Social Network Analysis in Behavioral Ecology

Matthew J. Hasenjager and Lee Alan Dugatkin[1]
Department of Biology, University of Louisville, Louisville, Kentucky, USA
[1]Corresponding author: E-mail: lee.dugatkin@louisville.edu

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1. INTRODUCTION

Social behavior is a pervasive feature of animal life (Alexander, 1974; Wilson, 1975; Davies, Krebs, & West, 2012; Alcock, 2013; Dugatkin, 2013). This ubiquity suggests that an animal's social environment will often play a

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critical role in influencing the development and expression of their behavior, as well as its fitness outcomes (Maynard Smith, 1982; Montiglio, Ferrari, & Réale, 2013; Stamps & Groothuis, 2010). Animal social groups are often characterized by complex, dynamic, and nonrandom patterns of social relationships (Croft, James, & Krause, 2008; Sih, Hanser, & McHugh, 2009; Davies et al., 2012; Alcock, 2013; Dugatkin, 2013). Therefore, in order to fully understand the evolution of social behavior, these aspects of social structure must be explicitly incorporated into models of animal behavior. Over the past few decades, behavioral ecologists have become increasingly cognizant of this fact. This recognition has led to fascinating novel insights in the study of social behavior and continues to generate new, potentially very important, hypotheses that are ripe for testing.

Social network theory provides both a conceptual framework and the analytical tools to explore the interplay between individual behavior, population structure, and population-level processes (Croft et al., 2008). Starting in the 1930s, social network theory has been widely used in sociology to study human relationships and social organization (Moreno, 1934; Lewin, 1951; Scott, 2000). More recently, these approaches have been applied toward the study of nonhuman social systems (Croft et al., 2008; Whitehead, 2008).

Social network theory views a social group as a system of interconnected elements which are usually—though not always—individuals (Newman, 2003). A social network can be graphically depicted as a collection of nodes, where each node represents an individual within the group. Social interactions or associations between two individuals are denoted by an edge connecting their two nodes together. Nodes can be assigned attributes—e.g., sex, body size, personality type—corresponding to the individual they represent. Edges, too, can vary in a number of properties. For example, edges can be weighted to indicate the relative frequency or intensity of a relationship, such as how often two individuals copulated, or directed to indicate asymmetric interactions—e.g., individual A groomed B, but not vice versa. The pattern of edges connecting nodes together, combined with the attributes possessed by the nodes and edges, makes up a group's social network.

Social network analysis (SNA) provides researchers with a wide variety of tools to explore different aspects of network dynamics, structure, and function. The structure of a social network can be described using a multitude of quantitative network measures that capture different aspects of social structure at the level of the dyad, the individual, and the population

(see examples in: Box 1; Croft et al., 2008; Wey, Blumstein, Shen, & Jordán, 2008; Whitehead, 2008). Networks often possess emergent properties arising from the complex ways in which nodes can interact with one another (Bradbury & Vehrencamp, 2011). Mathematicians have constructed several types of network models to better understand these emergent properties, their function in real-world networks, and how these networks form and evolve over time (Newman, 2003). These models can then be tapped by social network analysts for a number of purposes. For example, observed network measures can be compared to those generated from a simulated network to identify significant departures from null expectations, thereby revealing potentially important aspects of a population's social organization (Croft et al., 2008). Network modeling can also be used to determine the causal factors—e.g., individual behavior, environmental conditions—that drive observed network structure (Newman, 2003; Pinter-Wollman et al., 2014). Furthermore, a social network provides the substrate upon which population-level processes—e.g., disease transmission, information flow, or the emergence and maintenance of cooperation—may play out. Understanding the dynamics and structure of a population's social network provides us with predictive power with respect to these processes and can enhance our understanding of how social organization influences individual behavior (e.g., Croft et al., 2006; Hoppitt & Laland, 2013; Wilson et al., 2014).

SNA offers several advantages to behavioral ecologists when combined with more traditional methods of studying social structure and behavior. For one, SNA provides a holistic framework that directly links individual behavior to population structure. By population, we refer to a set of potentially interacting individuals in which the majority of interactions are among its members (Whitehead, 2008); in practical terms, the population refers to all the nodes making up a given social network. The ability of SNA to integrate individual behavior and population structure allows for a more sophisticated exploration of questions at both levels; many behaviors can only be fully understood when placed within the social context of the entire population. For example, the spread of social information, diseases, or parasites through a population depends not only on whom an individual directly interacts with, but also with whom their social partners interact (Godfrey, Bull, James, & Murray, 2009; Hoppitt & Laland, 2013; VanderWaal, Atwill, Isbell, & McCowan, 2014).

SNA also provides behavioral ecologists with a complex and detailed view of social structure applicable to a myriad of species and behavioral

Box 1 Terminology of Social Network Analysis

Social network theory views a social group as a system of interconnected individuals (Newman, 2003). **Social network analysis (SNA)** uses a variety of tools—e.g., visualization, descriptive measures, modeling, and simulations—to explore the dynamics that form a social network, the structure of that network, and the consequences of that structure for processes occurring over the network and the behavior of individuals within it. These analyses can scale from the individual level up to that of the population.

A social network can be visually represented as a series of **nodes** (also: **vertices**) representing individuals connected by **lines** (also: **edges, ties**) representing social relationships between two connected individuals. This visual representation is also known as a **sociogram** or **graph**. Ties can be **unweighted** (also: **binary**), where a tie between two nodes simply indicates the presence of a relationship (e.g., grooming), or **weighted**, where ties indicate the strength or frequency of an interaction (e.g., the number of times grooming occurred). Ties can also be **bidirectional** for symmetrical or reciprocated interactions, as is often the case for proximity, or they can be **directional** when interactions are asymmetrical or unreciprocated, such as if individual A groomed, but was never groomed by, individual B.

In addition to visual representation, a social network can also be represented as a **sociomatrix**, defined as the matrix of association or interaction measures between each pair of individuals in the population. Most quantitative network analyses are performed using this matrix.

Throughout this review, we use the term **social structure** to refer to the quality, content, and patterning of social relationships within a population (Hinde, 1976). The **population** will be defined as the collection of potentially interacting individuals on which a particular social network is based. A **community** is a set of nodes that are more densely interconnected to one another than they are to the wider network. The extent to which communities play an important role in dividing up a population can be assessed via Newman's (2004) **modularity** measure, which takes the difference between the proportion of total weights or edges connecting individuals within communities and the proportion expected if individuals associated at random.

A variety of network measures are available to describe different aspects of an individual's pattern of connectedness. Often, individual measures can be averaged across all individuals in the population—or across a class of individual—to provide population- or class-wide measures of social structure. Below, we introduce several commonly used network metrics and provide references in which they have been applied and/or where formulas for their calculation can be found.

Degree: the total number of connections a node has. In-degree and out-degree can be quantified for directional ties. For example, an individual's in-degree could be the number of social partners that have groomed it, while

Box 1 Terminology of Social Network Analysis (*cont'd*)

its out-degree would be the number of social partners it has groomed. Degree provides a measure of how well connected an individual is in its network—as well as its potential importance to overall network structure—based on its direct social partners.

Strength: the total weight of all ties connected to a node. In-strength and out-strength can be calculated for directional, weighted ties. Strength is the corresponding measure for weighted networks that degree is for binary ones. Strength also serves as a measure of gregariousness (Whitehead, 2008).

Clustering Coefficient: measures the extent to which a node's network neighbors are also connected with one another. The clustering coefficient averaged over the whole network provides a measure of how cliquish a network is; networks with high clustering are made up of highly interconnected social units (see Newman, 2003; Holme, Park, Kim, & Edling, 2007; Whitehead, 2008).

Eigenvector Centrality: a measure of how well connected a node is, taking into account not only the number and strength of direct connections, but also how well connected that node's neighbors are. Unlike degree or strength, eigenvector centrality also takes indirect connections into account. Computationally, eigenvector centrality is obtained from the first eigenvector of the sociomatrix (see Newman, 2004; Whitehead, 2008).

Reach: a measure of indirect connectedness; in a binary network, it measures the number of nodes *n* or fewer steps away from the focal node. See Whitehead (2008) for an example of how reach can be calculated for a weighted network. This measure might be particularly useful when a researcher is interested in the possibility of the spread of a behavioral trait or a type of interaction—e.g., agonistic behavior between individuals A and B causes B to direct agonistic behavior toward individual C (see Flack et al., 2006; Whitehead, 2008).

Path Length: the number of edges on the shortest pathway between two individuals. Path length measures how well connected two nodes are with each other.

Betweenness: the number of shortest path lengths between pairs of nodes in the network that pass through the focal node. Individuals that have high betweenness link together many individuals in the network and can therefore have particularly important effects on the flow of information, disease, or resources through a population. For example, imagine two clusters of individuals where the only connection between these clusters passes through a single intermediate individual. If a novel behavior arises in one cluster and spreads via social learning, the only way for that trait to reach the other cluster is through that intermediate individual (see Freeman, 1979; Lusseau & Newman, 2004; Whitehead, 2008).

Information Centrality: measures a similar property as betweenness, but also takes into account longer pathways weighted by the inverse of their length (see Stephenson & Zelen, 1989; McDonald, 2007; Vital & Martins, 2011, 2013).

(Continued)

Box 1 Terminology of Social Network Analysis (*cont'd*)

By viewing social groups as a system of interconnected nodes, social network theory highlights the potential for **emergent properties** to arise at the population level as a consequence of the complex patterns of relationships between individuals. Emergent properties are not predictable by considering each contributing factor in isolation from one another (Bradbury & Vehrencamp, 2011). In network terms, the structural properties of a network usually cannot be assessed by measuring the dyadic relationships of its constituent members in isolation. Only when these same relationships are allowed to interact with one another in the context of the whole population are we able to properly assess the structure and function of a network. Examples of emergent network properties include: population-wide resilience to loss of members (e.g., Lusseau, 2003), the formation of stable dominance hierarchies (e.g., Shizuka & McDonald, 2012), multitiered social structures (e.g., VanderWaal, Wand, et al., 2014), and the rate at which socially learned behaviors spread through a population (e.g., Whitehead & Lusseau, 2012; Aplin et al., 2015).

milieus. In this review, we define social structure as the nature, quality, and patterning of social relationships within a population, where a relationship summarizes the content, quality, and patterning of interactions between two individuals (Hinde, 1976); following Whitehead (2008), we use the terms social structure, social organization, social system, and society interchangeably. SNA incorporates information on individual behavioral variation and offers a wealth of network measures which provide an objective means of quantifying a population's social structure. This approach can complement conventional methods of describing animal societies—e.g., via group size, demography, mating system, or division of labor—that often downplay the variation and complexity of intragroup relationships or are only useful for specific taxonomic subgroups (Wilson, 1975; Wey et al., 2008; Whitehead, 2008). Furthermore, these network descriptors can facilitate comparative studies between populations and species to better understand how social structure and behavior is shaped by ecology and evolutionary history.

In addition to casting new light on old problems, a social network approach can highlight previously unconsidered or neglected social processes. If a social network is a system of interconnected nodes, then the potential exists for interactions between those nodes to involve nonlinear elements—e.g., competition, interference, or cooperation—which, in

turn, may generate emergent properties (Couzin, Krause, James, Ruxton, & Franks, 2002; Sumpter, 2006; Bradbury & Vehrencamp, 2011). The potential for animal social networks to facilitate emergent social phenomena has been traditionally underappreciated (Bradbury & Vehrencamp, 2014). The establishment of linear dominance hierarchies (e.g., Shizuka & McDonald, 2012), collective decision-making (e.g., Sueur, Deneubourg, & Petit, 2012), and the collective motion of animal groups (Bode, Wood, & Franks, 2011a) are all classic examples of emergent social processes; in each case, our understanding of the phenomenon has been enhanced by adopting a network-based approach.

Network theory is being simultaneously developed in a number of fields, including statistical physics, sociology, molecular biology, and computer science. As a result, the field is changing at a rapid pace, with concepts, approaches, and measures developed in one context often finding use in another. While not all developments can—or should—be applied toward the study of animal societies (James, Croft, & Krause, 2009), this rush of novel ideas from outside sources is sure to enrich behavioral ecology.

Our goal in this review is threefold. First, we will trace the history of the study of nonhuman social structure from early ethological ideas to modern social network theory. In so doing, we shall see that the fundamental questions and topics dealt with by social analyses have changed very little over time. However, the development of new conceptual frameworks and analytical techniques, as well as extensive cross-pollination from other disciplines, has allowed behavioral biologists to increasingly embrace the complexities seen in the natural world. Next, we will outline the concepts behind modern social network theory and discuss some of the new insights it has provided behavioral ecologists over the past decade. Here, we focus on social learning, collective movement and decision-making, animal personalities, and animal cooperation. While this by no means represents an exhaustive list of the potential topics to which SNA has been—or can be—applied, the above behaviors and phenomena possess many features—e.g., indirect effects, dependence on population structure, emergent properties—that network-based approaches are especially well suited to handle. Third, and finally, we will highlight intriguing new avenues of research as advancing technology and statistical methods allow researchers to address more nuanced questions regarding social behavior than ever before.

Just as SNA in behavioral ecology developed from earlier approaches to studying population structure and social behavior, SNA itself is evolving. Indeed, SNA has experienced an influx of new ideas and applications

over the past decade, as well as generated a wealth of novel insights. Since it has been several years since a number of reviews on the subject (Krause, Croft, & James, 2007; Croft et al., 2008; Wey et al., 2008; Whitehead, 2008; Sih et al., 2009), we feel the time is right to revisit it and review many of its recent developments. In this way, we hope to serve as a conceptual introduction to SNA for behavioral ecologists and a source of inspiration for future research.

2. A HISTORICAL PERSPECTIVE ON THE STUDY OF ANIMAL SOCIAL STRUCTURE

Drawing on developments from ethology, sociology, primatology, statistical physics, and behavioral ecology, the history of SNA in nonhuman systems is a rich one. While a comprehensive treatment is not possible here, we have distilled what we feel are the major developments leading up to the application of modern network analysis in behavioral ecology. The introduction to Whitehead (2008) and the review by Brent, Lehmann, and Ramos-Fernández (2011) provide more on this subject, with the latter dealing specifically with the study of nonhuman primate social structure. We do not review here the extensive sociological literature on network analysis except where it explicitly intersects with our primary objective—i.e., examining the evolution of network analysis in nonhuman systems. Interested readers should instead refer to several excellent treatments of that subject (Wasserman & Faust, 1994; Scott, 2000; Freeman, 2004; Borgatti, Mehra, Brass, & Labianca, 2009; Scott & Carrington, 2011).

2.1 Early Approaches

The evolutionary and ecological importance of animal social structure was formally recognized as early as the late nineteenth century (Crook, 1970; Whitehead, 2008). In 1878, Espinas proposed that animal societies were not simply random assemblages of individuals, but rather possessed structure and persisted as distinct entities over time (Espinas, 1878). Espinas argued that variation in animal social structures was related to ecological conditions rather than phylogenetic history. For example, the territories of carnivorous or piscivorous birds were often more defined and better defended than those of other avian species, but these territorial boundaries would break down during periods of high resource abundance. Espinas further argued that animal societies possessed emergent, group-level properties that arose from the complex web of social interactions within a population. He

even suggested that animal *societies* could be influenced by natural selection and evolve as entities in their own right.

Petrucci (1905, 1906) discussed animal territories and social organization in relation to individual, familial, and societal requirements, though he was careful to note that lower levels need not be present for higher levels to be in place—i.e., a society can form independently of familial concerns, while a family can be considered a social group in its own right. Like Espinas, Petrucci noted a correlation between environmental conditions and animal social structure, suggesting selection pressures played a role in shaping social organization. These early ideas lay fallow for some time before being rediscovered in the mid-twentieth century, in part due to neither author being biologists by trade, as well as the fact that contemporary biologists of the time were not particularly interested in such questions (Crook, 1970).

The first comprehensive attempt to place nonhuman social behavior within a larger conceptual framework came with the birth of ethology. For the most part, discrete social behaviors were believed to be innate and under control of special "centers" within the brain (Tinbergen, 1953). Over time, action-specific energy built up in these centers, requiring release which was provided by the presence or behavior of conspecifics. Lorenz (1937) likened the phenomenon to that of a lock and key. Natural selection shaped species to behaviorally respond in appropriate ways to unique combinations of stimuli (i.e., the "key") to which their brain was attuned (i.e., an innate perceptory pattern or the "lock"). While this system was believed to apply to any stimulus–response relationship, when the releasing stimulus involved a conspecific—i.e., a *kumpan* in Lorenz's terminology—signaler–receiver coevolution was possible over evolutionary time. This coevolutionary process could then give rise to specialized morphological structures and stereotyped motor patterns as seen, for example, in many avian courtship rituals. These morphologies and behaviors presumably evolved for the explicit purpose of influencing conspecifics.

To an early ethologist, social organization was simply the sum of the innate stimulus–response relationships corresponding to conspecifics (Tinbergen, 1953). Little consideration was given at the time to questions of group composition and how relationships were patterned within a group, nor how these structural elements might influence social behavior both between group members and over the course of an individual's life. Rather, dyadic interactions had been primarily studied as isolated phenomena detached from their wider social environment (Beer, 1976; Hinde, 1982). Intra- and interindividual variation in behavior was downplayed; instead,

innate, species-specific stereotyped behavior patterns were emphasized (Hinde, 1982).

This situation began to change in the 1950s as researchers started to question ethology's highly mechanistic explanations for behavior, as well as its tendency to neglect the full gamut of factors that could influence behavioral development and expression (Hinde, 1959; Kennedy, 1954; Lehrman, 1953). More explicit consideration was given to how genetic, ecological, and social factors interacted to produce variation in social structures and behavior (McBride, 1964; Lack, 1968). This transition came about in part due to recognition of significant intraspecies variability in primate social behavior that was not well explained by a system of innate, inherited releasing mechanisms (Crook, 1970). For example, harkening back to ideas raised by Espinas, studies found that vervet monkeys (*Chlorocebus pygerythrus*) living on a small island with rich food sources demonstrated territorial behavior not observed in vervet groups living in larger areas with sparser resources (Crook & Gartlan, 1966). The ecological conditions experienced by a group were an important determinant of social structure, while the ontogeny and expression of an individual's social behavior were critically influenced by both the ecological and social contexts experienced by that individual (McBride, 1964; Crook, 1970).

2.2 Searching for a Conceptual Framework

As interest in describing and comparing animal social structures between and within species grew, researchers recognized the need for a common framework within which they could work. C. R. Carpenter (1942a, 1942b, 1952) was one of the first to consider nonhuman primate social structure in a comparative sense. He developed species-specific models that described the spatial arrangement of individuals as determined by individual- and class-level patterns of affiliation and avoidance, though his work garnered little interest at the time (Sade, 1972). Drawing from prior classification schemes of social behavior in both sociology and ethology (Scott, 1945; Bales, 1951), Thompson (1958) sketched out a potential comparative framework of social structure that distinguished between social interactions that had either a positive or negative influence on group unity. Layered atop of this would be characteristics of the actors and recipients, such as sex or kinship, whether the interactions involved in- or out-group members, and their function (e.g., foraging, reproduction). The sum of these interactions formed the structure of a group, which could be characterized by: (1) the number of group members, (2) their density, (3) their cohesiveness—that is, the physical

proximity of group members, (4) the coordination exhibited among members when carrying out various tasks, and (5) group stability and permeability.

Noting the failure of earlier attempts to classify animal societies as resulting from an overly reductionist approach or a lack of generality by focusing too closely on taxon-specific social traits—e.g., eusociality, mating system, life cycles—E. O. Wilson advocated that researchers instead focus on social qualities that could be universally applied toward any study system (Wilson, 1975). He expanded on Thompson's (1958) list, devising a set of 10 qualities by which researchers could describe social structure: (1) group size, (2) demography, (3) cohesiveness, (4) amount and patterns of connectedness, (5) permeability, (6) compartmentalization—that is, the extent to which subgroups act as one unit, (7) role differentiation, (8) coordination of behavior, (9) information flow, and (10) fraction of time devoted to social behavior. Today, SNA allows researchers to study many of these qualities—e.g., cohesiveness, connectedness, compartmentalization, behavioral coordination, and information flow—under one integrated framework (Whitehead, 2008).

Behavioral ecologists, excluding those that worked with primates, were slow to adopt many of these social qualities (Whitehead, 2008); nonprimate social structures were primarily described by group size and demography (e.g., Jarman, 1974; Brosset, 1976). This stemmed both from a lack of analytical tools, as well as the misguided assumption that only primates had social systems that were sufficiently complex—e.g., involving individual recognition—to warrant such studies (Whitehead, 1997, 2008). Even cognitively advanced and highly social animals, such as cetaceans, were dismissed as having a relatively simple social organization (Gaskin, 1982). Primatologists, however, forged ahead with a number of approaches to describing, classifying, and comparing social systems (Silk, 2007; Brent et al., 2011).

Because sociologists also study primates—albeit usually focusing solely on humans—it is not all that surprising that there is a rich tradition of importing methods developed in sociology to study nonhuman primate social structure (Roney & Maestripieri, 2003). A particularly profitable import from sociology was the sociometric approach. Developed in the 1930s, sociometry sought to quantitatively describe the structure of human groups, and the positions of individuals within those groups, through application of mathematical graph theory (Moreno, 1934; Lewin, 1951). *The pattern of social relationships* between group members determined overall social structure and could be depicted as a set of nodes connected by edges—i.e., a sociogram (Box 1) (Moreno, 1934; Scott, 2000). Sociometric analyses

usually took the form of creating matrices that quantified some type of interaction between each pair of individuals in a group and used quantitative measures to describe the resulting pattern of social relationships. These analyses could be applied toward potentially any type of interaction, such as aggression, trade, affiliation, or communication.

