Behavioral Ecology

The official journal of the ISBE International Society for Behavioral Ecology

Behavioral Ecology (2014), 25(2), 242–255. doi:10.1093/beheco/art047

Invited Review

The dynamics of animal social networks: analytical, conceptual, and theoretical advances

Noa Pinter-Wollman,[a] Elizabeth A. Hobson,[b] Jennifer E. Smith,[c] Andrew J. Edelman,[d] Daizaburo Shizuka,[e,f] Shermin de Silva,[g] James S. Waters,[h] Steven D. Prager,[i] Takao Sasaki,[h] George Wittemyer,[g] Jennifer Fewell,[h] and David B. McDonald[j]

[a]BioCircuits Institute, University of California San Diego, 9500 Gilman Dr., La Jolla, CA 92093-0328, USA, [b]Department of Biology, New Mexico State University, PO Box 30001, MSC 3AF, Las Cruces, NM 88003, USA, [c]Biology Department, Mills College, 5000 MacArthur Boulevard, Oakland, CA 94613, USA, [d]Department of Biology, University of West Georgia, 1601 Maple Street, Carrollton, GA 30118, USA, [e]Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, IL 60637, USA, [f]School of Biological Sciences, University of Nebraska, Lincoln, 1400 R Street, Lincoln, NE 68588, USA, [g]Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, USA, [h]School of Life Sciences, PO Box 874601, Arizona State University, Tempe, AZ 85287-4601, USA, [i]Department of Geography, University of Wyoming, 1000 E University Avenue, Laramie, WY 82071, USA, and [j]Department of Zoology and Physiology, University of Wyoming, Dept. 3166, 1000 E University Avenue, Laramie, WY 82071, USA

Received 21 August 2012; revised 15 April 2013; accepted 1 May 2013; Advance Access publication 14 June 2013.

Social network analysis provides a broad and complex perspective on animal sociality that is widely applicable to almost any species. Recent applications demonstrate the utility of network analysis for advancing our understanding of the dynamics, selection pressures, development, and evolution of complex social systems. However, most studies of animal social networks rely primarily on a descriptive approach. To propel the field of animal social networks beyond exploratory analyses and to facilitate the integration of quantitative methods that allow for the testing of ecologically and evolutionarily relevant hypotheses, we review methodological and conceptual advances in network science, which are underutilized in studies of animal sociality. First, we highlight how the use of statistical modeling and triadic motifs analysis can advance our understanding of the processes that structure networks. Second, we discuss how the consideration of temporal changes and spatial constraints can shed light on the dynamics of social networks. Third, we consider how the study of variation at multiple scales can potentially transform our understanding of the structure and function of animal networks. We direct readers to analytical tools that facilitate the adoption of these new concepts and methods. Our goal is to provide behavioral ecologists with a toolbox of current methods that can stimulate novel insights into the ecological influences and evolutionary pressures structuring networks and advance our understanding of the proximate and ultimate processes that drive animal sociality.

Key words: **animal social networks, exponential random graph modeling, spatial behavior, social network analysis, temporal change, triadic motifs, variation.**

INTRODUCTION

Despite its long-term prevalence in sociology and physics (Wasserman and Faust 1994; Watts and Strogatz 1998; Barabasi and Albert 1999; Newman 2003), behavioral ecologists have only recently started to apply social network theory to investigate the ecological function and evolutionary development of social behavior (Krause et al. 2007; Croft et al. 2008; Wey et al. 2008; Sih et al. 2009; Croft et al. 2011). Network theory provides a holistic way to connect the functionality of a group to the behavior of its constituent individuals (Alon 2003; Fewell 2003). Within a network framework, individual animals are modeled as nodes

Address correspondence to N. Pinter-Wollman. E-mail: nmpinter@ucsd.edu.

within a group of more than 2 individuals and represented as a graph or network. Individuals are connected with links based on their co-occurrences in space or on their behavioral interactions. The links can be directed if the interaction has a clear instigator and a receiver or undirected if the interaction is in no particular orientation. Links can also be weighted, indicating the number or probability of interactions among individuals, or unweighted (binary), without information about the strength of the interaction (for more details, see Wey et al. 2008). The emergent patterns of interactions among individuals, occurring dynamically across space and time, can fundamentally shape the fitness of individuals within social groups and thus impact the demography and structure of populations (Lea et al. 2010; Barocas et al. 2011; Formica et al. 2012; Wey and Blumstein 2012).

