortativity and a heterogeneous distribution of node degree [Santos et al., 2006]. Indeed, Voelkl and Kasper [2009] demonstrated that cooperation can spread faster in networks of a size and degree of assortativity similar to those found in real nonhuman primate networks. Second, assortativity affects the way in which information flows among the nodes of a network. This was demonstrated by Voelkl and Noë [2010] in a simulation model of social learning in nonhuman primate networks in which information propagation was hampered in assortative networks compared with random or complete networks. Assortativity in these networks also implied a higher risk of extinction of learned behaviors. These results have important implications for studies of social learning, in which the assumption of equal mixing is prevalent. Finally, assortative mixing can lead to the formation of subgroups within a network, as suggested by Lusseau and Newman [2004]. Very high degrees of assortativity would imply, of course, that the network would become fragmented, with clusters corresponding to each class of individual. This is what Ramos-Fernández et al. [2009] found in spider monkeys (*Ateles geoffroyi*), with young adult males appearing as brokers between the male and female clusters.

Owing to the extraordinary proliferation of techniques and studies of networks in many scientific fields, it is important to distinguish those tools that are biologically meaningful to the study of nonhuman primate social structure from those that are best applied to other types of networks. For example, in many large and complex networks, such as those formed by collaborating scientists, the internet or interacting proteins, the degree distribution follows a power law [reviewed in Newman, 2003]. This implies that most of the nodes have a few connections, but a few nodes contain a large majority of the connections in the network (so-called hubs). Although this is an interesting property of some large networks, nonhuman primate social networks are too small [e.g. the largest groups of baboons reported by Stammbach [1987] contain up to 600 individuals] to allow for a significant test of the power law distribution [Clauset et al., 2009].

Nevertheless, it remains true that primate social networks are highly structured, with assortativity and centrality patterns that are quite different from those in random or regular networks [Kasper & Voelkl, 2009]. In this respect, one property of networks that has been suggested to have some biological relevance in nonhuman primate social networks is the so-called ''small-world'' effect [Watts & Strogatz, 1998], in which the average path length of the network is small compared with a random network, even though the mean clustering coefficient remains as high as in a random network [see Croft et al., 2004 and Lusseau, 2003 for examples in social networks of guppies and dolphins, respectively]. This effect greatly enhances the flow of information, because any two individuals, even if they belong to different clusters, can be linked through a relatively small number of nodes. Information flow through indirect connections might not be so relevant for nonhuman primate species living in stable groups, but in species with fission–fusion dynamics [Aureli et al., 2008], information about the location of feeding sites, for example, could in fact be transmitted through chains of common acquaintances even though the whole group is never found in the same place.

The small-world effect also implies that networks are particularly robust against the random loss of nodes [although a targeted removal of highly central nodes could rapidly decrease connectivity and fragment the network: Albert et al., 2000]. Indeed, this is what has been found in the few studies that have addressed this question in nonhuman primate networks, either by natural or by artificial removal of random or highly central individuals [Flack et al., 2006; Lehmann & Dunbar, 2009; Lusseau et al., 2011].

Inferential Analysis Tools: The Non-independent Nature of Relational Data

As with studies of human social networks, studies of nonhuman primate behavior nearly always deal with relational data. Unlike data based on attributes, relational data represent interactions or associations between pairs of individuals [Croft et al., 2008]. Relational data collected from multiple members of the same social group violate the assumption of independence required by traditional inferential statistical techniques [Kasper & Voelkl, 2009; Krause et al., 2009; Wasserman & Faust, 1994]. This is because individuals also interact with several members of their group, and interaction partners likewise interact with several other partners [Kasper & Voelkl, 2009]. In other words, the interactions of individual A may involve individuals B and C, while C may also interact with B [Hanneman & Riddle, 2005]. One of the most common ways to deal with this problem is to use permutation-based approaches, in which probability distributions are estimated directly from observed data sets [Hanneman & Riddle, 2005].