Drawing from these sociometric ideas, ethologist R. A. Hinde (1976) sought to provide a unifying conceptual framework for studies of primate social structure, though he also recognized its potential utility for nonprimate animals as well. The framework he proposed had three levels: interactions, relationships, and social structure, each of which influenced, and was influenced by, the other two levels (Figure 1). *Interactions* involve specific instances in which two individuals do something together or in which an individual directs an action toward another individual—e.g., two baboons

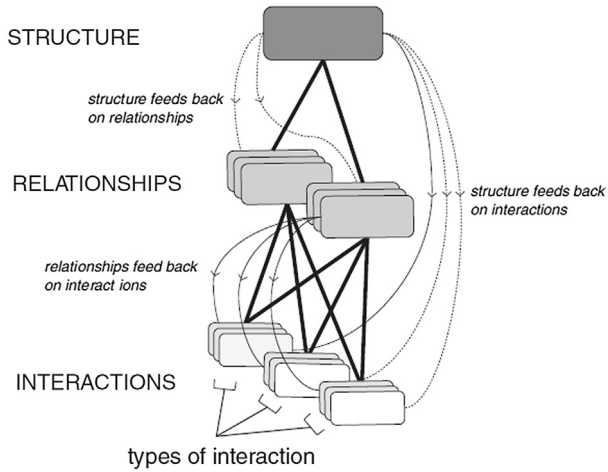

Figure 1 A simplification of Figure 1 from Hinde (1976) depicting a framework for the description of animal social structure. Successive interactions between two individuals make up their relationship, while the pattern of relationships within a population determines social structure. Feedbacks can occur between each level; for example, structure can influence the types of interactions likely to occur between two individuals. The relationship of two individuals accounts for all types of social interactions that have occurred between them—e.g., grooming, copulation, agonistic behavior—as well as the frequency and temporal patterning of those interactions. *Reprinted with permission from: Brent et al. (2011). Social network analysis in the study of nonhuman primates: a historical perspective.* American Journal of Primatology, 73, *720–730. Copyright © 2011 John Wiley and Sons. Originally adapted from: Hinde (1976). Interactions, relationships, and social structure.* Man, 11, *1–17. Adaptation reprinted here with permission from John Wiley and Sons, copyright © 1976.*

grooming one another or two fish shoaling together. Repeated interactions over time between two individuals form the basis of their *relationship*. Description of a relationship includes not only what two individuals do together, but how those interactions are patterned—e.g., the frequencies and timing of interactions, as well as the effect one type of interaction can have on another. Taken together, the nature and patterns of relationships within a group make up the *social structure* of that group. New properties emerge at each of Hinde's three levels—interactions, relationships, and structure—that are not present in the component units making up the lower levels. For example, the nature of an interaction results from the behavior of both individuals involved, each of which can act in a variety of ways depending on the identity of their partner. Hinde also discussed how various factors, such as kinship, sex, or age, might be expected to influence relationship patterns.

By clarifying the links between interactions, relationships, and the emergence of social structure, Hinde (1976) provided a conceptual framework that linked individual behavior to population structure and vice versa. In doing so, he underscored the importance of studying social behavior within the context of the whole population, as population structure could feed back to influence the nature of social interactions and relationships. Hinde's framework has proven itself to be widely applicable (e.g., Whitehead, 2008) and it was influential in prompting further development of sociometric approaches in nonhuman animals—e.g., block models (Pearl & Schulman, 1983)—as well as other forms of social analyses—e.g., ordination methods and lagged association rates (Kappeler, 1993; Whitehead, 1997; Whitehead & Dufault, 1999). Sociometry in particular was an important precursor to modern SNA (Brent et al., 2011), though it had some crucial limitations which we highlight below.

2.3 The Development of Sociometric Approaches in Primates

Sociometric approaches such as those advocated by Hinde (1976) were initially applied primarily to nonhuman primates and proved a fertile ground for researchers. For example, presenting social data as a sociogram allowed important, and sometimes nonintuitive, features of social structure to be highlighted in a much more accessible format as compared to data matrices. An early application of this technique to primate research was Sade's (1965) depiction of rhesus macaque (*Macaca mulatta*) grooming relationships as a network of nodes connected by lines indicating the direction and frequency

of grooming interactions between two individuals (Figure 2). Sociograms have been widely used to depict primate social relationships including: grooming (e.g., Soczka, 1974; Seyfarth, 1976, 1977; Cheney, 1978a; Fairbanks, 1980; Hanby, 1980b; Seyfarth, 1980; Pearl & Schulman, 1983; Mitani, 1986; Chepko-Sade, Reitz, & Sade, 1989; Nakagawa, 1992), proximity (Fairbanks, 1980; Hanby, 1980a; Seyfarth, 1980; Nakagawa, 1992), agonism (Hanby, 1980b; Pearl & Schulman, 1983), play (Soczka, 1974; Cheney, 1978b; Pearl & Schulman, 1983), and copulations (Cheney, 1978a; Pearl & Schulman, 1983). While there is a limit to the amount of usable information that can be effectively conveyed in a sociogram, they remain an invaluable graphical tool for SNA.

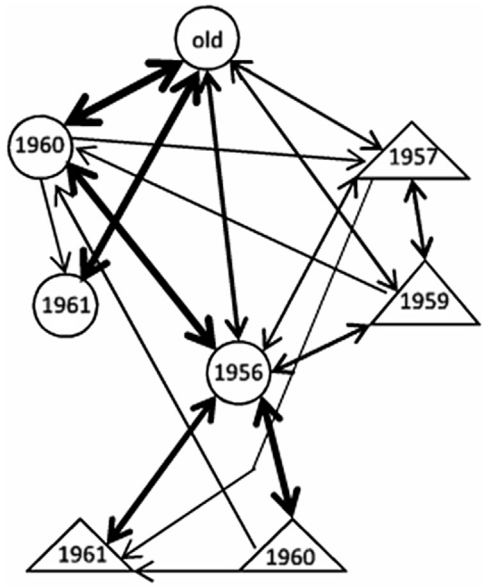

Figure 2 Sociogram of a rhesus macaque (*Macaca mulatta*) grooming network originally published by Sade (1965). Circles indicate females and triangles represent males. The lines between individuals indicate that grooming has occurred between these individuals; the thickness of the line is proportional to the frequency of grooming interactions. The arrows depict the direction of grooming—e.g., individual 1960 groomed, but was not groomed by, individual 1961. *Reprinted with permission from: Brent et al. (2011). Social network analysis in the study of nonhuman primates: a historical perspective.* American Journal of Primatology, 73, 720–730. *Copyright © 2011 John Wiley and Sons. Originally adapted from: Sade (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming.* American Journal of Physical Anthropology, 23, 1–17. *Adaptation reprinted here with permission from John Wiley and Sons, copyright © 1965.*

As an example of the utility of the sociometric approach, we turn to the rich history of studies on primate allogrooming (e.g., Sade, 1965; Kummer, 1968; Seyfarth, 1977). The structuring of grooming relationships was of particular interest to primatologists both because of the relatively high frequency at which grooming interactions occurred relative to other primate social behaviors and because other important behaviors and processes were suspected to be influenced by this structure—e.g., coalitionary support and the likelihood of receiving aggression (Rhine, 1973; Seyfarth, 1980; Seyfarth & Cheney, 1984). These studies revealed that grooming interactions were nonrandomly distributed within primate groups and that this structure was driven by a variety of social factors. For example, fewer than 15% of the possible dyads accounted for 62% of the grooming interactions in one group of rhesus macaques (*M. mulatta*), indicating a highly structured grooming network based on kinship (Sade, 1965). High-ranking females were preferred grooming recipients relative to low-ranking females in several species, including Chacma baboons (*Papio ursinus*) (Cheney, 1978a; Seyfarth, 1976), stump-tailed macaques (*Macaca arctoides*) (Rhine, 1973), and vervet monkeys (*C. pygerythrus*) (Seyfarth, 1980). However, females tended to instead groom individuals of adjacent social rank to themselves due to a number of influences—e.g., constraints imposed by higher-ranking individuals, kin-based preferences (Sade, 1965, 1972; Seyfarth, 1976; Cheney, 1978a; Seyfarth, 1980)—thereby demonstrating how studying dyadic relationships in isolation from the larger social environment can be misleading. Furthermore, sudden increases in grooming received were often observed for lactating females with infants, highlighting the dynamic elements of social structure (e.g., Seyfarth, 1976; Cheney, 1978a; Seyfarth, 1980).

Most sociometric analyses either focused on only one type of interaction (e.g., grooming) or examined multiple behaviors independent of one another. However, animals are embedded simultaneously within multiple networks, each of which might exert influence on the others. Pearl and Schulman (1983) attempted to combine multiple social networks into a single network through their application of block models to two social groups of rhesus macaques (*M. mulatta*). Sociomatrices for grooming, play, mating behaviors, proximity, threat displays, and fear grimaces were constructed and combined into one large matrix. Macaques were then partitioned into "blocks" such that the relationships individuals within a block share with those outside of their block are largely similar to one another. The behavioral profiles of these blocks were then compared within and between groups. A comparison of how different types of interaction related to one

another—for example, the relationship between proximity and play networks—suggested common factors influenced social structure in both groups despite dramatically different demographic profiles within, and ecological conditions experienced by, each population. One group was made up of about 25 wild individuals in the mountains of Pakistan, while the other was a large, free-ranging group containing about 100 individuals on the Caribbean island of Cayo Santiago. While these early block model studies were useful for considering multiple network types simultaneously, as well as potentially facilitating comparative studies of social structure, they tended to discard a great deal of information regarding an individual's network position that was of great interest to behavioral biologists. Block modeling has not been widely used in behavioral ecology, though it has seen continued use and development in other fields, including molecular biology (e.g., Wang & Qian, 2014) and sociology (e.g., Žiberna, 2014).

Even though it lacked a robust, quantitative methodology, sociometric analyses in primates presaged modern SNA in many ways. As in SNA, these early studies constructed a representation of social structure based on repeated interactions between group members, used numerical measures to describe this structure, and could graphically depict structural patterns using a sociogram. Also like SNA, sociometry sought to understand the reciprocal interplay between individual behavior and overall group structure (e.g., Sade, 1972; Hinde, 1976; Seyfarth, 1977; Hanby, 1980b; Sade, Altmann, Loy, Hausfater, & Breuggeman, 1988).

Sociometric studies were hamstrung by a lack of computational power, as well as by methodological issues (Brent et al., 2011). While Hinde (1976) had provided a useful conceptual framework for visualizing social structure, tools for quantitatively analyzing this structure lagged behind (Pearl & Schulman, 1983). Some network measures such as degree (i.e., the number of social partners an individual has) and strength (i.e., the frequency of interaction) were easily calculated by hand and were frequently used. Utilization of most other network metrics, however, had to await greater availability of computing power (though see: Sade, 1972; Kaplan & Zucker, 1980; Sade et al., 1988). Methods for assessing the statistical significance of nonindependent, relational data, such as is used in network studies, were infrequently applied (Sade & Dow, 1994). Comparing social structures between groups, populations, and species remained fraught with challenge (Sade, 1972; Chepko-Sade et al., 1989; Whitehead, 1997). Further, sociomatrices and sociograms represented a static image of a network that in reality was likely to be constantly changing as a result of environmental,

social, and demographic factors (Sade, 1965; Hanby, 1980b). While many of these issues remain challenges for SNA, progress has since been made on several of them.

A more important difference between modern SNA and these early sociometric studies is that SNA goes beyond simply describing and depicting network structure: SNA attempts to understand how that structure forms, what properties it might possess, and its function in ecological and evolutionary processes (e.g., Pinter-Wollman et al., 2014). For example, modern SNA might ask how network structure influences the flow of information through the network or how it impacts the use of behavioral strategies in the population. Furthermore, SNA emphasizes the potential for social structure to possess emergent properties, such as resilience in terms of network structure and function when faced with removal of individuals from the population (e.g., Lusseau, 2003). In these ways, as well as others, modern SNA encompasses much of the sociometric approach, but also amends it significantly by adding new concepts, questions, and techniques. Before we discuss the use of modern SNA in behavioral ecology, however, we first turn to some of the important contributions to social analyses made by nonprimatologists.

2.4 The Study of Social Structure Embraces Nonprimates

In the 1980s and 1990s, behavioral ecologists (many of whom were trained by primatologists) began to apply sociometric methods and related approaches to nonprimate species, including: ungulates (Clutton-Brock, Guinness, & Albon, 1982; Le Pendu, Briedermann, Gerard, & Maublanc, 1995), cetaceans (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990; Connor, Smolker, & Richards, 1992), and birds (Ekman, 1979; Myers, 1983). Contrary to earlier claims, it rapidly became apparent that nonprimates also possessed a great deal of complexity in their social interactions and organization. For example, male bottlenose dolphins (*Tursiops* spp.) were demonstrated to preferentially associate with one or two other males, forming long-term alliances through which members gained increased access to females (Connor et al., 1992). In some instances, two of these alliances would even cooperate, forming a superalliance that facilitated joint theft of a female from another alliance (Connor et al., 1992; Connor, Heithaus, & Barre, 1999). Many ungulate species were shown to possess seasonal variability in social organization, as well as nonrandom, preferential associations between individuals based on age and sex (e.g., Le Pendu et al., 1995; Underwood, 1981). By expanding work to nonprimate social systems, behavioral ecologists were able to study a wider variety of life histories,

mating systems, demographics, ecological contexts, and other factors relevant to social structure than they could previously. How this variation translated into variation in social structure—and how that, in turn, influenced the fitness outcomes of social behavior—provided innumerable avenues for fascinating research.

Analytical techniques were developed which could deal both with the much larger population sizes present in many nonprimate species relative to primate populations, as well as interaction or association data that were often much sparser than that available in primate studies (Whitehead & Dufault, 1999). For example, lagged association rates and other similar techniques allowed researchers to describe the temporal patterning of social relationships in a population. These temporal patterns are an important aspect of social structure, as the same average interaction rate between two individuals can have quite different interpretations if interactions persist at a low, but stable, frequency over time as compared to a high initial interaction frequency that quickly falls to zero. Myers (1983) calculated the likelihood of sanderling (*Calidris alba*) pairs remaining together over time intervals of hours, days, months, and years, finding that associations broke up quickly as birds moved throughout the foraging area and that associations did not persist over longer time periods. Underwood (1981) created what were basically survivor curves for the length of time two animals remained associated with one another, and found that individual eland (*Taurotragus oryx*) were often found together on consecutive days, but associations tended to quickly deteriorate after that.

These two approaches were further developed by Whitehead (1995, 1997) as the lagged association rate which calculates the probability of association τ time units since an earlier known association between two individuals. While a significant amount of data are needed to confidently characterize the temporal relationship for a particular dyad, the lagged association rate can be generalized over a class of individual, a community, or an entire population (Whitehead, 2008). In doing so, it provides a powerful approach that can be used even for species where social behaviors are difficult to observe and specific individuals are encountered rarely and opportunistically—e.g., sperm whales (*Physeter macrocephalus*) (Whitehead, 1995, 2008).

2.5 The Advent of Modern Social Network Analysis in Nonhuman Systems

It is difficult to draw a firm line dividing SNA from earlier sociometric methods. While some authors appear to see a clear delineation between

the work we have described above and SNA (Whitehead, 2008), others—e.g., Croft et al. (2008)—see SNA as further development of these early approaches that simultaneously embraces concepts, techniques, and methodologies from a wide range of disciplines in which network approaches have been applied, including sociology (Moreno, 1934; Homans, 1951; Wasserman & Faust, 1994; Hanneman & Riddle, 2005), business (Levine, 1972), economics (Burt, 1988), ecology (Harary, 1961; Solé & Montoya, 2001), physics (Newman, 2003, 2004), and molecular biology (Rausher, Miller, & Tiffin, 1999; MacCarthy, Seymour, & Pomiankowski, 2003; Kollmann, Løvdok, Bartholomé, Timmer, & Sourjik, 2005). While this can occasionally lead to misapplication of concepts and analyses that are not relevant when applied to animal groups (see James et al., 2009), it also allows researchers to explore social structure from a number of angles in order to better identify both the causal factors that drive observed patterns and the consequences of those patterns (Croft et al., 2008).

The main conceptual difference between early network approaches, such as sociometry, and modern SNA is that the latter emphasizes viewing a social network as a system of interconnected nodes that has the potential to generate complex properties and outcomes (Newman, 2003; Bradbury & Vehrencamp, 2014). Modern SNA does not just use descriptive measures to quantify individual- and population-level social structure, though that certainly remains an important part (Croft et al., 2008): It also seeks to understand the functional consequences of different types of network structure. SNA identifies emergent structural properties that arise from complex patterns of social relationships and explores how these properties influence individual behavior occurring within the network and social processes playing out over it (Newman, 2003). SNA also tries to understand the ecological factors and underlying social dynamics that result in the emergence of particular structural elements (e.g., Barabási & Albert, 1999; Wilson et al., 2014). To accomplish these goals, modern SNA has a wide array of tools at its disposal, including: descriptive measures, network models, simulations, and comparative approaches (e.g., Pinter-Wollman et al., 2014). While we will define concepts and terminology in the body of the text as they are used, readers can also refer to Box 1 where we provide definitions and corresponding references.

An early study explicitly applying elements of modern social network theory to nonhuman animals was Maryanski's (1987) work on gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) social organization. She used data from the literature to characterize the average relationship

between different age—sex classes in chimpanzee and gorilla groups in terms of strong or weak ties. Using this approach, Maryanski demonstrated similarities between chimpanzee and gorilla social structure in that most individuals maintained a handful of strong social ties, but the majority of their social connections, though fairly weak, were distributed throughout the regional population. This resulted in a large amount of interconnectedness at the population level which could have facilitated the movement of individuals and the transmission of social information throughout the population (e.g., Granovetter, 1973). Maryanski contrasted this with baboon (*Papio* spp.) groups where numerous strong ties existed within matrifocal social groups, but intergroup connections were rare. Many of the themes of Maryanski's work—such as a focus on emergent population structure and its implications for patterns of flow over the network—are shared by modern SNA. Her approaches were largely descriptive, however, and lacked many of the formal, quantitative elements embraced by network analysis today. Indeed, the recent surge of interest in SNA has in part been driven by the availability of modern computing power, as well as programs specifically designed for SNA (e.g., Borgatti, Everett, & Freeman, 2002; Whitehead, 2009), thereby allowing researchers to go beyond simple network metrics—such as degree and strength—and to apply a more rigorous statistical framework to their data (Croft et al., 2008; Brent et al., 2011).

A landmark paper that opened the floodgates for applying SNA to nonprimate species was David Lusseau's application of these techniques to a bottlenose dolphin (*Tursiops* spp.) population in Doubtful Sound, New Zealand. Lusseau (2003) analyzed a population of 64 dolphins and found a social network characterized by a high level of clustering—i.e., the network was fairly cliquish in that an individual's network neighbors were also likely to be associated with one another (Box 1). Despite these strongly associated subgroups, simulation studies in which randomly selected individuals and all their connections were removed from the network demonstrated the network's resilience to perturbation. Numerous pathways connected each dolphin to others in the population such that random removal of individuals did not fragment the larger network. Artificially constructed random networks with the same number of nodes and links as the real network fragmented much faster into isolated subgroups when experiencing the same level of random node removal. Targeted, nonrandom removal of especially highly connected individuals had a greater effect on overall social structure, but still did not fragment the network. Additional work on this population has demonstrated the existence of smaller communities within the larger

network, as well as the presence of particular individuals connecting these communities together who could potentially have a disproportionate influence on transmission processes occurring over the network (Lusseau & Newman, 2004; Lusseau, Whitehead, & Gero, 2008).

Lusseau's (2003) study was a major step forward in animal SNA. Rather than just describing the structure of the network, he utilized methods that allowed him to make wider inferences regarding both its structure and function. For example, the structure of the dolphin network was compared to that of random networks of equivalent size and density to emphasize potentially important aspects of dolphin social organization. Further, in testing whether particular pairs of dolphins were found together significantly more often than expected by chance, the permutation methods used to generate randomized networks maintained the underlying data structure—i.e., the observed group sizes and the number of times each individual was observed. These methods provided a more realistic null model for the observed data as compared to the node-label permutation methods more commonly used by sociologists (James et al., 2009). In addition, Lusseau focused on the emergent properties that could arise from network structure, such as facilitating rapid flow of social information and providing resilience in terms of network structure and function to the loss of population members.

Croft, Krause, and James (2004) applied SNA to a wild Trinidadian guppy (*Poecilia reticulata*) population in the Northern Range Mountains of Trinidad. All adult guppies were collected from a pool within the Arima River, individually marked with colored elastomer, and released back into the same pool. Shoals were then recaptured over a 7-day period to construct the social network. Croft et al. (2004) demonstrated that though guppies exhibit a highly dynamic, fission–fusion social system in which shoal membership can change rapidly as shoals meet with and diverge from each other, this population still possessed a highly structured social network. In particular, the network had a short mean path length and a high mean clustering coefficient, suggesting information and disease could spread rapidly throughout the population. The path length between two individuals is the smallest number of edges that lie between them on the network—e.g., a direct connection means a path length of 1—while the clustering coefficient measures the extent to which an individual's associates are themselves linked (Box 1). Persistent associations were present in this population between pairs of females even after accounting for body-size preferences, suggesting shoaling decisions could be based on active partner choice. These

associations persisted over several days, despite the fact that guppy shoals disperse at night and reform anew each morning (Croft et al., 2003). While a preference for familiar individuals had been demonstrated in guppies under laboratory conditions using binary choice trials (Griffiths & Magurran, 1997), Croft et al. (2004) provided compelling evidence that such preferences can also be expressed in wild populations.