Network methods help characterize social structures in new ways, providing an expanded opportunity to understand the ecological function and evolution of complex sociality in animals. However, current research utilizing a social network approach in behavioral ecology predominantly focuses on descriptive approaches that identify the structure of animal interactions but do not necessarily test hypotheses about function of interaction patterns. To understand the ecological and evolutionary processes underlying social network formation and organization, we need to compare social networks across species and study how changes in the environment, such as resource availability or population density, or during an animal's ontogeny, such as dispersal events, influence network structure. To advance the field of animal social networks from describing structures to testing ecologically and evolutionarily relevant hypotheses, current research needs to capitalize on theoretical, methodological, and analytical developments in parallel disciplines, such as epidemiology (Bansal et al. 2007), and the social (Snijders and Doreian 2010, 2012) and physical sciences (Newman 2003). Bringing in new techniques for analyzing animal social networks from the previously mentioned disciplines will allow behavioral ecologists to address novel questions about the formation and dynamics of animal social structures.

Here, we highlight methodological advances and conceptual challenges in the study of animal social networks, which are underutilized by the current behavioral ecological literature, and suggest how further development of these ideas will significantly advance the field. We divide this review into 3 broad topics. First, we summarize how methodological advancements, including network modeling and investigation of triadic motifs, can be used for sophisticated analyses and comparisons of animal social networks to illuminate mechanisms underlying network structures. Next, we focus on conceptual challenges and provide suggestions for incorporating temporal dynamics and spatial constraints into animal network studies, which we see as critical for understanding the processes that structure and maintain networks. Finally, we consider network variation at the individual, population, and species scales and describe how increased understanding of the causes and consequences of this variability can provide insights into the ecological influences and evolutionary pressures on networks. We hope to reenergize the use of social network theory in behavioral ecology by moving forward from introducing basic network methods (Wey et al. 2008) and highlighting technical constraints (Croft et al. 2011). We add to previous reviews of the topic (Krause et al. 2007; Sih et al. 2009) by suggesting new approaches and statistical tools that will address the biological questions social network theory can elucidate.

In each section, we include examples of how to apply these approaches and recommend relevant analytical tools that will facilitate the adoption of these advances (Table 1). We include examples of studies that have already implemented these concepts to reveal their current breadth across taxonomic groups (Table 2). In conclusion, we highlight unanswered questions that will be the focus of this next progression in socio-ecological research. Our goal is to summarize major methodological and theoretical advances in social network analysis to ensure behavioral ecologists are fluent with the available tools, analytical approaches, and underlying theory required to address questions regarding the generation and function of social complexity.

METHODOLOGICAL ADVANCES: UNDERSTANDING THE PROCESSES THAT UNDERLIE NETWORK STRUCTURES

Association patterns among individuals are generally nonrandom (Krause and Ruxton 2002; Krause et al. 2007). However, we have only a few functional explanations for why social networks are structured the way they are (one example is life-history stage; McDonald 2007). Advances in statistical methods suitable for network data can be used to better understand the factors that determine the structure of animal social networks. Here, we discuss how statistical network modeling and triadic motifs can be used to examine the mechanisms that underlie network structures and the ultimate function of networks.