Studies that have examined the exchange of behavioral services among nonhuman primates, e.g. the exchange of grooming for agonistic support, have often used permutation-based techniques, such as matrix correlations, to test their hypotheses [e.g. de Waal & Luttrell, 1986; Hemelrijk, 1994; Seyfarth, 1980; Silk, 1992]. Beyond these examples, however, the application of permutation-based statistics has been rare in primatology. SNA uses a host of permutation-based statistical techniques. These include the applications of bootstraps to generate confidence intervals for network-based data [e.g. Lusseau et al., 2008] and to perform inferential tests able to deal with the non-independent nature of relational data [Hanneman & Riddle, 2005]. The application of many of these approaches may be carried out within some of the recently developed SNA-specific software programs (e.g. UCINET).

Conceptual Frameworks Used in SNA and in Primatology: Sociometry and Role Theory

In the study of nonhuman primate social behavior, one conceptual framework has arguably formed the basis of the vast majority of research. In 1976, Robert Hinde proposed that nonhuman primate societies are organized according to the patterning of interactions between pairs of individuals, from which relationships, and consequently social structure, emerge (Fig. 2). With interactions between dyads at its core, Hinde's framework is fundamentally sociometric in nature (see above for a detailed description of sociometry). Although Hinde [1976] did not discuss sociometry explicitly, he was almost certainly influenced by it. For example, he acknowledged similarities between his framework and those used by social anthropologists, and referenced the work of individuals who were at the time actively involved in sociometric research [e.g. Barnes, 1972; Mitchell, 1969]. Hinde also referred to the studies by Sade [1972] and Kummer [1968] as rare examples of primatological research that integrate data on interactions in a manner that could lead to a greater understanding of social structure [Hinde, 1976, pp 1, paragraph 1]. Given that sociometry represents a major precursor to contemporary SNA, the sociometric nature of Hinde's framework highlights the similar origins of SNA and nonhuman primate behavioral research.

Despite wide-spread acceptance in studies of nonhuman primate social behavior, Hinde's framework has been difficult to implement in reality. This is especially true with regards to the abstraction from the overall patterning of relationships to the level of social structure. For instance, for a social network to be considered an accurate representation of social structure each link should represent the social relationship between two individuals. However, most networks studied so far by primatologists really consist of a single dimension (e.g. grooming). Multiplex networks, i.e. those that integrate multiple (behavioral) dimensions, have been used by sociologists since at least the 1970s, mostly for the purposes of finding meaningful subgroups [e.g. White et al., 1976]. Also, most of the computer programs used for representing and analyzing networks can deal with multiple dimensions in social interactions by generating aggregate indices or by performing Boolean multiplication on binary data (e.g. ''multiplex'' function in UCINET). However, the use of multiplex networks in primatology is rare.

In studies of nonhuman primates, Silk et al. [2006, 2010] defined a composite sociality index which linearly combines the behaviors that are most correlated in their study of chacma baboons (*Papio ursinus*): hourly rates of approaches, presents for grooming, grooming initiations, and the number of minutes of grooming per hour. Although not specifically aimed at studying social structure, these indices show wide variability across dyads and could be used to construct and analyze social networks of affiliation defined by several interaction types. Recently, Lusseau et al. [2011] argued that because the different interactions constituting relationships are not independent (e.g. two individuals cannot groom if they are not in proximity), the value of a tie cannot consist of a linear combination of different interactions, and networks should really be multidimensional objects (tensors, in mathematical terms). These authors develop methods to construct these objects and calculate the mean clustering coefficient and average path length in all dimensions. As such, we believe that SNA represents a promising way to truly study social structure in nonhuman primates as the overall patterning of social relationships.