Over the past decade, SNA has become an increasingly popular technique to probe aspects of social structure and to study behavior within the larger social context in which animals are embedded (Croft et al., 2008; Whitehead, 2008; Sih et al., 2009; Pinter-Wollman et al., 2014). It has been used in a number of taxa and applied to topics spanning the range of behavioral ecology (Wey et al., 2008; Sih et al., 2009). For example, SNA has allowed for detailed descriptions of social structure to be made for numerous species, including ants (e.g., *Odontomachus hastatus*) (Jeanson, 2012), blacktip reef sharks (*Carcharhinus melanopterus*) (Mourier, Vercelloni, & Planes, 2012), and reticulated giraffes (*Giraffa camelopardalis*) (VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014). Other studies have used SNA to examine the links between social structure and behavior, exploring topics that include song development in brown-headed cowbirds (*Molothrus ater*) (Miller, King, & West, 2008) and how behavioral type influences the composition and structure of cooperative breeding groups in a cichlid species (*Neolamprologus pulcher*) (Schürch, Rothenberger, & Heg, 2010).

SNA has also been used to explore how social structure influences population-level processes. Transmission pathways for the transfer of food items, and their implications for the spread of pathogens, have been explored in honeybee hives (*Apis* spp.) (Naug, 2008), while the structure of networks based on refuge sharing were found to be important predictors of parasite load and infection probability in both gidgee skinks (*Egernia stokesii*) and sleepy lizards (*Tiliqua rugosa*) (Godfrey et al., 2009; Leu, Kappeler, & Bull, 2010). Taking advantage of a 10-year data set on long-tailed manakins (*Chiroxiphia linearis*), David McDonald has employed SNA to address topics such as the importance of early life social connections in predicting later social rise and reproductive success (McDonald, 2007), and the extent to which kin selection has played a role in the evolution of obligate cooperative relationships in this species (McDonald, 2009).

SNA allows us to address several of the aspects of sociality laid out by Wilson (1975) in an integrated, quantitative framework that can facilitate objective comparison between individuals, populations, and species (Faust

& Skvoretz, 2002; Kelley, Morrell, Inskip, Krause, & Croft, 2011; Wilson, Krause, Dingemanse, & Krause, 2013). Even more exciting, as other fields utilizing network analysis develop in parallel with behavioral ecology, cross-pollination of concepts and techniques have occurred and will continue to, thereby enriching our field with an influx of new hypotheses and methods to test them. While network analysis in behavioral ecology has been largely descriptive up until now, that too is beginning to change as experimental manipulation, new technologies, advanced statistical techniques, and simulation modeling allow researchers to transition into an explicitly predictive and explanatory framework (Pinter-Wollman et al., 2014). We will touch on several of these new developments and approaches throughout the remainder of the review as we turn now to recent work that has been done using SNA and explore how a network-based approach has given us new insights into problems both old and new.

3. SOCIAL NETWORK ANALYSIS AND TOPICS IN BEHAVIORAL ECOLOGY

Sih et al. (2009) listed four concepts embraced by SNA that are of particular importance to behavioral ecology: (1) individuals differ in their social experiences, (2) indirect connections can be as important as direct ones, (3) individuals differ in the extent of their influence within the social network, and (4) the social network structure in one context can carry over to influence the network structure in other contexts. These four concepts offer a useful framework through which to appreciate the contributions SNA has made to our understanding of various topics in behavioral ecology, including: dominance hierarchies (Shizuka & McDonald, 2012; Dey, Reddon, O'Connor, & Balshine, 2013), sexual selection (Oh & Badyaev, 2010), disease ecology (Cross et al., 2004; Godfrey et al., 2009; VanderWaal, Artwill, et al., 2014), and the influence of social structure on fitness (Royle, Pike, Heeb, Richner, & Kölliker, 2012; Wey & Blumstein, 2012). Here, we have chosen to focus on SNA as it relates to: (1) social learning and information diffusion, (2) collective movement and decision-making, (3) animal personalities, and (4) cooperation. These topics were selected because we believe they provide excellent examples of how our understanding of social behavior can be enhanced by explicitly incorporating information on social structure and dynamics into models and analyses of animal behavior.

3.1 Social Learning and Culture

The ability of animals to learn environmentally relevant information and novel behavior patterns through observation of other individuals—or the by-products of their behavior—is termed social learning (Hoppitt & Laland, 2013). Classic examples include social learning of potato washing in Japanese macaques (*Macaca fuscata*) (Kawai, 1965), milk-bottle opening in great tits (*Parus major*) (Fisher & Hinde, 1949), and transfer of novel food preferences through breath odor in Norway rats (*Rattus norvegicus*) (Galef, Kennett, & Wigmore, 1984).

Early theoretical models exploring the adaptive value of social learning assumed a well-mixed population in which social learners copied others in a more or less random fashion (Boyd & Richerson, 1985; Rogers, 1988). The results of these models suggested that social learning did not automatically increase individual fitness as was generally assumed. Rather, negative frequency dependence for social learning resulted in a polymorphic equilibrium where the average fitness of social and asocial learners was equivalent (Rogers, 1988). This finding, known as Rogers' "paradox," flew in the face of common assumptions that the ability to use social learning *must* enhance fitness, using the success and growth of human populations as evidence. One way out of the "paradox" was by recognizing that social learning usually does not occur as random copying of others within a homogeneous population. Rather, humans and other animals are more likely to acquire social information in highly selective ways that are influenced by demonstrator characteristics, as well as by differential access to those demonstrators (Coussi-Korbel & Fragaszy, 1995; Laland, 2004; Hoppitt & Laland, 2013). In short, when exploring social learning dynamics, the social network structure matters.

3.1.1 Theoretical Models of Social Learning and Culture in Structured Populations

Recent theoretical studies have begun incorporating elements of social structure and learning strategies into their models to better explore how cultural traits spread through and persist in a population, the conditions that influence cultural trait diversity, and the fitness consequences of these traits. Given the obvious importance of culture in our societies, most work on these topics has focused on humans. From this body of research, it is clear that social structure can greatly influence how quickly, and to what extent, cultural information transmits through a population. For example, the mean network degree—i.e., the average number of connections an

individual has—predicts the ultimate spread of a cultural trait, while the extent to which a network is formed of smaller, semi-isolated subgroups influences how quickly an equilibrium state is reached through the loss of neutral cultural variants (Holme & Newman, 2006; Li & Hui, 2008; Meyers, Pourbohloul, Newman, Skowronski, & Brunham, 2005; Nardini, Kozma, & Barrat, 2008).

Fewer researchers have modeled cultural dynamics in nonhuman systems (Whitehead & Lusseau, 2012). Here, we will use the definition of culture as socially learned behavior that is shared by members of a group (Laland & Galef, 2009; Whitehead & Lusseau, 2012), though other definitions with more stringent requirements have also been used in the literature (Laland & Galef, 2009). Possible examples of nonhuman culture include nut cracking in chimpanzees (*P. troglodytes*) (Boesch, Marchesi, Marchesi, Fruth, & Joulian, 1994), potato washing in Japanese macaques (*M. fuscata*) (Kawai, 1965), and tool use in New Caledonian crows (*Corvus moneduloides*) (Hunt & Gray, 2003) and bottlenose dolphins (*Tursiops* spp.) (Krützen et al., 2005). By simulating transmission over small social networks with varied structural properties, researchers can gain insight into how putative cultural traits might spread through animal societies.

Voelkl and Noë (2008) constructed artificial networks of varying resemblance to commonly observed natural social structures, as well as simulating the real social network published in Sade's (1972) study of rhesus macaques (*M. mulatta*). When they examined transmission patterns over these networks, they found transmission rates were highest in a homogeneous network where every individual was equally connected to every other. A chain network where each individual had at most two connections possessed the slowest transmission rates. These highly artificial networks are extreme versions of egalitarian and hierarchical social structures respectively. Between these two extremes, networks with greater resemblance to real social networks observed for nonhuman primates had intermediate transmission rates. The decrease in transmission rate as networks became more hierarchical is consistent with empirical evidence that suggests that dominance relationships can impede the spread of social traits (e.g., Coussi-Korbel & Fragaszy, 1995; Huffman, 1996; Kendal et al., 2010).

Voelkl and Noë (2010) simulated information propagation in over 70 nonhuman primate sociopositive social networks—for example, networks based on grooming or social tolerance—previously published in the literature. In addition to using the unaltered social network, each network was also modified by: (1) shuffling the weighted edges between nodes to

randomize the connection pattern while maintaining the original network's distribution of edge weights, (2) creating an unweighted, binary network that maintained the connection pattern, and (3) creating a well-mixed, homogeneous network where each individual was connected to every other individual and all network ties were of equal strength (Figure 3). Information spread fastest in the well-mixed networks and slowest in the unaltered, original networks. This suggests that social transmission rates were hindered by both the pattern of social connections, as well as the unequal distribution of connection strength.

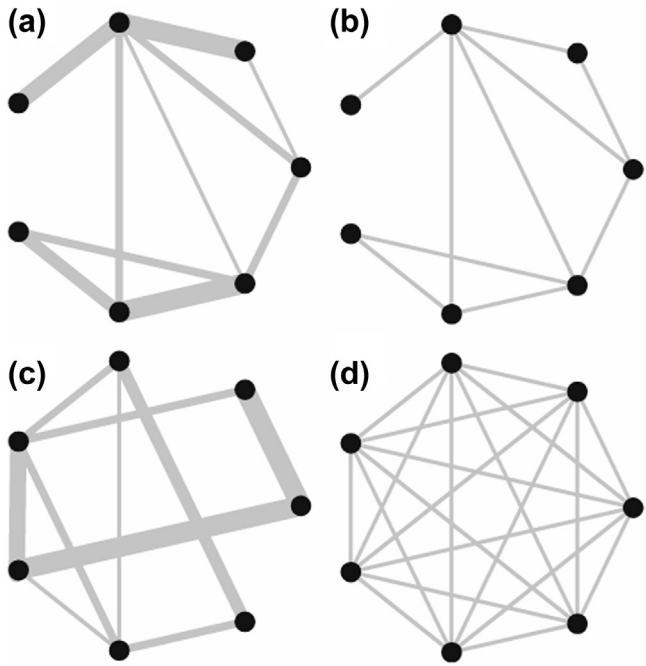

Figure 3 The four network types used in Voelkl and Noë's (2010) simulation study of social transmission in primate networks. (a) A network based on an actual primate social network where edge weights represent interaction frequency, (b) a network which maintains the connection pattern of the original network, but removes weighting so that all connections are of equal strength, (c) a network which maintains the distribution of edge weights from the original network, but the connections between nodes are randomized, and (d) a complete network where all possible connections are present and of equal weight. *Reprinted with permission from: Voelkl and Noë (2010). Simulation of information propagation in real-life primate networks: longevity, fecundity, fidelity.* Behavioral Ecology and Sociobiology, *64, 1449–1459. Copyright © 2010 Springer Science + Business Media.*

Whitehead and Lusseau (2012) recently simulated a number of social learning rules within networks of varying structure to explore the relative influence of both factors on cultural diversity. As networks became more modular, cultural diversity increased. Modularity was calculated as the difference between the proportion of total edge weights that connect individuals within the same subgroup and the expected proportion when assuming individuals associate at random (Newman, 2004). This score ranges from 0 for undifferentiated populations without clustering to 1 for a highly differentiated population where individuals only interact within, rather than between, subgroups. Within highly modular populations, clusters of individuals that were socially isolated from the larger population tended to embark on independent behavioral trajectories. This pattern was found regardless of the learning rule being used. Social structure might impose an upper limit on the overall behavioral diversity a network can realize, regardless of the learning mechanisms at work. The authors suggest that these predictions could be tested by comparing behavioral diversity and social structure in wild populations thought to exhibit cultural traditions, such as primates, cetaceans, and songbirds. Taken together, the above studies suggest that as a population becomes more structured—that is, less homogeneous—and/or access to other individuals becomes more limited, transmission occurs at a slower rate through the population with the added effect of possibly increasing the overall diversity of whatever it is that is being transmitted—e.g., novel behaviors, diseases.

The above simulation studies allow for generation of predictions which can then be tested in actual animal populations by quantifying the population's social structure, introducing a novel trait, and observing its spread (Voelkl & Noë, 2008; Whitehead & Lusseau, 2012). Potentially valuable new methods to accomplish these tasks have begun to be developed (e.g., network-based diffusion analysis (NBDA); see below). An area for future inquiry is to study these processes over dynamic networks in which connection patterns and strengths can shift over time (Whitehead & Lusseau, 2012). For example, if connections between parents and offspring begin strong in life and weaken as the offspring ages, vertical transmission rates should be highest early in an individual's life.

3.1.2 Network-Based Diffusion Methods

An early approach used to study social learning in freely interacting animal groups was diffusion curve analysis, in which the cumulative number of individuals that possess a trait over time is plotted. Traditionally, the shape

of the diffusion curve was used as an indicator of asocial or social learning (e.g., Lefebvre, 1995). An r-shaped curve was taken as evidence of asocial learning as, at the population level, it is indicative of individuals learning a trait at a roughly constant rate. Social learning was inferred from an s-shaped curve. The s-shape suggests few individuals possess the trait early on, resulting in a dearth of demonstrators and slow overall trait acquisition. As more individuals acquire the trait, more demonstrators are available to provide additional opportunities for naïve individuals to learn; under these conditions, rapid spread of the trait is predicted. Eventually, there are few uninformed individuals left and the overall rate of acquisition slows.

Using traditional diffusion curve analysis to understand social learning is problematic. These analyses assume all members of a population are equally likely to transmit or receive information and that the population is structured homogeneously with all individuals equally likely to interact with one another (Reader, 2000). Additionally, the shape of the curve is not as indicative of underlying learning processes as was initially assumed. Social learning may not result in a simple, s-shaped curve if populations exhibit some level of substructuring where the trait spreads quickly within, but slowly between, subgroups (Laland & Kendal, 2003; Reader, 2004). Similarly, if information is more likely to be learned from some individuals than others—e.g., due to transmission biases or directed social learning—the shape of the curve changes. Furthermore, an s-shaped curve can arise from asocial phenomena such as: neophobia, multistep tasks, or if variation in asocial learning rates exists between individuals (Reader, 2004; Hoppitt, Kandler, Kendal, & Laland, 2010).

To address these concerns, a new form of diffusion analysis has recently been developed. NBDA infers social learning if the spread of a trait through a population appears to follow the social network: that is, that social information is more likely to spread quickly between animals tightly linked in the network (Coussi-Korbel & Fragaszy, 1995; Franz & Nunn, 2009; Hoppitt & Laland, 2013). NBDA can be based on either the order in which individuals acquired the trait or the actual times of acquisition. These models can be used to compare strength of social transmission between contexts (e.g., open vs complex environments: Webster, Atton, Hoppitt, & Laland, 2013) or to test hypotheses related to different social learning strategies thought to be at work in a population (e.g., copying familiar individuals: Atton, Galef, Hoppitt, Webster, & Laland, 2014; vertical transmission: Allen, Weinrich, Hoppitt, & Rendell, 2013). Factors predicted to influence asocial rates of acquisition, such as neophobia or boldness, can also be

incorporated into the models to control for their effects (Hoppitt, Boogert, & Laland, 2010).

While still a new technique, NBDA has already been employed in both laboratory and field studies on a number of species, including: threespine sticklebacks (*Gasterosteus aculeatus*) (Atton, Hoppitt, Webster, Galef, & Laland, 2012; Webster et al., 2013; Atton et al., 2014), multiple species of Paridae songbirds (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Aplin et al., 2015), ring-tailed lemurs (*Lemur catta*) (Kendal et al., 2010), red-fronted lemurs (*Eulemur rufifrons*) (Schnoell & Fichtel, 2012), and humpback whales (*Megaptera novaeangliae*) (Allen et al., 2013). So far NBDA has been used primarily to study the spread of foraging information related to locating and accessing food, but it has the potential to address nearly any behaviorally transmitted trait—e.g., vocal traditions in cetaceans (Noad, Cato, Bryden, Jenner, & Jenner, 2000), mate-choice copying (Dugatkin, 1992), or defensive behaviors (Magurran & Higham, 1988; Mineka & Cook, 1988).

NBDA offers several important advantages for studying social transmission. Many social learning studies place individuals in binary choice tests following observation of informed demonstrators. While such studies have been useful in establishing the mechanisms and behavioral strategies by which individuals acquire and use social information (Galef, 2009; Hoppitt & Laland, 2013), animals are often tested under highly artificial conditions and restricted from acting within normal social contexts. NBDA's primary benefit is that it allows researchers to study social learning in naturalistic contexts with freely interacting groups of animals. Additionally, ecological, genetic, and social factors thought to influence the spread of a behavior can be considered simultaneously through inclusion of the appropriate variables in the NBDA model. This provides an attractive alternative to the ethnographic method which instead attempts to infer social learning in the wild through ruling out alternative genetic and ecological explanations (Laland & Janik, 2006). For example, lobtail feeding in humpback whales might be a behavioral specialization for foraging on a particular prey species: sand lance (*Ammodytes americanus*); the initial occurrence of this behavior in the humpback population in the Gulf of Maine coincided with both an increase in sand lance abundance and a dramatic decrease in the abundance of another important prey species for humpbacks: herring (*Clupea harengus*). Allen et al. (2013) found support using NBDA for both social transmission of lobtail feeding and for ecological effects—i.e., annual sand lance biomass—influencing acquisition of the lobtail technique.

One exciting possibility offered by NBDA that has only begun to be explored is examining the use of social learning strategies under various social and ecological conditions in freely interacting groups. For example, Atton et al. (2014) found that familiarity between two sticklebacks (*G. aculeatus*) facilitated discovery of a novel food source. The pattern of information acquisition in shoals made up of both familiar and unfamiliar fish was best described by a network allowing information flow only between familiar individuals; these results are largely consistent with a social learning strategy of "copy familiar individuals" (Galef, 2009).

Aplin et al. (2015) found strong evidence for a conformist strategy (i.e., "copy the majority") influencing the establishment and persistence of alternative, but functionally equivalent, novel behaviors in wild networks of great tits (*P. major*). Demonstrators from each subpopulation were trained in captivity to open a puzzle box with one of two options—pushing the blue half of a sliding door to the right or the red half to the left—in order to access the mealworms contained within. Demonstrators were then released back into their original subpopulations. Puzzle boxes with both options available were provided for each subpopulation and the timing and pattern of problem-solving were monitored. NBDA found overwhelming support for social transmission of these behaviors compared to asocial learning; birds with strong connections to solvers were much more likely to solve the task themselves. Despite both options—red and blue doors—being available for use, birds usually first solved the task with the option originally seeded into their subpopulation and continued to strongly prefer this option even after learning of the alternative. When the puzzle feeders were returned to the woods after a 9-month absence, each subpopulation still preferred their initially seeded technique despite significant population turnover. A cultural tradition—that is, a socially learned behavior shared within a group—appears to have been established in these populations, transmitted via the social network, and maintained through conformist biases for at least two generations.

Finally, an important feature of NBDA is that estimates of the *strength* of social transmission can be obtained. This is in contrast to earlier network-based diffusion methods that simply compared a test statistic to a null distribution generated with randomization techniques (e.g., Boogert, Reader, Hoppitt, & Laland, 2008; Morrell et al., 2008). For example, one of the approaches used in Boogert et al. (2008) used a weighted social network and the order in which individuals acquired a behavior (i.e., the diffusion chain). The average association strength between each individual and all

those who preceded it in the diffusion chain was summed over all individuals in the chain. This test statistic was then compared to a distribution of null values generated using randomized diffusion chains. If the trait was socially transmitted through strong network connections, the test statistic was expected to be in the upper 2.5% of the distribution. However, this method only indicates whether or not social transmission was likely occurring; it provides no estimates regarding the strength of social transmission. The effect size estimates possible using the latest forms of NBDA can facilitate comparisons of the strength of social learning between different contexts, populations, and species to better identify conditions that promote or may have selected for enhanced social transmission (e.g., Webster et al., 2013). It might even be possible to predict future spread of information through a population if given sufficient information on the effects of relevant factors on social transmission rates. This could have ramifications for management of wild and captive populations, such as seeding beneficial information or training to the individuals most likely to facilitate its rapid spread (Makagon, McCowan, & Mench, 2012).

Despite its potential utility, NBDA has weaknesses that require careful consideration from researchers prior to applying it. While NBDA facilitates studies of social learning under wild conditions, the ability for researchers to accurately identify when an individual has acquired the trait of interest is critical. Observation errors regarding this information can decrease the power of NBDA to detect social learning (Franz & Nunn, 2010). Analyses based only on the order of acquisition can be potentially more resistant to these errors, but may also have less statistical power to detect social learning than analyses that also incorporate information on the time of acquisition (Franz & Nunn, 2010; Hoppitt, Boogert, et al., 2010). Identifying an appropriate association measure is also critical. Ideally, a measure should be selected that reflects the probability that information will transmit between two individuals—e.g., a network based on how often individuals feed together might be more appropriate when considering the spread of foraging-related traits than a network based solely on spatial proximity (Hoppitt, Boogert, et al., 2010; Hoppitt & Laland, 2013).