Moving beyond descriptive statistics

To understand which physical and biological processes shape nonrandom social networks, a statistical network modeling approach can be used. In the past, researchers have examined network structures by comparing descriptive structural statistics (e.g., node degree and transitivity) between observed and randomly constructed networks (Croft et al. 2008). This type of statistical approach is easy to perform and can provide valuable insights into how the observed social network is different from a particular null hypothesis as expressed by a set of random networks (Croft et al. 2011). However, most if not all biological networks are nonrandom; thus, using random networks as null models may oversimplify the real-world complexities of many animal social systems. The next challenge is to decipher why particular nonrandom structures occur. Multiple deterministic and stochastic processes likely contribute to social network structure, and the effects of these processes cannot be rigorously teased apart through exploratory analyses of descriptive statistics alone. Advanced statistical modeling techniques offer a potential solution to evaluating the synergistic effects of multiple processes on animal social network structure.

Exponential random graph modeling (ERGM, or p* modeling) is a well-developed statistical technique, used extensively in the social sciences, that enables examination of the underlying mechanisms of network factors and processes that generate nonrandom network structures (Anderson et al. 1999; Robins et al. 2007). ERGM can be used to explore how network structures emerge from external factors and test how networks are shaped by their function. ERGM, closely related to logistic regression, uses stochastic modeling to determine the probability that a social link exists among individuals based on a set of predictor variables (Robins et al. 2007). Explanatory variables can take a variety of forms including individual attributes (e.g., age, social status, and reproductive condition), dyadic covariates (e.g., spatial distance, relatedness, and past interactions), and structural features (e.g., triad closure) (Goodreau et al. 2009). Social links can be directed or undirected in ERGM but must be binary (i.e., unweighted). ERGM (implemented in the R package *statnet*) is particularly suitable for the analysis of network data because it incorporates the inherent dependence among individuals in its estimation

Table 1

A summary of the analytical tools reviewed

Topic	Analysis method	Example for behavioral questions that can be addressed	Network properties[a]	Restrictions and caveats	Analysis packages	Link to software (if applicable)	Citations
Beyond descriptive statistics	ERGM	How do various factors (such as age, gender, genetic relatedness, and social status) differentially influence the structure of binary networks?	UD, D, B	Similar to logistic regression in interpretation, dependent variable must be binary; independent variables can be continuous	statnet (R)	http://csde.washington.edu/statnet/	Robins et al. (2007)
	MRQAP	How do various factors (such as age, gender, etc.) differentially influence the strength of associations (i.e., the structure of weighted networks)?	UD, D, W, B		UCInet, sna (R)	https://sites.google.com/site/ucinetsoftware/home	Dekker et al. (2007)
Deconstructing networks	Motif analysis (triads)	What is the frequency of transitive triads in dominance networks?	D, B	Careful consideration of randomization procedures to derive null hypotheses	igraph, statnet (R), Mfinder, MAVisto, FANMOD	http://csde.washington.edu/statnet/; http://www.weizmann.ac.il/mcb/UriAlon/groupNetworkMotifSW.html; http://mavisto.ipk-gatersleben.de/; http://theinf1.informatik.uni-jena.de/~wernicke/motifs/; http://igraph.sourceforge.net/	Handcock et al. (2003), Kashtan et al. (2004), Schreiber and Schwöbbermeyer (2005), Csardi and Nepusz (2006), Wernicke and Rasche (2006)
Temporal dynamics	Discrete visualization	What does the social network of x look like in different seasons?	UD, D, W, B	Temporal resolution should be appropriate to study species	Visone	http://visone.info/	Brandes and Wagner (2004)
	Discrete analysis	When does significant structural change occur in a social network?	UD, D, W, B		SNCD–ORA	http://www.casos.cs.cmu.edu/projects/ora/	McCulloh (2009)
	SAOM	Why do social ties and attributes change over time?	UD, D, B	Can handle some changes in number and identity of specific individuals	RSiena	http://www.stats.ox.ac.uk/~snijders/siena/	Snijders et al. (2010)
	Continuous analysis	How do the interactions among individuals change over time?	UD, D, B		Timeordered (R)	http://www.sourcecod.com/timeorderednetworks/	Blonder and Dornhaus (2011)
Spatial constraints	Community-detection algorithms	Can populations with high spatial overlap among individuals be subdivided into smaller, biologically meaningful, subnetworks?	UD, B, W	No spatial data needed	statnet (R), iGraph	http://igraph.sourceforge.net/; http://csde.washington.edu/statnet/; http://www.stats.ox.ac.uk/~snijders/siena/	Porter et al. (2009), Fortunato (2010)
	Spatially explicit approaches	Can social structure be inferred from spatiotemporal co-occurrence?	UD, W, B		GMMEvents (Matlab)	http://www.robots.ox.ac.uk/~parg/software.html	Psorakis et al. 2012
	ERGM and SAOM	Are interacting animals responding to social or spatial preferences?	UD, D, B	See above	RSiena, statnet (R)	See above	See above
Individual variation within networks	Knockout experiments	How does a certain individual affect network dynamics? Do individuals vary in their impact on the function of the network?	UD, D, W, B	Careful consideration of randomization procedures to derive null hypotheses	Experimental manipulation or computer simulation		Flack et al. 2006
Variation among networks	Compare standardized networks and data sharing	Do similar ecological and life-history constraints produce similar social structures in phylogenetically related species?	UD, D, W, B	Careful consideration of data collection methods and assumptions used when creating various networks	Dryad Digital Repository	http://datadryad.org/	
	Motif analysis	Do transient social networks have the same structure as long-lasting networks?	D, B	Careful consideration of randomization procedures to derive null hypotheses	See above	See above	See above