Another influential framework in primatology is role theory, which originated in social psychology and anthropology in the 1920s and 1930s [Mead, 1934, for an overview see: Roney & Maestripieri, 2003]. According to role theory, roles are the basic units of the social system, relationships are defined according to the respective roles of the individuals involved (e.g. mother–daughter), and social structure emerges from the cumulative outcome of individuals acting in various social roles [Fedigan, 1992]. Role theory was first adopted by primatologists in the 1960s. Although human roles were understood in the context of societal norms and expectations, roles in primates were defined as ''statistically probable behaviors in a given interactional and ecological setting'' [Reynolds, 1970]. Under the framework of role theory, primate researchers explored the roles of adult males [Fedigan, 1972], juveniles [Bernstein & Sharpe, 1966], and aged individuals [Pavelka, 1990], while other studies focused on what they called the control animal role [Bernstein, 1964; Smith, 1973]. Control animals were individuals who mediated intra-group conflict and led defensive attacks against external threats. Usually performed by the most dominant adult male, this role was immediately adopted by another male if the previous control animal was removed from the group [Bernstein, 1966, reviewed by Reynolds, 1970].

Around the same time that role theory gained popularity in primatology, aspects of this theory were incorporated into human-based network research [Scott, 2000]. Even though these studies saw social structure emerging from the patterning of interactions between individuals, and not roles, the concept that individuals could be reduced to a given role was adopted. This subsequently drove methodological advances in SNA and spawned considerable research efforts, investigating topics as diverse as traditional family roles to the impact of roles on the structure of the American economy [reviewed in Borgatti et al., 2009; Burt, 1987].

In the 1980s, role theory research largely fell out of favor with primatologists. This was due, in part, to criticisms that these studies produced little more than descriptions of the general activity patterns of members of given age, sex, and dominance classes [Roney & Maestripieri, 2003], which was further fuelled by accusations, probably based on misunderstandings of the theory and its implications [Fedigan, 1992], that role theory was necessarily connected to group selection [Wilson, 1975], and that social roles lacked clear operational definitions [Hinde, 1974].

Interestingly, recent years have seen renewed interest in social roles in primate behavior [e.g. Flack et al., 2005, 2006]. Conducted under the framework of SNA, this new research uses network-based metrics of individual centrality to define social roles quantitatively and to determine the individuals who occupy them. Individuals occupying particular roles may have a disproportionate influence on social structure, either because they act as brokers between otherwise isolated clusters [Ramos-Fernández et al., 2009], because they have more knowledge about their environment and can act as leaders in coordinated group movements [Lusseau, 2006] or because they serve a policing function, intervening to prevent escalation of conflicts among others [Flack et al., 2006]. The investigation of social roles under the framework of SNA could potentially form an important area of future nonhuman primate research.

CONCLUSIONS

SNA is a framework for the study of complex societies that owes its existence and continued development to the contributions of a wide-range of fields. The last 15 years have seen considerable advances in SNA-related analytical tools and computer software, resulting in the rapid expansion of the scope of application of SNA. Consequently, SNA has recently been used in a number of studies of animal behavior, including many studies of nonhuman primates. Although the rich history of nonhuman primate behavioral research includes the application of some of the techniques and concepts currently associated with SNA, there are also many social network-based methods that are novel and constitute valuable extensions to those traditionally used by primatologists. In this review, we have demonstrated that there is a complex and perhaps understated historical relationship between SNA and nonhuman primate behavioral research. We also hope to have identified areas in the study of nonhuman primate behavior in which a fresh perspective, using SNA, might prove fruitful.

ACKNOWLEDGMENTS

We were motivated to write this review by stimulating conversations with colleagues, in particular the participants of the symposium on social networks at the XXIII Congress of the International Primatological Society in Kyoto, Japan, to whom we wish to extend our great appreciation and thanks. Many thanks also to Cédric Sueur and Andrew King for their efforts in producing this special issue and for allowing us to contribute. Drew Marticorena and two anonymous reviewers provided helpful and much appreciated comments on the manuscript. L.J.N.B. is supported by the NIH (grant no. 1R01-MH-089484-01) and thanks Michael Platt, Stuart Semple, and Ann MacLarnon for their support. G.R.F. is supported by CONACYT grant J51278 and by the Instituto Politécnico Nacional. The production of this manuscript adhered to the American Society of Primatologists' principles for the ethical treatment of primates.

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