On a more conceptual note, NBDA uses a static network constructed from aggregated observations of association or interaction. If transmission processes occur at a fast rate relative to changes in network structure, then NBDA is a powerful technique. If instead transmission processes and structural changes occur over similar timescales, then a more fine-grained view of

social dynamics might be needed (Croft et al., 2008; Wilson et al., 2014). Furthermore, if acquiring a trait changes an individual's interaction patterns, then a social network constructed prior to when an individual acquired a trait might not accurately reflect its social relationships after trait acquisition. A model allowing for a dynamic network that can change over time might be more appropriate in this context (e.g., Blonder, Wey, Dornhaus, James, & Sih, 2012). New approaches are being developed that could help address some of these shortcomings; we will discuss a few of them—e.g., Markov chain models, dynamic networks—later in the review.

In addition to diffusion studies per se, attempts have been made to link particular network metrics with social learning. For example, high eigenvector centrality (Box 1) suggests an individual is well connected in its network and might therefore experience increased access to beneficial social information, resources, or mating opportunities. Formally, eigenvector centralities are taken from the first eigenvector of the matrix of associations or edges (Newman, 2004). In practical terms, an individual can have high eigenvector centrality if it has many connections in the network—i.e., high degree or strength—or if it is connected to individuals who have many connections. In squirrel monkeys (*Saimiri sciureus*), an individual's eigenvector centrality predicted the likelihood of, and the speed with which, it solved a foraging-related task when trained demonstrators were introduced into the group (Claidière, Messer, Hoppitt, & Whiten, 2013).

Information centrality measures the extent to which one individual links pairs of other individuals together, thereby providing an indicator of how important an individual is in influencing the flow of information through its network (Stephenson & Zelen, 1989). It is similar to the betweenness of a node, but betweenness only counts the number of shortest paths between pairs of nodes that pass through the node of interest (Freeman, 1979). In comparison, information centrality takes into account all possible pathways weighted by the inverse of their length. Vital and Martins (2011) found that individuals who were characterized by high information centrality were of greater importance to group function than noncentral individuals in zebrafish (*Danio rerio*) shoals. Removal of these central fish disrupted the ability of the group to learn foraging-related cues, while removal of other fish had little effect (Vital & Martins, 2011). An intriguing direction for future research is suggested by the strain-related differences found in Vital and Martins' study which hint at underlying genetic bases to both zebrafish social organization and learning.

3.1.3 Transmission Dynamics Using Markov Chain Models

A recent development in the analysis of animal networks with important implications for understanding transmission processes is the use of Markov chain models which allow for exploration of the social dynamics that drive the formation of a network (Wilson et al., 2014). Wilson et al. (2014) conducted repeated focal follows of wild female guppies (*P. reticulata*) in their native habitat of Trinidad, periodically recording whether or not the focal fish was shoaling with another female and if so, with who. From these observations, they constructed Markov chain models describing shoaling dynamics, where the shoaling behavior of an individual at time $t + 1$ depends solely on its behavioral state at time t, and each behavioral state—e.g., shoaling, swimming alone—is associated with a unique set of transition probabilities describing the likelihood of future states. Simulated outputs from a number of Markov chain models were compared to the observed data to assess goodness-of-fit (Figure 4). Wilson et al. (2014) found that the best-fitting model had focal individuals selecting shoaling partners with individual-specific probabilities, suggesting active social preferences were at work in this population. These Markov chain models were then used to generate simulated networks whose structure was compared to that of real networks constructed from the observed shoaling partner data. These comparisons found that when models without individual-specific shoaling preferences were used to generate simulated networks, the structure of these networks differed significantly from that of the real networks. This difference was not found when models that included individual-specific shoaling preferences were used instead to generate the simulated networks, suggesting these preferences played an important role in determining population structure.

Wilson et al.'s (2014) Markov chain models can be used to analyze and predict transmission processes over networks with a potentially high level of accuracy. These models were used in a disease transmission simulation where it was found that individual partner preferences slowed down infection rates relative to a model assuming a homogeneous social structure with no partner preferences. For this approach to work, some knowledge is needed regarding the length of time required for transmission to occur between two individuals. Animals can then be observed at an appropriate frequency to capture social dynamics at a fine enough scale to properly model the transmission process of interest (e.g., information, disease, parasites). By constructing Markov chain models that explicitly incorporate factors predicted to influence social learning dynamics, such as age, familiarity, or kinship, predictions could potentially be made regarding the

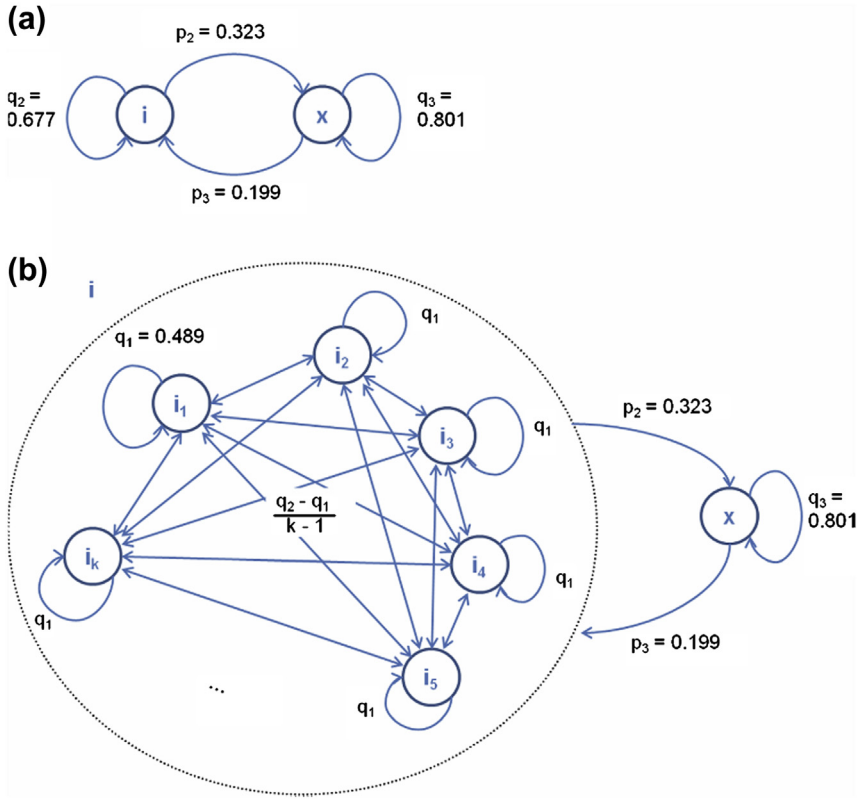

Figure 4 Markov chain models of Trinidadian guppy (*Poecilia reticulata*) shoaling dynamics. (a) The simplest possible model where an individual can either be shoaling (*i*) or alone (*x*). The probabilities of switching state are given by p_2 and p_3, while the probabilities of maintaining the same state are given by q_2 and q_3. (b) An elaboration of the simplest model, in which an additional term is included describing shoaling state *i* in the presence of *k* possible partners. Individuals are selected as shoaling partners with equal probabilities, and the focal individual remains with the current shoaling partner with probability q_1. An elaboration of this model which incorporates individual-specific shoaling preferences provided the best fit to the empirical data (see text). *Reprinted with permission from: Wilson et al. (2014). Dynamic social networks in guppies (*Poecilia reticulata*).* Behavioral Ecology and Sociobiology, *68, 915–925. Copyright © 2014 Springer Science + Business Media.*

importance of various social learning strategies within a population (Laland, 2004; Hoppitt & Laland, 2013). This approach could also facilitate comparisons of social learning between populations and species.

The use of Markov chains in animal social network studies is still relatively new and its effectiveness has not yet been extensively tested. For instance, it

remains unclear to what extent population density might influence the transition probabilities of the Markov chains and consequently limit comparative studies. Nevertheless, it offers an intriguing next step for modeling transmission dynamics over networks, as well as exploring the processes that shape social structure. Wilson et al.'s (2014) approach could be especially appropriate for modeling social dynamics and network structure in animal species where associations and interactions are often short-lived.

While using Markov chains to model network dynamics is relatively unexplored in the behavioral ecology literature, it has a longer history of use in sociology (Wasserman, 1977; Leenders, 1995; Snijders, 2001; Snijders, van de Bunt, & Steglich, 2010; Pinter-Wollman et al., 2014). For example, stochastic actor-based models can explore how characteristics of actors, dyadic relationships between pairs of actors, and the actors' positions in their network drive changes in network structure over time. These models use a time series of networks, where the networks are constructed for the same group of actors at each time point. Changes in network structure between time points are modeled as a Markov process where future network structure is determined only by the current state of the network, mediated through the behavior of the nodes. The main difference between stochastic actor-based models and the Markov chain models used by Wilson et al. (2014) is that the former is modeling the changes between multiple observed networks over time, while the latter attempts to identify the social dynamics at work in a population and use them to infer the structure of the population's social network.

3.2 Collective Movement and Decision-making

In principle, large-scale, complex, and synchronized movement of animal groups—e.g., fish shoals, bird flocks, insect swarms—might be the result of self-organization based on simple behavioral rules played out at the local level between adjacent group members (Sumpter, 2006). Interacting with neighbors based on rules-of-thumb such as "avoid collisions" and "move toward and align with conspecifics" can result in a cohesive and responsive animal group that can potentially acquire information more effectively than a lone individual could and rapidly disseminate that information to its members (Couzin et al., 2002; Ioannou, Couzin, James, Croft, & Krause, 2011). Minor variation in these local rules can lead to rapid and discrete shifts in group structure; for example, simulated fish shoals can shift from swarming behavior to a torus structure and finally to parallel directional movement by simply varying the range over which an individual aligns with group

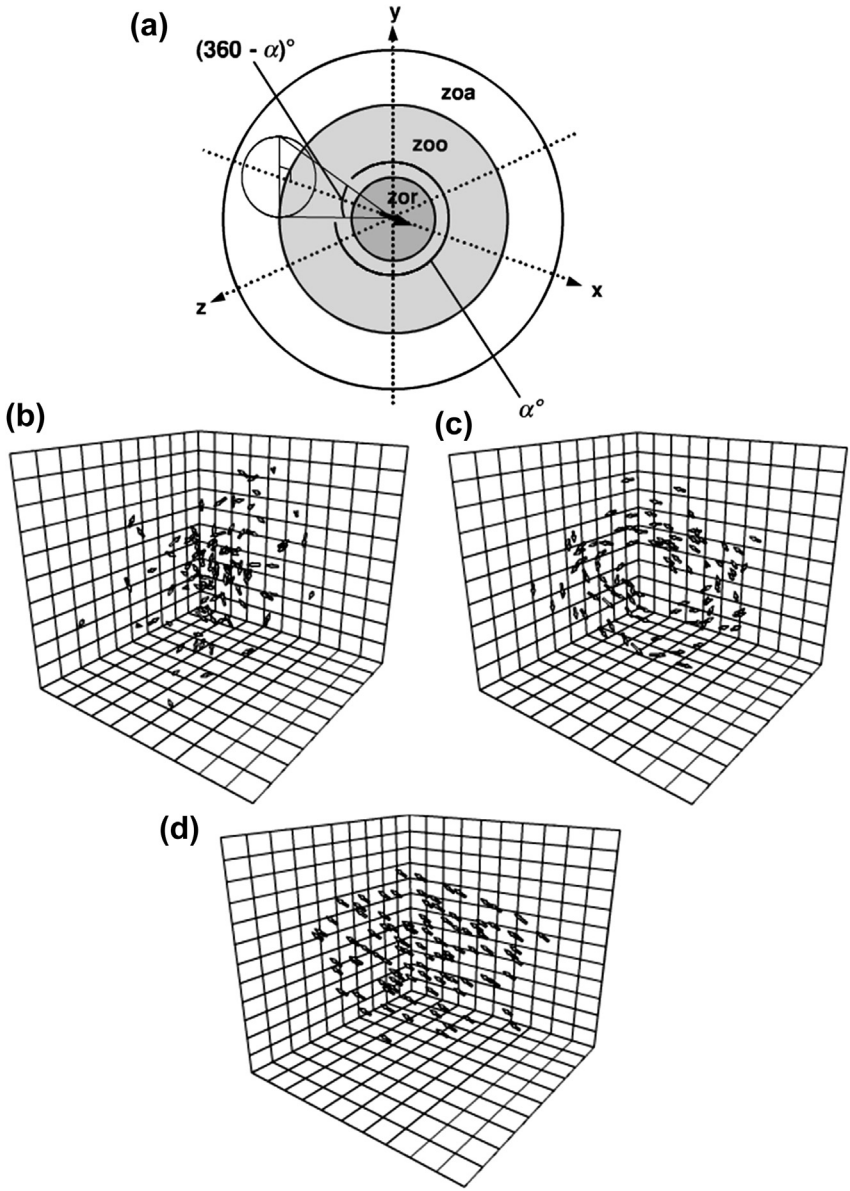

Figure 5 A model of collective motion. (a) An individual is centered within three zones governing its local rules. These are: the zone of repulsion (zor), zone of orientation (zoo), and zone of attraction (zoa). An individual's field of perception is determined by α. (b) Swarm, (c) torus, and (d) parallel directional formations. *Reprinted with permission from: Couzin et al. (2002). Collective memory and spatial sorting in animal groups.* Journal of Theoretical Biology, 218, *1–11. Copyright © 2002 Elsevier.*

members (Figure 5) (Couzin et al., 2002). Each of these formations can be characterized by its influence on group properties, such as cohesion or the speed of information transmission between group members.

Most work on collective movement, however, has not considered how individual-level rules might be influenced by the underlying social structure of a group. Researchers have simply assumed that the same collective movement rules apply to any conspecifics detected within an individual's perceptual zone (Couzin et al., 2002; Hemelrijk & Hildenbrandt, 2008). Yet, empirical work has shown that phenotypic assortment and social preferences for particular individuals influence animal grouping patterns (e.g., Griffiths & Magurran, 1997; Croft et al., 2009; Aplin et al., 2013). Incorporating such preferences—embodied within a group's social network—into models of collective motion and decision-making will help to generate new, testable predictions for the field (Bode et al., 2011a).

Research suggests that subtle behavioral variation is sufficient to consistently influence spatial position in a moving group (Couzin et al., 2002); variation in social preferences is predicted to have a similar effect (Bode, Wood, & Franks, 2011b). In addition, if animals are more likely to be consistently found in certain spatial locations within a group, this may facilitate the development of social preferences between adjacent individuals (Bode et al., 2011a). Differences in information status, speed of travel, behavior, and other variables can result in passive assortment (Krause, Butlin, Peuhkuri, & Pritchard, 2000; Reebs, 2000; Couzin et al., 2002), which might then transform into active preferences expressed within the social network.

A caveat about the relationship between spatiotemporal proximity and animal social networks is in order here. In many species and contexts, gathering a good record of the interactions occurring between individuals can be prohibitively difficult (Whitehead, 2008). Social relationships in these networks are often inferred based on the frequency of association instead. Whether two animals are associating or not is usually based on group membership—i.e., "the gambit of the group" (Whitehead & Dufault, 1999)—where group is defined as animals maintaining spatiotemporal proximity for primarily social reasons. While spatiotemporal proximity often correlates with the likelihood two animals will engage in some social interaction, animals might also group for nonsocial reasons. For example, animals might aggregate around some resource or environmental feature, such as a watering hole or roosting site (Krause & Ruxton, 2002). In such circumstances, group membership provides much less, if any, meaningful information about social structure (Whitehead, 2008). In other contexts, animals might group for social reasons,

but "the gambit of the group" as it is normally implemented, such as through use of a chain rule, can be misleading. For instance, it seems unlikely that every herring (*C. harengus*) shares a meaningful social relationship within a school of potentially thousands of individuals spread out over hundreds of meters (Mackinson, 1999). Instead, it is more likely that an individual fish would maintain many fewer—if any—persistent, social relationships and is most likely to interact with the individuals immediately around it at any one time—i.e., those within its perceptual zone (Couzin et al., 2002).

Many of the studies we review in this section distinguish between a network of social preferences and the interactions that occur within an individual's perceptual zone (e.g., Bode et al., 2011a, 2011b). The former quantifies stable preferences that change relatively slowly compared to interactions occurring in the latter, which form and break as individuals move near to and away from one another. Additionally, several of these studies, particularly those dealing with group movement toward some resource, demonstrate how the outcomes of self-organized, collective behavior can be influenced by a combination of both social and nonsocial processes. We examine three ways in which social network structure influences different aspects of collective behavior. The first considers collective motion in animal groups that are not actively navigating toward some goal. The second section then considers group navigation and leadership effectiveness. Finally, we turn to topics related to group decision-making and the initiation of group movement.

3.2.1 Collective Motion in Nonnavigating Groups

Simulations that incorporate social preferences which bias individual movement toward or away from particular individuals have found that the spatial arrangement of individuals within a moving group reflect the group's social network structure. Qiu and Hu (2010) constructed social networks with weighted edges representing the relative influence each individual had over one another's movement decisions. During collective motion, individual movements were biased toward network neighbors that had greater influence—i.e., stronger edge weights. When the social network resembled a linear chain where each individual had a strong connection with only one other individual, moving groups likewise assumed a linear formation (Figure 6(a)). Conversely, where one or a few individuals had particularly high centrality—i.e., they had many strong connections directed toward them—relative to other group members, moving groups formed relatively compact structures as socially peripheral individuals attempted to remain close to these strongly connected, central individuals (Figure 6(b)).

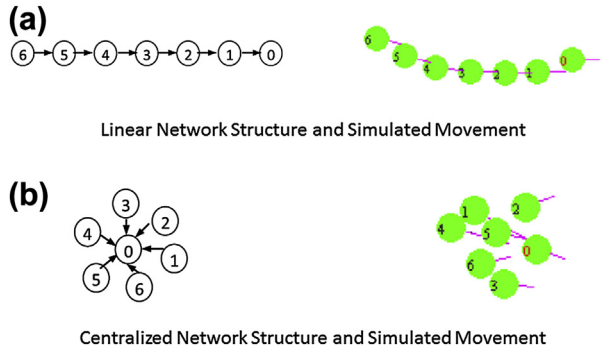

Figure 6 Network structure can influence the resulting spatial structure during agent-based simulations of collective motion. (a) A linear network structure in which each individual shares a strong social connection with just one other individual results in a linear formation during collective motion. (b) A highly centralized network structure in which one individual possesses a greater number of strong social connections relative to other group members results in a compact, clustered formation during collective motion. *Reprinted with permission from: Qiu and Hu (2010). Modeling group structures in pedestrian crowd simulation.* Simulation Modelling Practice and Theory, 18, *190–205. Copyright © 2010 Elsevier.*

Hemelrijk and Kunz (2005) noted similar clustering around preferred associations when they constructed a model incorporating social preferences resembling familiar and unfamiliar associations, with the assumption that familiar individuals preferred one another's company. In their simulations, distinct clusters of familiar individuals were detected within the moving collective. Bode et al. (2011b) explored the influence of various social network structures on collective movement in the absence of navigation. Socially central individuals—i.e., those with numerous strong ties to others in the network—were more likely to also occupy spatially central positions within the moving group. Highly centralized networks that had one or two "key"—i.e., socially central—individuals were found to be tightly cohesive during collective motion. In contrast, strongly interconnected subgroups, such as communities within the network, facilitated fragmentation of the larger group. The most cohesive groups, however, were those that lacked any strong connections, suggesting that a more homogeneous social structure facilitated cohesive collective motion.

3.2.2 Collective Navigation

If one or a few individuals possess accurate environmental information, they can lead uninformed group members toward a target, such as a food source, resulting in accurate group navigation (Couzin, Krause, Franks, & Levin,

2005). Bode, Franks, and Wood (2012) asked whether an underlying social network expressing individual preferences influenced the ability of leaders to guide group movement. Leaders in their simulations had a preferred direction—that is, they acted as if they were informed regarding the location of a desired destination—while nonleaders had no preferred direction (Figure 7(a)). Leaders also had to balance a nonsocial tendency to navigate toward their preferred direction with a social tendency to respond to the movements of group members. At one extreme, leaders only navigated, with no regard for the behavior of group mates. At the other end, no navigation occurred and the leader only moved according to local interaction rules modified by social preferences. Navigational success for the leader increased with its navigational tendency (Figure 7(b)). However, if leaders paid too little attention to the behavior of group members (i.e., they focused solely on navigation), group fragmentation could result (Figure 7(c)). Fragmentation became less likely when a leader had more and stronger social ties to other group members—that is, when leaders possessed high network centrality. The most effective collective navigation was achieved when leaders had high centrality coupled with moderation in their navigational tendencies (Figure 7(d)).