[a]Network properties: D, directed; UD, undirected; B, binary (unweighted); W, weighted.

methods. The main statistical benefit of employing an ERGM approach is the ability to rigorously evaluate how multiple covariates contribute to the overall social network structure. For example, researchers can use ERGM to examine how multiple covariates such as age, social status, spatial distance, and relatedness differentially influence the social network structure of a study population or group. However, this approach has not yet been applied to understand what processes shape animal social systems (Table 2).

Multiple Regression Quadratic Assignment Procedure (MRQAP) is another method that can be used to investigate the synergistic effects of multiple factors on network structure (Dekker et al. 2003; Dekker et al. 2007; Croft et al. 2011). In contrast to ERGM, MRQAP can be used with weighted (i.e., nonbinary) networks, in which the strength of the links is known because both the dependent and independent matrices can be continuous measures. MRQAP tests have been used to determine social affinity patterns while controlling for factors such as spatial location, sex, and relatedness (Mann et al. 2012) and to test whether similarity in age, sex, or relatedness predicted networks of affiliative and agonistic interactions (Wey and Blumstein 2010). MRQAP can be implemented using UCInet and the *sna* R package.

In an effort to move the field of animal social networks beyond the descriptive stage, we encourage the adoption and development of the above mentioned, as well as novel statistical network modeling techniques. In doing so, behavioral ecologists will enhance their understanding of the mechanisms underlying the structures of animal social networks and the robustness of their conclusions.

Deconstructing networks

Another strategy for examining the processes that shape animal social networks is comparing the networks of various species to understand how ecological pressures and evolutionary history structure interaction patterns. One of the major challenges in applying a comparative approach to network studies is deciding which measures of network structure can be logically compared across multiple, potentially widely divergent, species and networks that vary in size and density (Croft et al. 2008). An increasingly popular approach is to deconstruct networks into subcomponents and compare the relative frequencies of these subcomponents across networks (Holland and Leinhardt 1976; Milo et al. 2002; Faust 2007). This class of analysis, commonly termed "motif analysis," allows a bottom-up examination of network structure and function and facilitates comparison across networks to reveal shared, general organizing principles.

The motif method deconstructs a network into its constituent subgraphs, that is, subsets of connected nodes within the network (Figure 1A). A network of any size can be deconstructed into sets of dyad (2-node), triad (3-node), or *n*-node subgraphs, each of which represents a unique pattern of interactions among individuals. Such patterns are relevant in behavioral ecology, for example, when considering dominance networks in which transitive triads (A→B, B→C, and A→C, Figure 1B) represent a linear hierarchy among 3 individuals, whereas cyclical triads (A→B, B→C, and C→A, Figure 1B) represent the absence of a clear hierarchy (McDonald and Shizuka 2013). The frequency of each type of subgraph can then be compared with those frequencies in other empirical networks, or various random networks, to illuminate the underlying function of the observed network structure (Milo et al. 2002). Such an approach has been successfully applied to the comparison of the frequency of cyclical and transitive triads across multiple empirical networks, revealing that animal dominance networks are orderly and tend to have fairly high temporal stability of the rank orders (McDonald and Shizuka 2012). Furthermore, the type of subgraph structure each individual participates in may explain its role in the network. In a directed 3-node network, there are 16 possible configurations of triads, ranging from null triads (no interactions) to completely reciprocal relations between all 3 nodes (Figure 1B). Because the number of subgraphs increases exponentially with their size, analysis of subgraphs larger than 3 or 4 nodes is currently prohibitory because of computational demands. However, because the goal of motif analysis is to compare among networks using tractable components, the size of the compared components is not relevant, as long as they are biologically meaningful.

The study of subgraphs of 3 nodes (triads) is particularly well suited for examining directed social interactions in animals, for example, in the context of dominance relations and information exchange. The triad analysis approach was first conducted by sociologists to study patterns of transitivity in human friendship choices, that is, the likelihood that if A chooses B as a friend and B chooses C, A also chooses C (Davis et al. 1971; Holland and Leinhardt 1976). Transitivity of social relations is also of interest to behavioral ecologists studying dominance hierarchies in animal groups. For example, a "linear" dominance hierarchy is one in which all triadic dominance relations are transitive, and "linearity" indices are used to measure how closely a group conforms to a linear hierarchy (De Vries 1995). However, measures of linearity become unreliable when not all individuals interact, thus creating "missing data" (Shizuka and McDonald 2012). Focusing directly on the transitivity of triadic relations can yield alternative measures of dominance hierarchy structure that are resilient to missing data (Shizuka and McDonald 2012) and reveal previously underappreciated levels of similarity among dominance hierarchies of different taxa (McDonald and Shizuka 2013). Recently, the analysis of triadic configurations or "triadic motifs" has also been applied to identify differences in information flow among a variety of complex biological, technological, and sociological networks (Milo et al. 2002, 2004; Faust 2007; Stouffer et al. 2007). Examining triadic motifs in information networks of animals, for example, the interactions among social insects in a colony, can uncover the prevalence of triads that facilitate efficient information flow, thus illuminating the mechanisms underlying complex group behaviors (Waters and Fewell 2012).

Most network analysis software, including R packages "igraph" (Csardi and Nepusz 2006) and "statnet" (Handcock et al. 2003), provide methods for counting the frequencies of triadic configurations (called "triad census"). These tools can be used in combination with custom randomization procedures to carry out triad motif analysis (Shizuka and McDonald 2012 provide example codes). Other software specifically designed for motif analysis are also widely available: Mfinder (Kashtan et al. 2004), MAVisto (Schreiber and Schwöbbermeyer 2005), and *FANMOD* (Wernicke and Rasche 2006). In all cases, we advocate careful consideration of randomization procedures to derive statistical metrics because the choice of the randomization design determines the null hypothesis, thus affecting the interpretation of the results (Artzy-Randrup et al. 2004).