Although Bode, Franks, et al.'s (2012) models have not been explicitly tested, some empirical results do support their general conclusions. Leadership during flight in homing pigeon (*Columba livia*) groups can be influenced by individual navigational experience and route fidelity (Freeman, Mann, Guilford, & Biro, 2011; Flack, Pettit, Freeman, Guilford, & Biro, 2012)—that is, those pigeons with higher navigational tendencies were more effective leaders. Vital and Martins (2013) quantified the social network structure of small zebrafish (*D. rerio*) groups and identified "key" and "nonkey" fish based on individual information centrality (see Box 1). In each group, either a "key" or "nonkey" fish—i.e., those individuals with the highest or lowest centrality respectively—was trained on how to reach a safe location when faced with an aversive stimulus. When transferred back into their groups, "key" individuals were better able to influence collective group avoidance behavior than "nonkey" fish. Swaney, Kendal, Capon, Brown, and Laland (2001) found that trained guppies (*P. reticulata*) that were familiar to the rest of the group were better able to lead group mates toward a food source as opposed to trained demonstrators that were unfamiliar to the group. The most effective leaders, though, were the familiar guppies that were relatively poorly trained, as the well-trained fish tended to leave their group mates behind. This seems to parallel Bode, Franks, et al.'s (2012) finding that

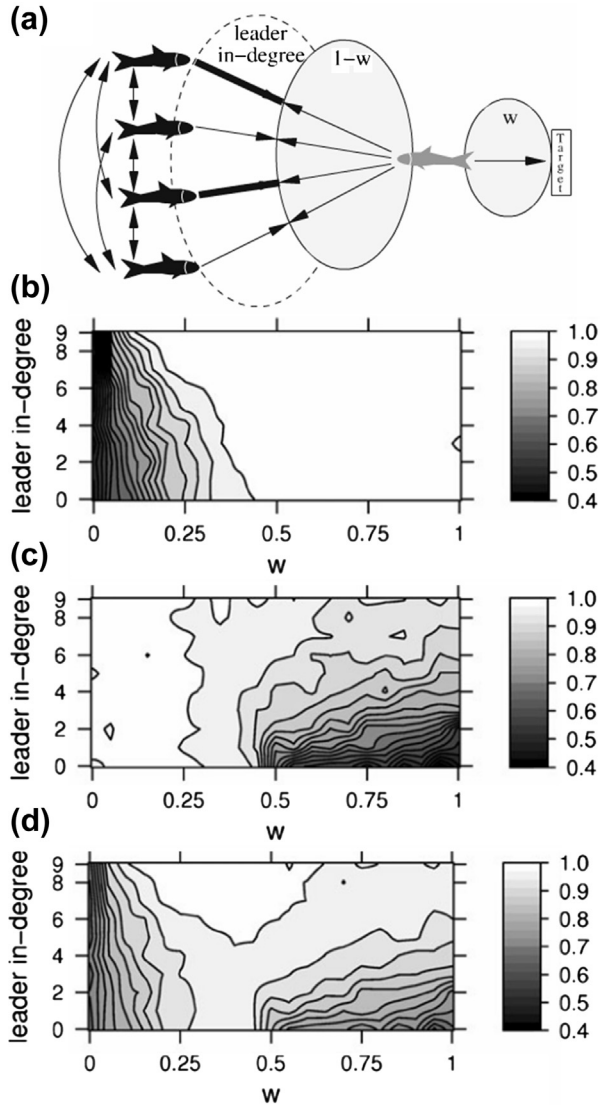

Figure 7 (a) The informed individual in gray has a navigational tendency, *w*, countered by social tendencies, $1 - w$. Arrows indicate social preferences, with stronger preferences indicated by thicker lines. (b) Navigational success of the leader increased with *w*; as in-degree increased, a smaller *w* was needed for success. (c) The scale on the right denotes the fraction of the total group that was found in the same cohesive group as the leader. More fragmentation was observed as *w* increased, but this was countered to some extent by higher leader in-degree. (d) The square root of the product of the measures from (b) and (c) provided a combined measure where high values indicated successful group navigation. The most effective group navigation occurred when leaders had high in-degree and moderate navigational tendencies. *Reprinted with permission from: Bode, Franks, et al. (2012). Leading from the front? Social networks in navigating groups.* Behavioral Ecology and Sociobiology, 66, *835–843. Copyright © 2012 Springer Science + Business Media.*

individuals focused solely on navigation facilitate fragmentation of the larger group, potentially by outpacing other group members and robbing them of effective leadership.

In the absence of informed leaders, animal groups can still accomplish cohesive and accurate navigation. Under what is known as the "many-wrongs principle," pooling imperfect individual navigational information can facilitate collective navigation as individual errors are averaged out at the group level (Simons, 2004). Bode, Wood, and Franks (2012) used simulations to examine how social network structure influenced such leaderless group-level navigation. Each individual in the model moved based on both innate, but imperfect, navigational tendencies toward the target direction, as well as social tendencies toward nearby conspecifics. Social preferences were determined by a network of strong and weak connections. Two models of network formation were considered, with the placement of strong connections selected either (1) based on preferential attachment, resulting in a few, very strongly connected nodes (Barabási & Albert, 1999), or (2) at random. To represent the absence of social structure, the control treatment used a network where all individuals were connected to one another and all connections were equally strong. Bode, Wood, et al. (2012) found that relative to the control treatment, either type of social network acted to reduce group navigation error when individuals were biased in favor of interacting with conspecifics rather than following their own navigational knowledge. Conversely, when individuals focused more on nonsocial navigation, group-level accuracy was no longer influenced by the social network. Overall, these simulations suggest that over an evolutionary timescale, natural selection could favor some level of social structure in group-living organisms due to its facilitation of collective navigation.

The relative scarcity of work combining these two fields can be partially traced to logistical and methodological limitations. It can be difficult enough to track individual wild animals over course timescales, let alone record the fine-grained details needed for studies of collective motion. Novel automated tracking and recording systems are being developed that offer opportunities to begin investigating these topics in greater detail by allowing high-resolution data of individual identities, positions, and movements to be collected for wild animal populations (e.g., Krause et al., 2013; Nagy et al., 2013; Farine et al., 2014; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2014).

Researchers have only recently begun to cohesively integrate SNA with studies of collective motion. Given the intriguing results of these initial

studies, however, further synthesis of these fields is likely to greatly advance our understanding of the underlying mechanics and dynamics of emergent social behavior. Questions abound: how does the relationship between social structure and information pooling during collective navigation vary across ecological contexts (e.g., within a structurally complex environment)? Does social structure mediate or hinder group cohesion when conflicts of interest occur between group members? How do networks characterized both by preferred and avoided relationships influence collective motion and navigation? How are the costs and benefits of leadership balanced against the costs and benefits of maintaining social relationships? Additionally, comparative studies examining the interaction between social networks and collective motion across contexts and between populations and species will allow us to unravel the role natural selection plays in influencing emergent social phenomena.

3.2.3 Initiation of Group Movement and Group Decision-making

To this point, we have only considered collective motion in continually moving animal groups without considering how initiation of group movement occurs. Another body of work uses the term collective movement to refer to the sequence of events that include a predeparture period (sometimes with recruitment behaviors involved), initiation of movement, and group movement if the initiator was successful (Petit & Bon, 2010). In these studies, the focus is on such questions as what individual characteristics are possessed by successful initiators of group movement, and how do animals decide whether to join a departing group or remain where they are?

Joining decisions during the initiation of collective movement have been well studied in primate groups. Jacobs, Sueur, Deneubourg, and Petit (2011) proposed several rules which brown lemurs (*Eulemur fulvus fulvus*) might in principle follow in their decision-making process. Joining decisions could be based on: (1) individual-specific needs and motivations, (2) the identity or characteristics of the initial leader, (3) the total number of animals who have joined, (4) the total number of kin who have joined, and (5) the affiliative relationships shared with those who have joined. Agent-based simulations of brown lemur behavior found that decisions based on the affiliative relationships shared with those who have joined best fit the data, suggesting that the social network of affiliative behavior predicted group-level movement patterns for brown lemurs. Similar results have been found for Tonkean macaques (*Macaca tonkeana*) (Sueur, Petit, & Deneubourg, 2009, 2010), rhesus macaques (*M. mulatta*) (albeit modified by kinship

patterns: Sueur et al., 2010), and in herds of heifers (*Bos taurus*) and ewe lambs (*Ovis aries*) (Ramseyer, Boissy, Thierry, & Dumont, 2009).

Sueur et al. (2012) further explored how collective movement patterns and group decision-making style were influenced by social network structure by running agent-based simulations using networks varying in their centralization. Highly centralized networks were dominated by one individual with the most and the strongest connections relative to other group members. Specifically, these individuals possessed the highest eigenvector centrality of the group (see Box 1). More decentralized networks were characterized by less disparity in eigenvector centrality between the central individual and its group mates until, in a completely decentralized network, all group members were equally central. In highly centralized networks, the central individual had the greatest recruitment success during initiation of collective movement. As networks became less centralized, leadership effectiveness became more evenly distributed in the group. Finally, in a completely decentralized network, every individual was equally successful as a leader. The interaction between social structure and decision-making style was nonlinear, suggesting that the latter is an emergent property of the former (Bradbury & Vehrencamp, 2011); once a critical level of network decentralization was reached, group decision-making rapidly shifted from an unshared to a shared consensus in which each group member had equal say in collective decisions (Conradt & Roper, 2005). Results of these simulations were very much in line with the empirical data on movement initiation and joining decisions in a number of primate species, including: Tonkean macaques (*M. tonkeana*), rhesus macaques (*M. mulatta*), brown lemurs (*E. fulvus fulvus*), and white-faced capuchins (*Cebus capucinus*).

Social network structure can also influence the dynamics of permanent group fissions, with important consequences for patterns of gene flow, population dynamics (e.g., growth rate), colonization of new habitats, and the potential extinction of local or regional populations (Lefebvre, Ménard, & Pierre, 2003; Jones, 2005; Strier, Boubli, Possamai, & Mendes, 2006). For example, a population of northern muriqui monkeys (*Brachyteles hypoxanthus*) located in a small forest reserve in Brazil underwent a permanent fission event over the course of 2003–2005 when a subgroup broke off from the main population (Strier et al., 2006). Tokuda et al. (2014) retroactively employed SNA to examine how social structure might have influenced the dynamics of the fission process. Newman's modularity method (Newman, 2004, 2006) was used to detect subgroups of individuals within the larger population. Modularity—i.e., the extent to which association

occurs within, as opposed to between, subgroups—in the population increased over time as the point of fission approached. Females that were more peripheral to the main group—i.e., those that had relatively lower strength and eigenvector centrality—began to associate as a separate subgroup that eventually broke off from the larger group (Figure 8). Ecological factors, such as foraging competition, were implicated in the permanent split in the female population, while the subgroup of males that subsequently joined the new female subgroup likely did so for reproductive opportunities (Tokuda et al., 2014). Restructuring of the social network over time during repeated temporary fissions appears to have resulted in permanent group division; simulation studies appear to provide support for this interpretation (Sueur & Maire, 2014).

Initiation of collective movement cannot occur without a leader. In contrast to our earlier discussion regarding leadership during collective navigation, here we will use the term leader to refer to individuals who attempt—successfully or unsuccessfully—to initiate group movement. What characteristics are possessed by successful versus unsuccessful leaders? Is leadership a stable role, consistently occupied by one or a few group members, or is it a temporary position taken up by individuals based on current knowledge or motivation? Dominance relationships or social rank appear to influence leadership in at least some species. In feral horses (*Equus ferus caballus*), higher-ranked individuals successfully recruited more followers when departing from the group, and horses tended to join collective movements in rank order (Krueger, Flauger, Farmer, & Hemelrijk, 2014). In contrast, individual position within sociopositive social networks was not associated with leadership success. Similarly, dominance rank was strongly associated with successful initiation of collective movement in rhesus macaques (*M. mulatta*) (Sueur & Petit, 2008).

Dominance rank is not always correlated with leadership success (e.g., Nagy et al., 2013). In some cases, it might be the individuals that possess the most knowledge or experience that take up leadership roles (Couzin et al., 2005; Bode, Franks, et al., 2012). In the bottlenose dolphin (*Tursiops* spp.) population living in Doubtful Sound, New Zealand, two particular behaviors are used to coordinate cohesive group movement on a local scale: a side-flop to initiate travel and an upside-down lobtail maneuver to signal cessation of movement (Lusseau, 2007). Only a subset of individuals performed these group-coordinating behaviors; side-flops were only successful when used by certain males, while upside-down lobtailing was likewise only successful when employed by particular females. By examining the social

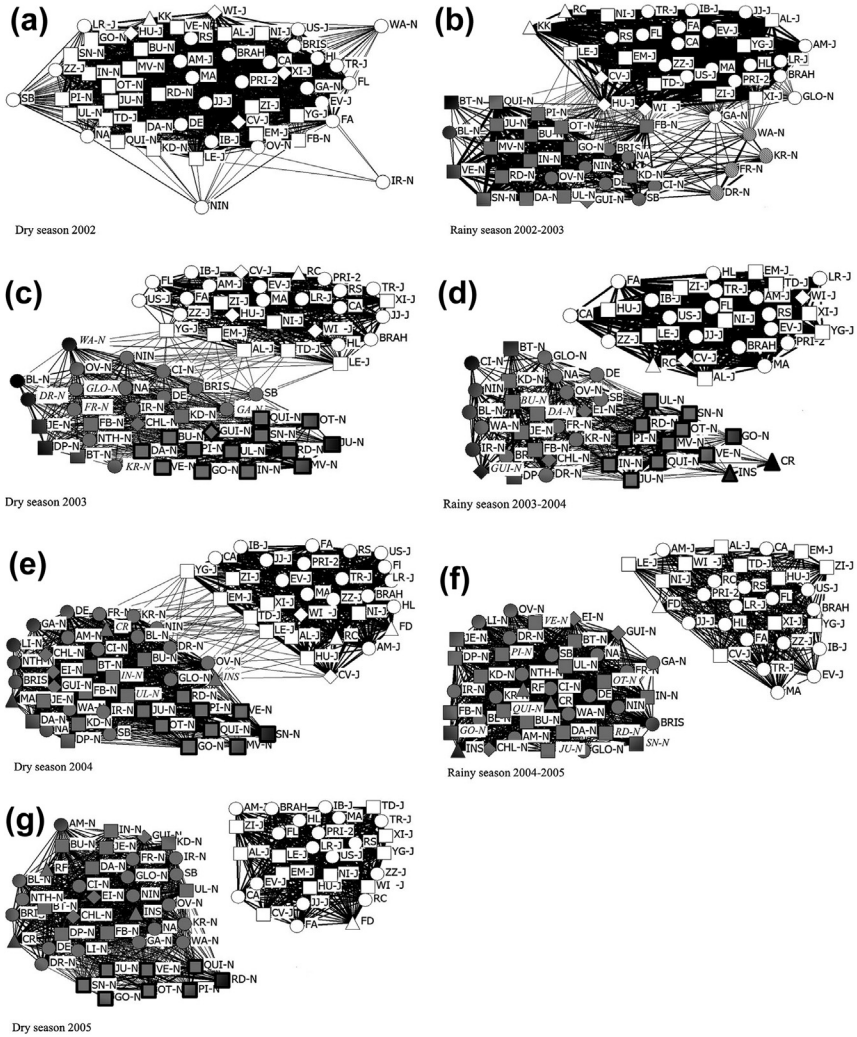

Figure 8 Social networks for a northern muriqui (*Brachyteles hypoxanthus*) population that underwent permanent group fission between the dry season in 2002 (a) and the dry season in 2005 (g). Clusters of individuals detected by Newman's modularity method are indicated by different shading, hatching, and border width in panels (b)—(g). Circles: adult females, squares: adult males, triangles: subadult females, and diamonds: subadult males. Additional figure information can be found in Tokuda et al. (2014). *Reprinted with permission from: Tokuda et al. (2014). Males follow females during fissioning of a group of northern muriquis.* American Journal of Primatology, *76, 529—538. Copyright © 2014 John Wiley and Sons.*

network position of signaling and nonsignaling dolphins, it was discovered that signalers had higher betweenness scores than nonsignalers: that is, signalers were more likely to associate with individuals in multiple subcommunities. Such individuals might have possessed greater knowledge regarding the likelihood that potential conspecific competitors were nearby or which resource patches had recently been visited. The possibility of eavesdropping by competitors might have resulted in greater reliance during coordination of collective movement on these local, short-distance signals compared to long-distance vocal communication.

Taken together, the above studies indicate that social network structure, as well as an individual's network position, influences individual leadership effectiveness, joining decisions, and group decision-making style in many species. While self-organization of group-level behavior can occur via local rules, it can often be misleading to assume these rules are blind to the identity of individuals with which an animal interacts. A feature worth noting in several of the above studies is the melding of model simulations with collection of empirical data on animal collective movements (e.g., Jacobs et al., 2011; Sueur et al., 2012). Through use of model simulations, predictions can be generated and then compared to empirical data in order to infer which explanation best accounts for all aspects of the data. These studies offer excellent examples of predictive approaches using SNA. Further work might incorporate ecological and social factors into the models to explore their potential influence on group decision-making, as well as compare explanatory models between species to assess whether similar or different behavioral mechanisms are at play.

3.3 Animal Personalities

Animal personality is typically defined as consistent individual differences in behavioral responses within and across contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih & Bell, 2008). Animal personality research has typically focused on behavioral traits predicted to be ecologically relevant, such as aggression, boldness, sociability, activity level, and explorative tendencies (Wolf & Weissing, 2012). Consistent between-individual differences in these and other behavioral traits have been reported for a wide range of animal taxa (Sih, Bell, & Johnson, 2010).

The existence of animal personalities is predicted to have substantial impacts on social structure and dynamics, as well as to be influenced in turn by social organization (Krause, James, & Croft, 2010; Wolf & Krause, 2014). Personality types have been shown to differ in the strength and

distribution of their interactions with group members and to assort with others based on personality (e.g., Pike, Samanta, Lindström, & Royle, 2008; Croft et al., 2009; Aplin et al., 2013). Some personality types can occupy prominent or influential network positions, thereby wielding disproportionate influence over network dynamics compared to other group members (Flack, Girvan, de Waal, & Krakauer, 2006; Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014).

Network metrics themselves might even be used to describe an individual's social personality if an individual consistently occupies a similar network position over time and/or across contexts (Blumstein, Petelle, & Wey, 2013; Wilson et al., 2013). In animal personality research, traits are usually measured in individuals under standardized conditions to ensure the trait of interest can be kept distinct from other behavioral responses, as well as to ensure the animal is presented with the same situation each time it is tested (Réale et al., 2007). Variation in these measures can then be related to behavior in naturalistic contexts. However, measurements of social behavior within isolated dyadic interactions can often be very different compared to measurements made within a realistic social environment (Krause et al., 2010; Webster & Ward, 2011). The extent to which network measures can be used as indicators of social personality traits presents an interesting direction for future research.

Much work on animal personalities has centered on an individual's position along the bold–shy axis—that is, an individual's tendency to act in a risk-prone or risk-averse fashion (Réale et al., 2007). For example, bolder individuals are more likely to approach a novel object or investigate a potential predator (e.g., Croft et al., 2009; Kurvers, Nolet, Prins, Ydenberg, & van Oers, 2012). Variation along this axis has also been linked to fitness consequences—e.g., bolder individuals may have higher reproductive success than shy individuals, but experience decreased survival (Smith & Blumstein, 2008). The first studies to examine the links between personality variation and network structure were done comparing network positions of bold and shy fish. Pike et al. (2008) assayed wild-caught threespine sticklebacks (*G. aculeatus*) in the lab for boldness—measured here as the latency to resume feeding following a mild startle response—and then formed small groups of six fish. Groups were composed of all bold individuals, all shy individuals, or a mixture of both phenotypes. In general, as the proportion of bold individuals increased in the group, mean association strength decreased and mean clustering coefficient increased. The clustering coefficient (Box 1) measures the extent to which an individual's social associates are themselves associated.

Bold fish had weaker associations with others, but distributed those associations evenly over the rest of the group, while shy fish had a few, relatively strong, connections focused on a small number of individuals. In mixed networks, bold and shy fish showed comparable patterns as above. Differences in social network structure between groups might have been linked to the different movement patterns expressed by bold and shy individuals. Shy fish were far less likely to move if they were near a conspecific, possibly resulting in the development of strong associations between these pairs. Conversely, bold fish did not base their movement decisions on the presence of others. Similar results to Pike et al. (2008) have also been found in a wild social network of guppies (*P. reticulata*) in that shy individuals formed stronger associations on average than did bold fish (Croft et al., 2009).

Aplin et al. (2013) explored the link between personality and social structure in a wild population of great tits (*P. major*). Tits were outfitted with passive integrated transponder (PIT) tags that could be read by automated recording equipment setup on artificial feeders placed throughout the woods. This allowed for continuous passive monitoring of social structure in these flocks based on co-occurrence at feeding stations. A subset of the PIT-tagged population were captured and then tested in a captive environment to assess their exploration tendencies—used as a proxy for the extent to which individuals were risk-prone fast explorers or risk-averse slow explorers—before being released back into the wild. The cofeeding network derived from joint feeder arrivals demonstrated nonrandom social structure that was associated with variation in personality types (Figure 9(a)). Fast explorers were found to have higher degree and betweenness and weaker association strength than slow explorers: that is, fast explorers had more numerous, but weaker social contacts than slow explorers and were more likely to move between flocks (Figure 9(b) and (c)). These results remained significant after controlling for differences between personality types in movement patterns and space use. Temporal stability in association patterns was also linked to personality, with slow explorers having a higher likelihood of remaining with prior associates—especially with other slow explorers—while fast explorers had more unstable associations. Bonds between two fast explorers were often especially weak and unstable. While female birds did not assort by personality, male birds preferred to associate with individuals that had similar personality types to themselves.

The work reviewed thus far has demonstrated a correlation between an individual's personality type and their network position, as well as between behavioral variation at the population level and overall network structure.

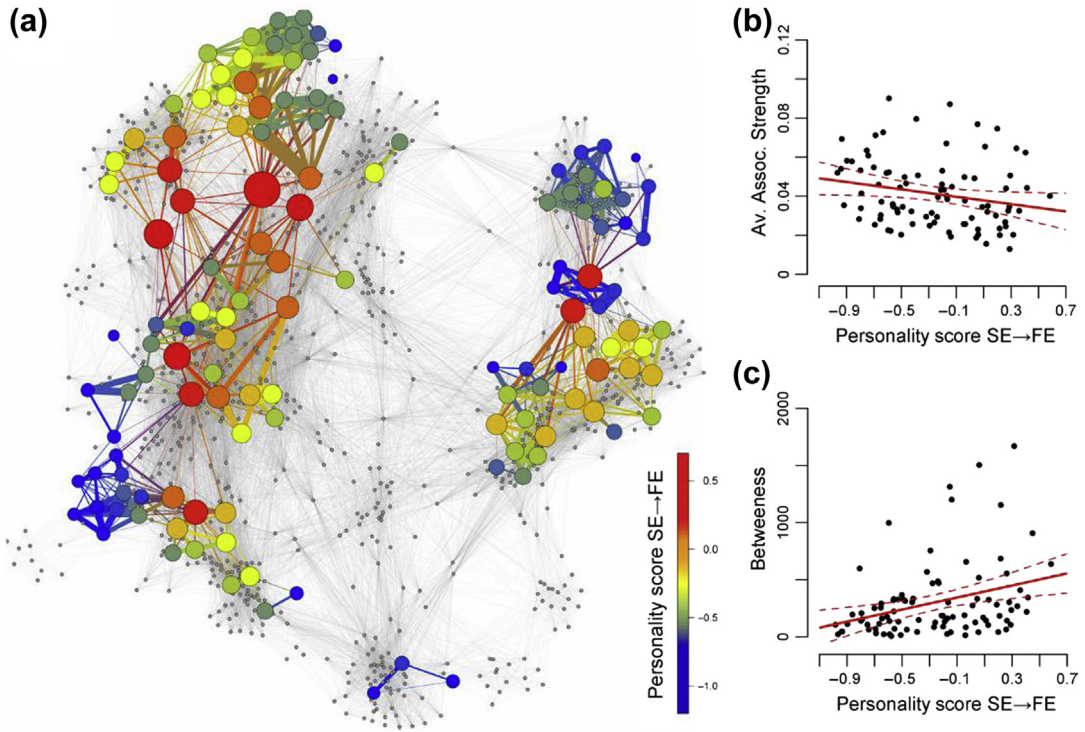

Figure 9 (a) A social network of great tits (*Parus major*) based on co-occurrence at feeding stations. Shading represents personality score ranging from risk-averse (SE) to risk-prone (FE) birds. Gray nodes indicate individuals who were not screened for personality. Node size indicates degree for birds with known personality. (b) The relationship between average association strength and personality score. (c) The relationship between individual betweenness and personality score. Dashed lines represent 95% confidence intervals. *Reprinted with permission from: Aplin et al. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*).* Ecology Letters, 16*, 1365–1372. Copyright © 2013 John Wiley and Sons.*

Future work might explore the links between personality type and dynamic processes taking place over the network, as well as how the relative mixture of personalities within a group influences emergent phenomena. For example, prior work has demonstrated differences in how individual personality influences use of social information (e.g., Kurvers et al., 2010; Trompf & Brown, 2014). Techniques such as NBDA could be used to explore how different personality types affect information transmission through a network. In Aplin et al.'s (2013) bird population, for example, information might flow most efficiently between slow-exploring birds and their tightly linked associates, while fast explorers might play an important role in transmitting information between different flocks. If the behavior of shy individuals results in the formation of small, tightly linked clusters, those subgroups may be buffered from exposure to pathogens, as well as find it easier to maintain cooperative relationships. In contrast, bolder animals could individually have faster access to new social information and thus be able to capitalize more quickly on social opportunities or obtain better access to resources. Individuals might even attempt to select or modify their social environment to best take advantage of these potential benefits or to shield themselves from social costs (e.g., Oh & Badyaev, 2010).

A hallmark of self-organized collective movement is that if individual behavior is consistent, then collective group formations will reassemble into the same form (statistically speaking) following perturbation (Couzin et al., 2002). An intriguing parallel might exist when considering the interactions between social structure and dynamics and animal personalities. We have seen above how personality type is linked to social network structure and temporal dynamics, as well as how it might influence processes occurring over the network. We might then predict that a given mixture of personality types, whether in one group or over multiple groups, will consistently give rise to the same social structure and its associated properties, with important evolutionary implications—particularly if personality and/or network position is heritable (e.g., Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; Dingemanse et al., 2009; Fowler, Dawes, & Christakis, 2009). Social organization can also influence the emergence of personalities, whether via frequency-dependent selection, social niche specialization, or reputation building (Wolf & Weissing, 2010). Future work might, therefore, examine whether separate populations embark on independent trajectories as their social structure influences the emergence of individual personalities and, consequently, the eventual mixture of personality types at the population level. Alternately,

independent populations might instead converge on one or more stable behavioral mixtures.

3.4 Cooperation

Although evolutionary biologists have been interested in cooperation and altruism ever since Darwin (Dugatkin, 2006), only recently have these subjects been addressed from a social network perspective (Nowak & May, 1992; Nowak & Sigmund, 1992; Nowak, Tarnita, & Antal, 2010; Wilson, Pollock, & Dugatkin, 1992). In a widely cited study, Ohtsuki, Hauert, Lieberman, and Nowak (2006) found that cooperation in a structured population can persist if $b/c > k$, where b is the benefit of a cooperative act received by any who are connected to the cooperator, c is the cost to the cooperator for the act, and k is the average degree of the network (Figure 10). Their "rule" indicates that cooperation is favored when individuals possess only a small number of social ties. Santos, Pacheco, and Lenaerts (2006a) found similar results; a heterogeneous social network promoted the persistence of cooperation. This occurred even in the presence of ties that connected otherwise "socially distant" individuals, thereby allowing clusters of cooperators to be more easily invaded by defectors. Turning to real-life networks, simulations using 70 nonhuman primate social networks found that primate social structure often—though not always—facilitated cooperation (Voelkl & Kasper, 2009).

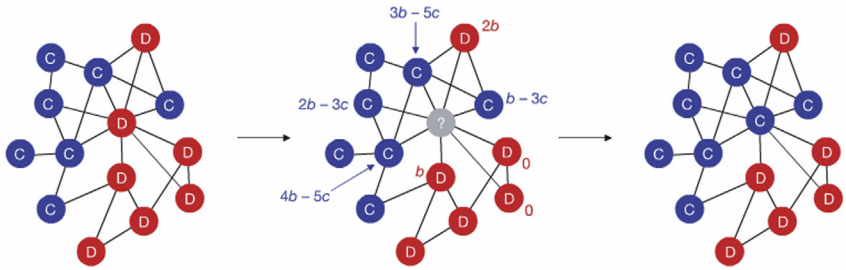

Figure 10 Each individual obtains a payoff (P) derived from interactions with its network neighbors. Cooperators (C) pay a cost, c, for each neighbor to receive a benefit, b. Defectors (D) pay no costs, nor provide any benefits. At each time step, a random individual dies—denoted in the figure by the node marked "?". Neighbors of the now-vacant node compete to occupy it with their offspring, with success proportional to individual fitness. Individual fitness is given by $1 - w + wP$, where w is the strength of selection. *Reprinted by permission from Macmillan Publishers Ltd from: Ohtsuki et al. (2006). A simple rule for the evolution of cooperation on graphs and social networks.* Nature, 441, *502–505. Copyright © 2006.*

If cooperators are capable of assorting with other cooperators and avoiding defectors, cooperation can persist even in networks with higher levels of overall connectedness. For example, Santos, Pacheco, and Lenaerts (2006b) found that cooperation was better able to persist when individuals were able to swiftly modify their local network in response to defection. Given that animals are often likely to have some influence over their network connections, we might expect to observe such assortative patterns in the wild (e.g., Croft et al., 2006). In general, mechanisms that allow for assortment favor the evolution of cooperation and altruism (Wilson & Dugatkin, 1997; McNamara & Leimar, 2010; Nowak et al., 2010).

Cooperation can also be favored by selection when policing behavior that punishes defectors and/or maintains group stability is in place (Foster & Ratnieks, 2001; Ratnieks & Wenseleers, 2005). Flack et al. (2006) used SNA to study policing by male pig-tailed macaques (*Macaca nemestrina*). Social networks for grooming, play, contact sitting, and proximity were recorded for a captive macaque group. Subsequently, three high-ranking males who were known to engage in impartial, third-party conflict interventions were repeatedly removed from the group and social networks were again recorded. When these males were absent, aggressive behaviors became more common and affiliative behaviors less so (Flack, Krakauer, & de Waal, 2005). Their removal also contributed to several structural modifications in the social networks (Flack et al., 2006). Mean reach—i.e., the number of nodes two or fewer steps away from the focal individual (Box 1)—and mean degree decreased for play and grooming networks, mean clustering coefficient increased for proximity networks, and macaques were more likely to assort by degree in play, grooming, and contact-sitting networks. Taken together, these structural changes suggest that in the absence of policing behavior, animals adjusted their social networks in a manner consistent with theoretical predictions regarding the maintenance of cooperation by maintaining a smaller and less diverse network of connections (Ohtsuki et al., 2006; Santos et al., 2006a). While cooperative behaviors per se were not explicitly studied by the authors, their work offers an intriguing example of how behavior can modify the social network in ways that can either facilitate or inhibit cooperative relationships.

Coalitions involve two or more individuals cooperating with one another during potentially costly competitive or aggressive interactions (de Waal & Harcourt, 1992). Using a long-term data set on chimpanzee (*P. troglodytes*) troops in Gombe National Park, Tanzania that contains both behavioral and genetic records, Gilby et al. (2013) used SNA to investigate the potential

fitness benefits of coalitionary behavior for male chimpanzees. They found that reproductive success was significantly and positively correlated with individual betweenness in the coalitionary network—that is, males that had numerous coalition partners that were not themselves allied with one another sired more offspring and were more likely to rise in social rank.

Alliances, defined as long-term coalitionary relationships, are common in bottlenose dolphins (*Tursiops* spp.) (Connor, 1992; Connor et al., 1992; Connor et al., 1999; Wiszniewski, Brown, & Möller, 2012). In some populations, male dolphins will form associations with one to a few other males in order to gain access to females, either by cooperatively herding them or by stealing females from other male alliances. In some cases, second- and even third-order alliances have been observed in which multiple smaller alliances join together into one superalliance (Connor et al., 1999). Wiszniewski et al. (2012) used SNA to examine alliance structure in a dolphin population near Port Stephens, Australia in which males often form strong, long-lasting bonds with one to three other males, while females have a weaker and more dispersed social structure. Male alliance composition was recorded over an 8-year period and analyzed in 2-year increments. While most males—i.e., 69–80%—in a given 2-year period were part of an alliance, the relative stability of these alliances varied greatly. Some lasted for the entire eight years of the study, while others lasted for less than two. Wiszniewski et al.'s (2012) analysis found that a male's social network position was linked to alliance stability. Members of stable alliances maintained particularly tight connections within their alliance, but had very few associations outside it. Conversely, members of less stable alliances maintained a large contact network in the general population. The causes and functional consequences of this variation in alliance structure and stability, however, remain unknown.

A large body of theoretical work now exists exploring the evolution of cooperation in structured populations and providing many predictions ripe for empirical testing (see Nowak et al., 2010). Relatively less work has been done in free-living animal groups, with many questions yet to be answered. SNA provides an integrated framework that allows researchers to explore both the outcomes of cooperation on social behavior and population structure, as well as predict the likelihood of future cooperation given information about a population's social network. For example, theoretical work has associated particular structural elements with either facilitating or inhibiting the emergence and maintenance of cooperation (e.g., Ohtsuki et al., 2006; Santos et al., 2006a). The presence of these elements in animal populations

allow for predictions to be made regarding the likelihood of observing cooperation. Comparative studies of social structure between species that differ in their cooperative relationships might also help to answer such questions (e.g., McDonald, 2007; Ryder, McDonald, Blake, Parker, & Loiselle, 2008). The outcomes of cooperative behaviors can also be studied using a social network approach. When cooperation—or a lack of it—is observed between two individuals, we might predict their social relationship will change as a result, as might their relationship with any potential eavesdroppers. Cooperation might be more likely in the presence of eavesdroppers, especially if those eavesdroppers are well connected. Development of dynamic network models—e.g., time-ordered networks (Blonder et al., 2012)—should shed some light on these questions by allowing us to examine how individuals shift their behavior based on social context and "rewire" their network connections over time.

Social responsiveness—the likelihood of an individual adjusting its behavior according to past interactions with particular individuals—is predicted to facilitate cooperation when past transgressions are remembered, thereby providing one mechanism by which cooperators can assort with one another and "rewire" their social ties (McNamara, Stephens, Dall, & Houston, 2009; McNamara & Leimar, 2010). If defectors can be identified from prior direct experience, or via eavesdropping on past interactions, socially responsive individuals can adjust their behavior during future interactions with known defectors. Alternately, socially responsive individuals can facilitate cooperative behavior by threatening to terminate interactions with cheaters and seek out a more favorable social partner (McNamara & Leimar, 2010). At the same time, personality differences between population members are predicted to result in socially responsive individuals (Wolf & Weissing, 2010; Wolf & Krause, 2014). Such responsiveness will only be favored if: (1) behavioral variation is present, and (2) past behavior of a potential social partner can in part predict their future behavior—i.e., they exhibit behavioral consistency (Wolf, van Doorn, & Weissing, 2011). As such, the composition of personality types within a population is predicted to influence the extent to which social responsiveness is favored. This suggests the presence of at least two potential pathways by which the mixture of personality types within a population can influence cooperative behavior: (1) by influencing social network structure in ways that facilitate or inhibit cooperative behavior (e.g., Ohtsuki et al., 2006; Santos et al., 2006a), or (2) by influencing the level of social responsiveness (e.g., Santos et al., 2006b; McNamara & Leimar, 2010). However, when socially responsive individuals change their future

behavior based on past interaction, this can be reflected by structural changes in their local network, as well as population-level shifts in social structure. Since social structure is also likely to influence the development of individual personalities (Wolf & Weissing, 2010; Montiglio et al., 2013), this would suggest a potential feedback loop between social network structure, the behavioral composition of the population, social responsiveness, and the emergence or maintenance of cooperation. These potential links present an intriguing direction for future research.

4. FUTURE DIRECTIONS FOR SOCIAL NETWORK ANALYSIS IN BEHAVIORAL ECOLOGY

Until recently, much of SNA in nonhuman systems has dealt with how best to describe social structure in terms of interaction patterns, preferred and avoided relationships, assortment of individuals within the network, and delineating substructures within the larger global structure. Less attention has been paid to the "why" of these topics. What influences tie formation or dissolution? What ecological and social factors influence network dynamics and structure? How does social structure change over different timescales? What affect does social structure have over processes that occur on the network? What are the mechanisms by which social network position influences behavior, and what is the functional significance of both an individual's position in the network and of overall population structure? While several of the studies we have discussed in this review have begun to provide answers to some of these questions, a great deal of work remains to be done.

A general call has recently been sounded to move SNA in behavioral ecology away from a predominately descriptive framework toward a more predictive one that seeks to explore the functional consequences of network structure and dynamics for the evolutionary ecology of social behavior (Hobson, Avery, & Wright, 2013; Bradbury & Vehrencamp, 2014; Pinter-Wollman et al., 2014; Wilson et al., 2014). Pinter-Wollman et al. (2014) provide an excellent review of recent advances in technology, analytical methods, and conceptual thinking in SNA. To avoid treading old ground, we refer the interested reader to their comprehensive coverage and will instead focus on two topics—comparative approaches and dynamic networks—that we feel have particular relevance for the subject areas we have addressed in this review.

4.1 Comparative Approaches

Comparative studies are a powerful method for assessing ecological and evolutionary hypotheses (Harvey & Pagel, 1991). Since social structure is derived from behaviors shaped via natural selection, it is predicted to reflect selective pressures and phylogenetic history (e.g., Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007; Kelley et al., 2011). However, network comparisons are often not straightforward, particularly when networks vary in size and connectedness (Croft et al., 2008). Many measures, such as path length and the clustering coefficient, vary with the number of nodes and edges in the network, and can be biased by sampling error. Following Croft et al. (2008), when networks of a similar size and density cannot be compared, network measures can be rescaled prior to comparison or, if the goal is to compare the network position of individuals or classes of individuals between networks, the ranks of a network measure can be used instead of its actual values. Alternately, network comparisons can make use of models that either control for network size, density, and other structural features (e.g., Watts & Strogatz, 1998), or that can parameterize a network's structure so that those parameters can be compared instead between networks (e.g., Faust & Skvoretz, 2002).

Even when measures of global network structure cannot be compared directly between networks, it can still be highly informative to compare smaller-scale network patterns and the social dynamics that inform network structure. To that end, here we briefly discuss two recently applied techniques—Markov chain network models and motif analysis—that we hope will facilitate further comparative analyses and offer fresh insights into many of the topics we have previously discussed.

Transition probabilities from Markov chain models can be directly compared between populations and species to explore how the underlying behavioral dynamics that result in social structure are influenced by ecological context and evolutionary history (Figure 4) (Wilson et al., 2014). While this approach is very new, it offers the tantalizing combination of allowing comparisons to be made regarding both the dynamics leading to network formation—i.e., the transition probabilities—as well as the processes that act over the network itself (see Section 3.1.3).

While these models were initially applied in behavioral ecology toward understanding shoaling decisions in freshwater fish, they can be modified and applied to other behaviors, including foraging, mating, and agonistic interactions. More complex models could incorporate multiple types of

behavior at once, facilitating exploration of how behavioral processes are influenced by different forms of social behavior. For example, in principle, a model combining proximity patterns with agonistic interactions could be used to describe the effects of social eavesdropping and/or audience effects on dominance interactions in freely interacting animal groups. In practical terms, a different set of transition probabilities might govern agonistic interactions when individuals are in the presence of an audience and/or potential eavesdroppers as compared to when third-party individuals are absent. Agonistic networks could be simulated from models that take these third-party effects into account and compared with networks generated from models that ignore them to highlight their structural consequences. Comparative analyses using such models might reveal important evolutionary or ecological influences on the prevalence or importance of eavesdropping or audience effects in different environments, populations, or species. Networks generated from these Markov chain models might also be searched for structural aspects associated with the behavioral process of interest; motif analysis might prove helpful in this regard (see below).

Animals are embedded in multiple social networks, each of which might influence the others (e.g., Pearl & Schulman, 1983; Flack et al., 2006; Barrett, Henzi, & Lusseau, 2012). Creating composite Markov chain models that incorporate two or more types of social behavior simultaneously—e.g., agonistic, sexual, and/or affiliative interactions—would allow researchers to take such network dependencies into account. Markov chain models could be constructed for each behavior separately, as well as for each combination of behaviors. Networks could then be generated from these models to assess the influence of different social behaviors on population structure; comparisons with empirical data could be used to infer which behaviors were most important for driving observed patterns.

Motif analysis has recently been applied toward understanding the structural components of animal social networks (Faust, 2006, 2007, 2010; Shizuka & McDonald, 2012; Ilany, Barocas, Koren, Kam, & Geffen, 2013; McDonald & Shizuka, 2013). Motif analysis deconstructs a network into subcomponents (e.g., triad configurations, see Figure 11), the relative frequencies of which can be compared across networks (Milo et al., 2002; Milo et al., 2004). Certain subcomponent configurations are predicted to facilitate specific network processes and properties such as information processing (Waters & Fewell, 2012) and stable dominance hierarchies (Shizuka & McDonald, 2012). Comparison of the relative frequencies of those configurations across populations might be used to infer the importance of

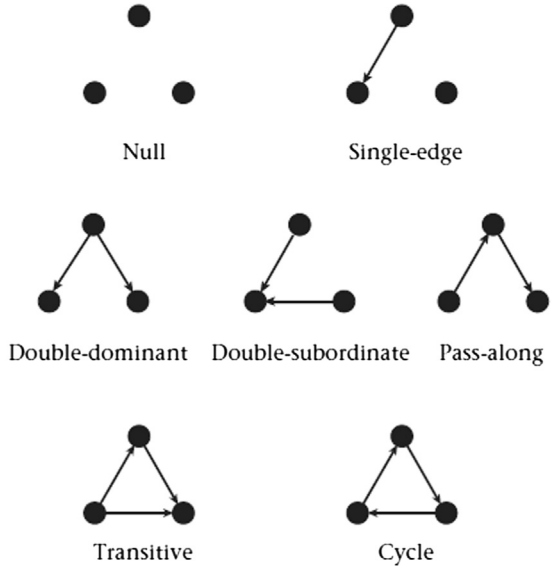

Figure 11 Examples of triad configurations with no symmetrical relationships—i.e., no double-headed arrows. *Reprinted with permission from: Shizuka and McDonald (2012). A social network perspective on measurements of dominance hierarchies.* Animal Behaviour, *83, 925–934. Copyright © 2012 Elsevier.*

certain processes in a population and their consequences for group function. Care must be taken in comparative analyses to control for differences in dyadic connection patterns, as these constrain the possible configurations for higher-level three- and four-node subcomponents (Faust, 2006, 2007, 2010); within these constraints, however, significant departures from expected frequencies can be informative. In other cases, the expected frequency of particular subcomponent configurations is independent of group size (e.g., Shizuka & McDonald, 2012), making motif analysis an attractive option for network comparisons.

Motif analysis is best used with directed interactions (Box 1, Pinter-Wollman et al., 2014). A challenge will be to identify potential instances of directed interaction when "direction" is not obvious. In some cases, direction is clear, such as when two animals engage in an agonistic contest during which one individual emerges victorious. It is not as obvious in other cases: for example, individual A might exert influence on both individuals B and C during their agonistic interaction—e.g., A creates an audience effect. In this case, it might be difficult to identify this directed influence from A on individuals B and C, particularly in freely interacting groups. Nevertheless,

the emphasis motif analysis places on relationship patterns above the dyadic level—e.g., triadic—suggests it might be fruitfully applied toward the study of audience effects, eavesdropping, and other aspects of communication networks that are not often explicitly tackled by SNA. Technological advances allowing for greater monitoring of signaling interactions within a wider community—e.g., microphone arrays recording songbird interactions (Foote, Fitzsimmons, Mennill, & Ratcliffe, 2010)—could be especially helpful in this regard.

Motif analysis of leader–follower relationships could allow researchers to assess the extent to which the leadership hierarchy in an animal group is dominated by transitive or cyclical relationships, with potentially important implications for group function. For example, if leader–follower interaction patterns are dominated by cyclical triads, greater leadership or navigational tendencies might be required for effective group navigation. Benefits of group cohesion might select for transitive, stable leadership patterns even when no clear asymmetries exist in individual ability, experience, or information (Krause & Ruxton, 2002; McDonald & Shizuka, 2013). Similarly, the effectiveness of collective navigation has been linked to the frequency of particular four-node motifs (Bode, Wood, et al., 2012). Comparisons of the frequency of different leadership subcomponent configurations in various environments, or between different species, might reveal ecological or evolutionary influences on aspects of collective animal behavior.

Motif analysis is currently constrained primarily to censuses of three- and four-node subcomponents. This is because the number of possible configurations of a subcomponent increases exponentially with the total number of nodes making up that subcomponent. Analysis of subcomponents larger than about four nodes is therefore computationally prohibitive (Pinter-Wollman et al., 2014). However, as long as subcomponents are biologically meaningful—e.g., as when transitive triads indicate stable dominance relationships—their size may not be particularly important.

4.2 Dynamic Networks

A population's social network structure is rarely static, changing often as the result of demographic processes and behavioral responses to both external and internal changes. Despite widespread recognition of this fact, the dynamics of network topology have generally been neglected in the behavioral ecology literature (Blonder et al., 2012; Hobson et al., 2013; Pinter-Wollman et al., 2014). Most studies are based on a single, static network constructed from observed interactions and associations accumulated over

some time span—i.e., a time-aggregated network. When temporal network dynamics have been considered, this has generally been accomplished by comparing a series of time-aggregated networks, each of which was compiled over some interval of interest—e.g., seasons or years. Methods are available to study such longitudinal changes in network structure and to identify the factors influencing the probabilities of individuals changing their social relationships over time (e.g., Croft et al., 2008; Snijders et al., 2010; Pinter-Wollman et al., 2014), though these methods have been infrequently applied in behavioral ecology.

Many processes, including information flow, disease transmission, and cooperative interactions, can occur over timescales much shorter—e.g., seconds to minutes—than a longitudinal approach using time-aggregated networks can address (Waters & Fewell, 2012). What's more, network processes and topological changes to network structure might occur over similar timescales and interact with each other in feedback loops. Knowledge of the temporal sequence of interactions is particularly important if one suspects that such feedback loops are at work (Blonder et al., 2012). For example, an animal that becomes infected with parasites might modify its behavior, or others might modify their behavior toward it by attempting to avoid that individual; these changes influence the subsequent likelihood of disease transmission through the population (e.g., Croft et al., 2011). This sort of feedback has been modeled using "adaptive" or "coevolutionary" networks (Gross & Blasius, 2008), but has rarely been addressed in empirical studies on animal groups. Reciprocal feedbacks between network structure and flow dynamics might be best analyzed via time-ordered network models (Blonder et al., 2012; Pinter-Wollman et al., 2014).

Time-ordered analyses maintain data in time-stamped streams of observations, keeping a continuous record of the order, timing, and duration of interactions (Figure 12(a)). With this information in hand, it is possible to trace potential transmission pathways that take into account the actual order in which interactions occurred, as well as directly observe topological changes in the network (Blonder et al., 2012). Furthermore, aggregating interaction data over intervals can break the data stream down into a series of traditional time-aggregated networks (Figure 12(b)). Time-ordered network models are especially well suited for investigating transmission processes; researchers can use these models to: identify permitted pathways of flow, determine the relative importance of individuals in terms of their influence over these processes, and estimate the speed and efficiency of transmission within the network. While behavioral ecology has only recently begun to make use of these

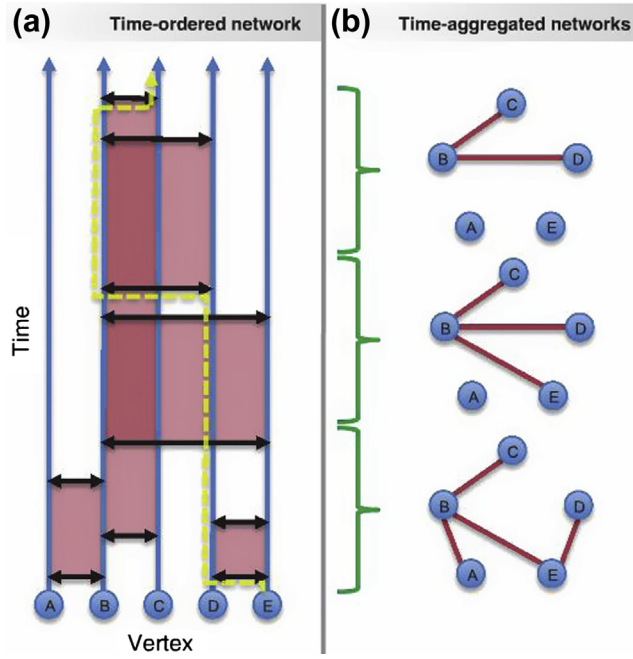

Figure 12 (a) A time-ordered network in which the precise sequence of interactions between individuals can be seen as time progresses. (b) Time-aggregated networks derived from the time-ordered data over specified intervals of time. *Reprinted with permission from: Blonder et al. (2012). Temporal dynamics and network analysis.* Methods in Ecology and Evolution*, 3, 958–972. Copyright © 2012 John Wiley and Sons.*

models (e.g., Blonder & Dornhaus, 2011), they have been used more extensively in a number of other fields, including physics (e.g., Kostakos, 2009; Holme & Saramäki, 2012), engineering (e.g., Kuhn & Oshman, 2011), and the computer sciences (e.g., Kempe, Kleinberg, & Kumar, 2002; Santoro, Quattrociocchi, Flocchini, Casteigts, & Amblard, 2011). Their use in behavioral ecology is likely to become more common in the future given parallel advancements in technology that allow researchers to continuously track individual animals. Social association data can now be collected automatically at high spatial and temporal resolution—e.g., via GPS devices or PIT systems (Aplin et al., 2013; Krause et al., 2013; Farine et al., 2014; Strandburg-Peshkin et al., 2014).

Time-ordered network analyses could be used to complement and offer further insight into many of the topics we have discussed in this review. For example, during collective motion and navigation, links can be formed as individuals move toward one another and dissolve as they move apart. Passive

mechanisms, such as individual body condition, can influence spatial location within a moving group; if animals repeatedly interact with the same individuals during these movements, passive associations might transform into active social preferences (Bode et al., 2011a). An examination of time-ordered data, as well as the time-aggregated networks that can be derived from it, could reveal whether accumulated short-term interactions during collective motion can facilitate development of more stable, long-term associations, and potentially cast light on the mechanisms by which this could occur.

Time-ordered networks might also be useful for assessing the influence of perturbations—e.g., changes in group composition, the arrival of a predator, or anthropogenic disturbances—on network structure and dynamics. An intriguing possibility that could be addressed with these techniques is whether there is variation in the extent to which individuals modify their social connections in response to perturbation. Some individuals might be very socially reactive, frequently and quickly modifying their social connections according to changing conditions or internal physiology, while others might be more socially stable and attempt to maintain the same pattern and/or intensity of connections regardless of context.

5. CONCLUSION

Starting from the musings and keen observations of naturalists and other early thinkers, the study of animal social structure and behavior has transformed over time, drawing concepts and techniques from fields as diverse as ecology, mathematics, sociology, statistical physics, evolutionary theory, and behavioral ecology. Animal SNA is now a vibrant, integrative discipline in which new insights are being generated monthly, allowing for a deeper and more holistic understanding of social structure and behavior than ever before. We have shown in this review how SNA has enriched our knowledge of behavioral ecology, as well as contributed to our understanding of many other fields. The origins of culture, the age-old problem of cooperation, and how complex, emergent group phenomena arise from individual behavior can only be fully understood when they are embedded within an explicit social context. New technologies melded with theoretical and statistical advances are expanding the horizons of SNA and taking it in novel directions at an impressive rate. We eagerly look forward to the exciting new insights sure to develop from these endeavors in the coming decades and beyond.

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REFERENCES

Alcock, J. (2013). *Animal behavior* (10th ed.). Sunderland, MA: Sinauer Associates.

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics, 5*, 325–383.

Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science, 340*, 485–488.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature, 518*, 538–541.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters, 16*, 1365–1372.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society of London B: Biological Sciences, 279*, 4199–4205.

Atton, N., Galef, B. J., Hoppitt, W., Webster, M. M., & Laland, K. N. (2014). Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. *Proceedings of the Royal Society of London B: Biological Sciences, 281*, 20140579.

Atton, N., Hoppitt, W., Webster, M. M., Galef, B. G., & Laland, K. N. (2012). Information flow through threespine stickleback networks without social transmission. *Proceedings of the Royal Society of London B: Biological Sciences, 279*, 4272–4278.

Bales, R. F. (1951). *Interaction process analysis: A method for the study of small groups*. Cambridge, MA: Addison-Wesley.

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

Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 367*, 2108–2118.

Beer, C. (1976). Some complexities in the communication behavior of gulls. *Annals of the New York Academy of Sciences, 280*, 413–432.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. *Report of the International Whaling Commission (Special Issue), 12*, 383–405.

Blonder, B., & Dornhaus, A. (2011). Time-ordered networks reveal limitations to information flow in ant colonies. *PLoS One, 6*, e20298.

Blonder, B., Wey, T. W., Dornhaus, A., James, R., & Sih, A. (2012). Temporal dynamics and network analysis. *Methods in Ecology and Evolution, 3*, 958–972.

Blumstein, D. T., Petelle, M. B., & Wey, T. W. (2013). Defensive and social aggression: repeatable but independent. *Behavioral Ecology, 24*, 457–461.

Bode, N. W. F., Franks, D. W., & Wood, A. J. (2012). Leading from the front? Social networks in navigating groups. *Behavioral Ecology and Sociobiology, 66*, 835–843.

Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011a). Social networks and models for collective motion in animals. *Behavioral Ecology and Sociobiology, 65*, 117–130.
Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011b). The impact of social networks on animal collective motion. *Animal Behaviour, 82*, 29–38.
Bode, N. W. F., Wood, A. J., & Franks, D. W. (2012). Social networks improve leaderless group navigation by facilitating long-distance communication. *Current Zoology, 58*, 329–341.
Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution, 26*, 325–338.
Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origin and spread of innovations in starlings. *Animal Behaviour, 75*, 1509–1518.
Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *UCINET 6 for Windows: Software for social network analysis*. Harvard, MA: Analytic Technologies.
Borgatti, S. P., Mehra, A., Brass, D. J., & Labianca, G. (2009). Network analysis in the social sciences. *Science, 323*, 892–895.
Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer Associates.
Bradbury, J. W., & Vehrencamp, S. L. (2014). Complexity and behavioral ecology. *Behavioral Ecology, 25*, 435–442.
Brent, L. J. N., 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.
Brosset, A. (1976). Social organization in the African bat, *Myotis boccagei*. *Zeitschrift für Tierpsychologie, 42*, 50–56.
Burt, R. S. (1988). The stability of American markets. *American Journal of Sociology, 94*, 356–395.
Carpenter, C. R. (1942a). Characteristics of social behavior in non-human primates. *Transactions of the New York Academy of Sciences: Series II, 4*, 248–258.
Carpenter, C. R. (1942b). Societies of monkeys and apes. *Biological Symposium, 8*, 177–204.
Carpenter, C. R. (1952). Social behavior of non-human primates. Structure et physiologie des sociétés animales. *Colloques Internationaux du Centre National de la Recherche Scientifique, 34*, 227–246.
Cheney, D. L. (1978a). Interactions of immature male and female baboons with adult females. *Animal Behaviour, 26*, 389–408.
Cheney, D. L. (1978b). The play partners of immature baboons. *Animal Behaviour, 26*, 1038–1050.
Chepko-Sade, B. D., Reitz, K. P., & Sade, D. S. (1989). Sociometrics of *Macaca mulatta* IV: network analysis of social structure of a pre-fission group. *Social Networks, 11*, 293–314.
Claidière, N., Messer, E. J. E., Hoppitt, W., & Whiten, A. (2013). Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Current Biology, 23*, 1251–1255.
Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: Behavior and ecology of two sexes*. Chicago, IL: University of Chicago Press.
Connor, R. C. (1992). Dolphin alliances and coalitions. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 415–443). Oxford, UK: Oxford University Press.
Connor, R. C., Heithaus, M. R., & Barre, L. M. (1999). Superalliance of bottlenose dolphins. *Nature, 397*, 571–572.
Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America, 89*, 987–990.
Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology and Evolution, 20*, 449–456.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour, 50*, 1441–1453.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature, 433*, 513–516.

Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology, 218*, 1–11.

Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., et al. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy *Poecilia reticulata*. *Oikos, 100*, 429–438.

Croft, D. P., Edenbrow, M., Darden, S. K., Ramnarine, I. W., van Oosterhout, C., & Cable, J. (2011). Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies *Poecilia reticulata*. *Behavioral Ecology and Sociobiology, 65*, 2219–2227.

Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton, NJ: Princeton University Press.

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

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology, 63*, 1495–1503.

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

Crook, J. H. (1970). Introduction—Social behaviour and ethology. In J. H. Crook (Ed.), *Social behaviour in birds and mammals: Essays on the social ethology of animals and man* (pp. xxi–xl). London, UK: Academic Press.

Crook, J. H., & Gartlan, J. S. (1966). Evolution of primate societies. *Nature, 210*, 1200–1203.

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

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology* (4th ed.). Hoboken, NJ: Wiley-Blackwell.

Dey, C. J., Reddon, A. R., O'Connor, C. M., & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behaviour, 85*, 395–402.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour, 64*, 929–938.

Dingemanse, N. J., van der Plas, F., Wright, J., Réale, D., Schrama, M., Roff, D. A., et al. (2009). Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. *Proceedings of the Royal Society of London B: Biological Sciences, 276*, 1285–1293.

Dugatkin, L. A. (1992). Sexual selection and imitation: females copy the mate choice of others. *The American Naturalist, 139*, 1384–1389.

Dugatkin, L. A. (2006). *The altruism equation: Seven scientists search for the origins of goodness*. Princeton, NJ: Princeton University Press.

Dugatkin, L. A. (2013). *Principles of animal behavior* (3rd ed.). New York, NY: W. W. Norton & Company.

Ekman, J. (1979). Coherence, composition, and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *P. cristatus*. *Ornis Scandinavica, 10*, 56–68.

Espinas, A. (1878). *Des sociétés animales: Étude de psychologie comparée*. Paris, FR: Libraire Germer Ballière.

Fairbanks, L. A. (1980). Relationships among adult females in captive vervet monkeys: testing a model of rank-related attractiveness. *Animal Behaviour, 28*, 853–859.

Farine, D. R., Strandburg-Peshkin, A., Brugere, I., Li, V. J., Berger-Wolf, T. Y., & Crofoot, M. C. (August 2014). Self-organisation in a dynamic network of wild Anubis baboons. In *Presentation at the 15th conference of the International Society for Behavioral Ecology. New York, NY*.

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

Faust, K. (2007). Very local structure in social networks. *Sociological Methodology, 37*, 209–256.

Faust, K. (2010). A puzzle concerning triads in social networks: graph constraints and the triad census. *Social Networks, 32*, 221–233.

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

Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds, 42*, 347–357.

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

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

Flack, A., Pettit, B., Freeman, R., Guilford, T., & Biro, D. (2012). What are leaders made of? The role of individual experience in determining leader-follower relations in homing pigeons. *Animal Behaviour, 83*, 703–709.

Foote, J. R., Fitzsimmons, L. P., Mennill, D. J., & Ratcliffe, L. M. (2010). Black-capped chickadee dawn choruses are interactive communication networks. *Behaviour, 147*, 1219–1248.

Foster, K. R., & Ratnieks, F. L. W. (2001). Convergent evolution of worker policing by egg eating in the honeybee and common wasp. *Proceedings of the Royal Society of London B: Biological Sciences, 268*, 169–174.

Fowler, J. H., Dawes, C. T., & Christakis, N. A. (2009). Models of genetic variation in human social networks. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 1720–1724.

Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society of London B: Biological Sciences, 276*, 1829–1836.

Franz, M., & Nunn, C. L. (2010). Investigating the impact of observation errors on the statistical performance of network-based diffusion analysis. *Learning and Behavior, 38*, 235–242.

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

Freeman, L. C. (2004). *The development of social network analysis: A study in the sociology of science*. Vancouver, BC: Empirical Press.

Freeman, R., Mann, R., Guilford, T., & Biro, D. (2011). Group decisions and individual differences: route fidelity predicts flight leadership in homing pigeons (*Columba livia*). *Biology Letters, 7*, 63–66.

Galef, B. G., Jr. (2009). Strategies for social learning: testing predictions from formal theory. *Advances in the Study of Behavior, 39*, 117–151.

Galef, B. G., Jr., Kennett, D. J., & Wigmore, S. W. (1984). Transfer of information concerning distant foods in rats: a robust phenomenon. *Animal Learning & Behavior, 12*, 292–296.

Gaskin, D. E. (1982). *The ecology of whales and dolphins*. London, UK: Heinemann.

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., et al. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology, 67*, 373–381.

Godfrey, S. S., Bull, C. M., 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.

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

Griffiths, S. W., & Magurran, A. E. (1997). Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour, 53*, 945–949.

Gross, T., & Blasius, B. (2008). Adaptive coevolutionary networks: a review. *Journal of the Royal Society Interface, 5*, 259–271.

Hanby, J. P. (1980a). Relationships in six groups of rhesus monkeys I: networks. *American Journal of Physical Anthropology, 52*, 549–564.

Hanby, J. P. (1980b). Relationships in six groups of rhesus monkeys II: dyads. *American Journal of Physical Anthropology, 52*, 565–575.

Hanneman, R. A., & Riddle, M. (2005). *Introduction to social network methods*. Riverside, CA: University of California, Riverside.

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

Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.

Hemelrijk, C. K., & Hildenbrandt, H. (2008). Self-organized shape and frontal density of fish schools. *Ethology, 114*, 245–254.

Hemelrijk, C. K., & Kunz, H. (2005). Density distribution and size sorting in fish schools: an individual-based model. *Behavioral Ecology, 16*, 178–187.

Hinde, R. A. (1959). Unitary drives. *Animal Behaviour, 7*, 130–141.

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

Hinde, R. A. (1982). *Ethology: Its nature and relations with other sciences*. New York, NY: Oxford University Press.

Hobson, E. A., Avery, M. L., & Wright, T. F. (2013). An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. *Animal Behaviour, 85*, 83–96.

Holme, P., & Newman, M. E. J. (2006). Nonequilibrium phase transition in the coevolution of networks and opinions. *Physical Review E, 74*, 056108.

Holme, P., Park, S. M., Kim, B. J., & Edling, C. R. (2007). Korean university life in a network perspective: dynamics of a large affiliation network. *Physica A: Statistical Mechanics and Its Applications, 373*, 821–830.

Holme, P., & Saramäki, J. (2012). Temporal networks. *Physical Reports, 519*, 97–125.

Homans, G. C. (1951). *The human group*. London, UK: Routledge and Kegan Paul.

Hoppitt, W. J. E., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology, 263*, 544–555.

Hoppitt, W., Kandler, A., Kendal, J. R., & Laland, K. N. (2010). The effect of task structure on diffusion dynamics: implications for diffusion curve and network-based analyses. *Learning and Behavior, 38*, 243–251.

Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton, NJ: Princeton University Press.

Huffman, M. A. (1996). Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In C. M. Heyes, & B. G. Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 267–289). San Diego, CA: Academic Press.

Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London B: Biological Sciences, 270*, 867–874.

Ilany, A., Barocas, A., Koren, L., Kam, M., & Geffen, E. (2013). Structural balance in the social networks of a wild mammal. *Animal Behaviour, 85*, 1397–1405.

Ioannou, C. C., Couzin, I. D., James, R., Croft, D. P., & Krause, J. (2011). Social organisation and information transfer in schooling fish. In C. Brown, J. Krause, & K. N. Laland (Eds.), *Fish cognition and behavior* (2nd ed.). (pp. 217–239). Hoboken, NJ: Wiley-Blackwell.

Jacobs, A., Sueur, C., Deneubourg, J. L., & Petit, O. (2011). Social network influences decision making during collective movements in brown lemurs (*Eulemur fulvus fulvus*). *International Journal of Primatology, 32*, 721–736.

James, R., Croft, D. P., & Krause, J. (2009). Potential banana skins in animal social network analysis. *Behavioral Ecology and Sociobiology, 63*, 989–997.

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. *Behaviour, 48*, 215–267.

Jeanson, R. (2012). Long-term dynamics in proximity networks in ants. *Animal Behaviour, 83*, 915–923.

Jones, C. B. (2005). *Behavioral flexibility in primates: Causes and consequences*. New York, NY: Springer.

Kaplan, J. R., & Zucker, E. (1980). Social organization in a group of free-ranging patas monkeys. *Folia Primatologica, 34*, 196–213.

Kappeler, P. M. (1993). Variation in social structure: the effects of sex and kinship on social interactions in three lemur species. *Ethology, 93*, 125–145.

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates, 6*, 1–30.

Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J., & Croft, D. P. (2011). Predation risk shapes social networks in fission-fusion populations. *PLoS One, 6*, e24280.

Kempe, D., Kleinberg, J., & Kumar, A. (2002). Connectivity and inference problems for temporal networks. *Journal of Computer and System Sciences, 64*, 820–842.

Kendal, R. L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L., et al. (2010). Evidence for social learning in wild lemurs (*Lemur catta*). *Learning and Behavior, 38*, 220–234.

Kennedy, J. S. (1954). Is modern ethology objective? *Animal Behaviour, 2*, 12–19.

Kollmann, M., Løvdok, L., Bartholomé, K., Timmer, J., & Sourjik, V. (2005). Design principles of a bacterial signaling network. *Nature, 438*, 504–507.

Kostakos, V. (2009). Temporal graphs. *Physica A: Statistical Mechanics and Its Applications, 388*, 1007–1023.

Krause, J., Butlin, R. K., Peuhkuri, N., & Pritchard, V. L. (2000). The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biological Reviews, 75*, 477–501.

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology, 62*, 15–27.

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365*, 4099–4106.

Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., & Rutz, C. (2013). Reality mining of animal social systems. *Trends in Ecology and Evolution, 28*, 541–551.

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, UK: Oxford University Press.

Krueger, K., Flauger, B., Farmer, K., & Hemelrijk, C. (2014). Movement initiation in groups of feral horses. *Behavioural Processes, 103*, 91–101.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 8939–8943.

Kuhn, F., & Oshman, R. (2011). Dynamic networks: models and algorithms. *ACM SIGACT News, 42*, 82–96.

Kummer, H. (1968). *Social organization of Hamadryas baboons: A field study*. Chicago, IL: University of Chicago Press.

Kurvers, R. H. J. M., Nolet, B. A., Prins, H. H. T., Ydenberg, R. C., & van Oers, K. (2012). Boldness affects foraging decisions in barnacle geese: an experimental approach. *Behavioral Ecology, 23*, 1155–1161.

Kurvers, R. H. J. M., van Oers, K., Nolet, B. A., Jonker, R. M., van Wieren, S. E., Prins, H. H. T., et al. (2010). Personality predicts the use of social information. *Ecology Letters, 13*, 829–837.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London, UK: Chapman and Hall.

Laland, K. N. (2004). Social learning strategies. *Learning and Behavior, 32*, 4–14.

Laland, K. N., & Galef, B. G., Jr. (Eds.). (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology and Evolution, 21*, 542–547.

Laland, K. N., & Kendal, J. R. (2003). What the models say about social learning. In D. Fragaszy, & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 33–55). Cambridge, UK: Cambridge University Press.

Le Pendu, Y., Briedermann, L., Gerard, J. F., & Maublanc, M. L. (1995). Inter-individual associations and social structure in a mouflon population (*Ovis orientalis* musimon). *Behavioural Processes, 34*, 67–80.

Leenders, R. T. A. J. (1995). Models for network dynamics: a Markovian framework. *Journal of Mathematical Sociology, 20*, 1–21.

Lefebvre, L. (1995). Culturally-transmitted feeding behaviour in primates: evidence for accelerating learning rates. *Primates, 36*, 227–239.

Lefebvre, D., Ménard, N., & Pierre, J. S. (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.

Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behaviour. *The Quarterly Review of Biology, 28*, 337–363.

Leu, S. T., Kappeler, P. M., & Bull, C. M. (2010). Refuge sharing network predicts ectoparasite load in a lizard. *Behavioral Ecology and Sociobiology, 64*, 1495–1503.

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

Lewin, K. (1951). *Field theory in social science: Selected theoretical papers*. New York, NY: Harper.

Li, P. P., & Hui, P. M. (2008). Dynamics of opinion formation in hierarchical social networks: network structure and initial bias. *The European Physical Journal B, 61*, 371–376.

Lorenz, K. Z. (1937). The companion in the bird's world. *The Auk, 54*, 245–273.

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

Lusseau, D. (2007). Evidence for social role in a dolphin social network. *Evolutionary Ecology, 21*, 357–366.

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

Lusseau, D., Whitehead, H., & Gero, S. (2008). Incorporating uncertainty into the study of animal social networks. *Animal Behaviour, 75*, 1809–1815.

MacCarthy, T., Seymour, R., & Pomiankowski, A. (2003). The evolutionary potential of the *Drosophila* sex determination gene network. *Journal of Theoretical Biology, 225*, 461–468.

Mackinson, S. (1999). Variation in structure and distribution of pre-spawning Pacific herring shoals in two regions of British Columbia. *Journal of Fish Biology, 55*, 972–989.

Magurran, A. E., & Higham, A. (1988). Information transfer across fish shoals under predator threat. *Ethology, 78*, 153–158.

Makagon, M. M., McCowan, B., & Mench, J. A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science, 138*, 152–161.

Maryanski, A. R. (1987). African ape social structure: is there strength in weak ties? *Social Networks, 9*, 191–215.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.

McBride, G. (1964). A general theory of social organization and behaviour. *University of Queensland Papers, Faculty of Veterinary Science, 1*, 75–110.

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences, 104*, 10910–10914.

McDonald, D. B. (2009). Young-boy networks without kin clusters in a lek-mating manakin. *Behavioral Ecology and Sociobiology, 63*, 1029–1034.

McDonald, D. B., & Shizuka, D. (2013). Comparative transitive and temporal orderliness in dominance networks. *Behavioral Ecology, 24*, 511–520.

McNamara, J. M., & Leimar, O. (2010). Variation and the response to variation as a basis for successful cooperation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365*, 2627–2633.

McNamara, J. M., Stephens, P. A., Dall, S. R. X., & Houston, A. I. (2009). Evolution of trust and trustworthiness: social awareness favours personality differences. *Proceedings of the Royal Society of London B: Biological Sciences, 276*, 605–613.

Meyers, L. A., Pourbohloul, B., Newman, M. E. J., Skowronski, D. M., & Brunham, R. C. (2005). Network theory and SARS: predicting outbreak diversity. *Journal of Theoretical Biology, 232*, 71–81.

Miller, J. L., King, A. P., & West, M. J. (2008). Female social networks influence male vocal development in brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour, 76*, 931–941.

Milo, R., Itzkovitz, S., Kashtan, N., Levitt, R., Shen-Orr, S., Ayzenshtat, I., et al. (2004). Superfamilies of evolved and designed networks. *Science, 303*, 1538–1542.

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

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In B. G. Galef, Jr., & T. R. Zentall (Eds.), *Social learning: Psychological and biological perspectives* (pp. 51–73). Hillsdale, NJ: Lawrence Erlbaum.

Mitani, M. (1986). Voiceprint identification and its application to sociological studies of wild Japanese monkeys (*Macaca fuscata yakui*). *Primates, 27*, 397–412.

Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: an ecological and evolutionary overview. *Animal Behaviour, 89*, 53–62.

Montiglio, P. O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 368*, 20120343.

Moreno, J. L. (1934). *Who shall survive? A new approach to the problem of human interrelations*. Washington, DC: Nervous and Mental Disease Publishing Co.

Morrell, L. J., Croft, D. P., Dyer, J. R. G., Chapman, B. B., Kelley, J. L., Laland, K. N., et al. (2008). Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour, 76*, 855–864.

Mourier, J., Vercelloni, J., & Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Animal Behaviour, 83*, 389–401.

Myers, J. P. (1983). Space, time and the pattern of individual associations in a group-living species: sanderlings have no friends. *Behavioral Ecology and Sociobiology, 12*, 129–134.

Nagy, M., Vásárhelyi, G., Pettit, B., Roberts-Mariani, I., Vicsek, T., & Biro, D. (2013). Context-dependent hierarchies in pigeons. *Proceedings of the National Academy of Sciences of the United States of America, 110*, 13049–13054.

Nakagawa, N. (1992). Distribution of affiliative behaviors among adult females within a group of wild patas monkeys in a nonmating, nonbirth season. *International Journal of Primatology, 13*, 73–96.

Nardini, C., Kozma, B., & Barrat, A. (2008). Who's talking first? Consensus or lack thereof in coevolving opinion formation models. *Physical Review Letters, 100*, 158701.

Naug, D. (2008). Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behavioral Ecology and Sociobiology, 62*, 1719–1725.

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

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

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

Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N., & Jenner, K. C. S. (2000). Cultural revolution in whale songs. *Nature, 408*, 537.

Nowak, M. A., & May, R. M. (1992). Evolutionary games and spatial chaos. *Nature, 359*, 826–829.

Nowak, M. A., & Sigmund, K. (1992). Tit for tat in heterogeneous populations. *Nature, 355*, 250–253.

Nowak, M. A., Tarnita, C. E., & Antal, T. (2010). Evolutionary dynamics in structured populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365*, 19–30.

Oh, K. P., & Badyaev, A. V. (2010). Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist, 176*, E80–E89.

Ohtsuki, H., Hauert, C., Lieberman, E., & Nowak, M. A. (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature, 441*, 502–505.

Pearl, M. C., & Schulman, S. R. (1983). Techniques for the analysis of social structure in animal societies. *Advances in the Study of Behavior, 13*, 107–146.

Petit, O., & Bon, R. (2010). Decision-making processes: the case of collective movements. *Behavioral Processes, 84*, 635–647.

Petrucci, R. (1905). *Les origines naturelles de la propriété: Essai de sociologie comparée*. Instituts Solvay. Travaux de l'Institut de Sociologie. Notes et Memoires. Fasc. 3. Bruxelles, BE: Misch et Thron.

Petrucci, R. (1906). *Origine polyphylétique, homotypie et non-comparabilité directe des sociétés animales*. Instituts Solvay. Travaux de l'Institut de Sociologie. Notes et Memoires. Fasc. 7. Bruxelles, BE: Misch et Thron.

Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society of London B: Biological Sciences, 275*, 2515–2520.

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., et al. (2014). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology, 25*, 242–255.

Qiu, F., & Hu, X. (2010). Modeling group structures in pedestrian crowd simulation. *Simulation Modelling Practice and Theory, 18*, 190–205.

Ramseyer, A., Boissy, A., Thierry, B., & Dumont, B. (2009). Individual and social determinants of spontaneous group movements in cattle and sheep. *Animal, 3*, 1319–1326.

Ratnieks, F. L. W., & Wenseleers, T. (2005). Policing insect societies. *Science, 307*, 54–56.

Rausher, M. D., Miller, R. E., & Tiffin, P. (1999). Patterns of evolutionary rate variation among genes of the anthocyanin biosynthetic pathway. *Molecular Biology and Evolution, 16*, 266–274.

Reader, S. M. (2000). *Social learning and innovation: Individual differences, diffusion dynamics and evolutionary issues* (Ph.D. thesis). Cambridge, UK: University of Cambridge.

Reader, S. M. (2004). Distinguishing social and asocial learning using diffusion dynamics. *Learning and Behavior, 32*, 90–104.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*, 291–318.

Reebs, S. G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal Behaviour, 59*, 403–409.

Rhine, R. J. (1973). Variation and consistency in the social behavior of two groups of stumptail macaques (*Macaca arctoides*). *Primates, 14*, 21–35.

Rogers, A. R. (1988). Does biology constrain culture? *American Anthropologist, 90*, 819–831.
Roney, J. R., & Maestripieri, D. (2003). Social development and affiliation. In D. Maestripieri (Ed.), *Primate psychology* (pp. 171–204). Cambridge, MA: Harvard University Press.
Royle, N. J., Pike, T. W., Heeb, P., Richner, H., & Kölliker, M. (2012). Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society of London B: Biological Sciences, 279*, 4914–4922.
Ryder, T. B., McDonald, D. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2008). Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proceedings of the Royal Society of London B: Biological Sciences, 275*, 1367–1374.
Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology, 23*, 1–17.
Sade, D. S. (1972). Sociometrics of *Macaca mulatta* I. Linkages and cliques in grooming matrices. *Folia Primatologica, 18*, 196–223.
Sade, D. S., Altmann, M., Loy, J., Hausfater, G., & Breuggeman, J. A. (1988). Sociometrics of *Macaca mulatta*: II. Decoupling centrality and dominance in rhesus monkey social networks. *American Journal of Physical Anthropology, 77*, 409–425.
Sade, D. S., & Dow, M. M. (1994). Primate social networks. In S. Wasserman, & J. Galaskiewicz (Eds.), *Advances in social network analysis: Research in the social and behavioral sciences* (pp. 152–166). Thousand Oaks, CA: Sage Publications.
Santoro, N., Quattrociocchi, W., Flocchini, P., Casteigts, A., & Amblard, F. (2011). Time-varying graphs and social network analysis: temporal indicators and metrics. *arXiv*, 1102.0629.
Santos, F. C., Pacheco, J. M., & Lenaerts, T. (2006a). Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 3490–3494.
Santos, F. C., Pacheco, J. M., & Lenaerts, T. (2006b). Cooperation prevails when individuals adjust their social ties. *PLoS Computational Biology, 2*, 1284–1291.
Schnoell, A. V., & Fichtel, C. (2012). Wild redfronted lemurs (*Eulemur rufifrons*) use social information to learn new foraging techniques. *Animal Cognition, 15*, 505–516.
Schürch, R., Rothenberger, S., & Heg, D. (2010). The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365*, 4089–4098.
Scott, J. P. (1945). Group formation determined by social behavior: a comparative study of two mammalian societies. *Sociometry, 8*, 42–52.
Scott, J. (2000). *Social network analysis: A handbook* (2nd ed.). Thousand Oaks, CA: Sage Publications.
Scott, J., & Carrington, P. J. (2011). *The SAGE handbook of social network analysis*. Thousand Oaks, CA: Sage Publications.
Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour, 24*, 917–938.
Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology, 65*, 671–698.
Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour, 28*, 798–813.
Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature, 308*, 541–543.
Shizuka, D., & McDonald, D. B. (2012). A social network perspective on measurements of dominance hierarchies. *Animal Behaviour, 83*, 925–934.
Sih, A., & Bell, A. M. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior, 38*, 227–281.

Sih, A., Bell, A., & Johnson, J. C. (2010). Behavioral syndromes. In D. F. Westneat, & C. W. Fox (Eds.), *Evolutionary behavioral ecology* (pp. 516–530). Oxford, UK: Oxford University Press.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology, 63*, 975–988.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 362*, 539–559.

Simons, A. M. (2004). Many wrongs: the advantage of group navigation. *Trends in Ecology and Evolution, 19*, 453–455.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology, 19*, 448–455.

Snijders, T. A. B. (2001). The statistical evaluation of social network dynamics. *Sociological Methodology, 31*, 361–395.

Snijders, T. A. B., van de Bunt, G. G., & Steglich, C. E. G. (2010). Introduction to stochastic actor-based models for network dynamics. *Social Networks, 32*, 44–60.

Soczka, L. (1974). Ethologie sociale et sociometrie: analyse de la structure d'un groupe de singes crabiers (*Macaca fascicularis = irus*) en captivite. *Behaviour, 50*, 254–269.

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

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews, 85*, 301–325.

Stephenson, K., & Zelen, M. (1989). Rethinking centrality: methods and examples. *Social Networks, 11*, 1–37.

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (August 2014). Leadership and collective motion in Anubis baboons using high-resolution GPS tracking. In *Presentation at the 15th conference of the International Society for Behavioral Ecology. New York, NY.*

Strier, K. B., Boubli, J. P., Possamai, C. B., & Mendes, S. L. (2006). Population demography of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva Particular do Patrimônio Natural-Felìciano Miguel Abdala, Minas Gerais, Brazil. *American Journal of Physical Anthropology, 130*, 227–237.

Sueur, C., Deneubourg, J. L., & Petit, O. (2012). From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus). *PLoS One,* 7, e32566.

Sueur, C., & Maire, A. (2014). Modelling animal group fission using social network dynamics. *PLoS One, 9*, e97813.

Sueur, C., & Petit, O. (2008). Shared or unshared consensus decision in macaques? *Behavioural Processes, 78*, 84–92.

Sueur, C., Petit, O., & Deneubourg, J. L. (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. L. (2010). Short-term group fission processes in macaques: a social networking approach. *The Journal of Experimental Biology, 213*, 1338–1346.

Sumpter, D. J. T. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 361*, 5–22.

Sundaresan, S. R., Fischhoff, I. R., Dushoff, J., & Rubenstein, D. I. (2007). Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia, 151*, 140–149.

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour, 62*, 591–598.

Thompson, W. R. (1958). Social behaviour. In A. Roe, & G. G. Simpson (Eds.), *Behavior and evolution* (pp. 291–310). New Haven, CT: Yale University Press.

Tinbergen, N. (1953). *Social behaviour in animals, with special reference to vertebrates*. London, UK: Methuen.

Tokuda, M., Boubli, J. P., Mourthé, Í., Izar, P., Possamai, C. B., & Strier, K. B. (2014). Males follow females during fissioning of a group of northern muriquis. *American Journal of Primatology, 76*, 529–538.

Trompf, L., & Brown, C. (2014). Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Animal Behaviour, 88*, 99–106.

Underwood, R. (1981). Companion preference in an eland herd. *African Journal of Ecology, 19*, 341–354.

VanderWaal, K. L., Atwill, E. R., Isbell, L. A., & McCowan, B. (2014). Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *Journal of Animal Ecology, 83*, 406–414.

VanderWaal, K. L., Wang, H., McCowan, B., Fushing, H., & Isbell, L. A. (2014). Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). *Behavioral Ecology, 25*, 17–26.

Vital, C., & Martins, E. P. (2011). Strain differences in zebrafish (*Danio rerio*) social roles and their impact on group task performance. *Journal of Comparative Psychology, 125*, 278–285.

Vital, C., & Martins, E. P. (2013). Socially-central zebrafish influence group behavior more than those on the social periphery. *PLoS One, 8*, e55503.

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.

Voelkl, B., & Noë, R. (2010). Simulation of information propagation in real-life primate networks: longevity, fecundity, fidelity. *Behavioral Ecology and Sociobiology, 64*, 1449–1459.

de Waal, F. B. M., & Harcourt, A. H. (1992). Coalitions and alliances: a history of ethological research. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 1–19). Oxford, UK: Oxford University Press.

Wang, Y., & Qian, X. (2014). Functional module identification in protein interaction networks by interaction patterns. *Bioinformatics, 30*, 81–93.

Wasserman, S. S. (1977). *Stochastic models for directed graphs* (Ph.D. dissertation). Cambridge, MA: Harvard University.

Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications*. Cambridge, UK: Cambridge University Press.

Waters, J. S., & Fewell, J. H. (2012). Information processing in social insect networks. *PLoS One, 7*, e40337.

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

Webster, M. M., Atton, N., Hoppitt, W. J. E., & Laland, K. N. (2013). Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *The American Naturalist, 181*, 235–244.

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews, 86*, 759–773.

Wey, T. W., & Blumstein, D. T. (2012). Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology, 66*, 1075–1085.

Wey, T., Blumstein, D. T., 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. (1995). Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology, 6*, 199–208.

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

Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology, 63*, 765–778.

Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior, 28*, 33–74.

Whitehead, H., & Lusseau, D. (2012). Animal social networks as substrate for cultural behavioural diversity. *Journal of Theoretical Biology, 294*, 19–28.

Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.

Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: a key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology, 67*, 163–173.

Wilson, A. D. M., Krause, S., James, R., Croft, D. P., Ramnarine, I. W., Borner, K. K., et al. (2014). Dynamic social networks in guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology, 68*, 915–925.

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

Wilson, D. S., Pollock, G. B., & Dugatkin, L. A. (1992). Can altruism evolve in purely viscous populations? *Evolutionary Ecology, 6*, 331–341.

Wiszniewski, J., Brown, C., & Möller, L. M. (2012). Complex patterns of male alliance formation in a dolphin social network. *Journal of Mammalogy, 93*, 239–250.

Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology and Evolution, 29*, 306–308.

Wolf, M., van Doorn, G. S., & Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society of London B: Biological Sciences, 278*, 440–448.

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365*, 3959–3968.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution, 27*, 452–461.

Žiberna, A. (2014). Blockmodeling of multilevel networks. *Social Networks, 39*, 46–61.