TEMPORAL AND SPATIAL DYNAMICS: CONCEPTUAL CHALLENGES IN THE STUDY OF ANIMAL SOCIAL NETWORKS

Interactions among animals are dynamic processes, yet many studies of animal social networks examine static structures. Animals may modify their social interactions in response to changes in external conditions such as climate, predation pressure, and social

Table 2

Examples of studies that consider the topics discussed, by species

Species	Beyond descriptive statistics	Triads	Temporal dynamics	Spatial constraints	Individual variation	Variation among networks
Meta-analyses	Faust and Skvoretz (2002)	Shizuka and McDonald (2012)				Faust and Skvoretz (2002), Kasper and Voelkl (2009), Lehmann and Dunbar (2009), Shizuka and McDonald (2012)
Mammals						
Primates						
Homo sapiens (human)[a]	Faust and Skvoretz (2002), Goodreau et al. (2009)	Davis et al. (1971), Holland and Leinhardt (1976)				
Pan troglodytes (chimpanzee)					Lehmann and Dunbar (2009), Kanngiesser et al. (2011)	
Papio hamadryas ursinus (chacma baboon)			Henzi et al. (2009)			
Ateles geoffroyi (spider monkey)			Ramos-Fernández et al. (2009)			
Macaca mulatta (rhesus macaque)					Colvin (1983), Sueur and Petit (2008)	Sueur and Petit (2008)
Macaca nemestrina (pigtailed macaque)					Flack et al. (2006)	
Macaca tonkeana (tonkean macaque)					Sueur and Petit (2008)	Sueur and Petit (2008)
Ungulates						
Elephas maximus (Asian elephant)			de Silva et al. (2011)		de Silva et al. (2011)	de Silva and Wittemyer (2012)
Loxodonta africana (African elephant)			Wittemyer et al. (2005)	Pinter-Wollman et al. (2009)		de Silva and Wittemyer (2012)
Procavia capensis (rock hyrax)					Barocas et al. (2011)	
Equus grevyi (Grevy's zebra)						Sundaresan et al. (2007)
Equus hemionus khur (Indian wild ass)						Sundaresan et al. (2007)
Syncerus caffer (African buffalo)			Cross et al. (2004)			
Cetaceans						
Orcinus orca (killer whale)			Foster et al. (2012)		Williams and Lusseau (2006)	
Sotalia guianensis (Guiana dolphin)			Cantor et al. (2012)	Cantor et al. (2012)		
Tursiops spp. (bottlenose dolphin)	Mann et al. (2012)	Connor et al. (2001)	Connor et al. (2001), Ansmann et al. (2012)		Lusseau and Newman (2004), Wiszniewski et al. (2010)	

Table 2
Continued

Species	Beyond descriptive statistics	Triads	Temporal dynamics	Spatial constraints	Individual variation	Variation among networks
Carnivores						
Neophoca cinerea (Australian sea lion)				Lowther et al. (2012)		
Zalophus wollebaeki (Galápagos sea lion)				Wolf et al. (2007), Wolf and Trillmich (2008)		
Crocuta crocuta (spotted hyena)		Smith et al. (2010)	Holekamp et al. (2012)		Smith et al. (2010), Holekamp et al. (2012)	
Nasua nasua (ring-tailed coati)					Hirsch et al. (2012)	
Suricata suricatta (meerkat)					Madden et al. (2009), Madden et al. (2011)	
Rodents						
Marmota flaviventris (yellow-bellied marmot)	Wey and Blumstein (2010)				Blumstein et al. (2009), Lea et al. (2010), Wey and Blumstein (2012)	
Spermophilus columbianus (Columbian ground squirrel)					Manno (2008)	
Microtus ochrogaster (prairie vole)				Streatfeild et al. (2011)	Streatfeild et al. (2011)	
Bats						
Nyctalus lasiopterus (giant noctule bat)				Fortuna et al. (2009)		
Myotis bechsteinii (Bechstein's bat)			Kerth et al. (2011)			
Birds						
Carpodacus mexicanus (house finch)					Oh and Badyaev (2010)	
Chiroxiphia linearis (long-tailed manakin)			McDonald (2007)	McDonald (2009)		
Parus major (great tit)				Psorakis et al. (2012)		Royle et al. (2012)
Pipra filicauda (wire-tailed manakin)					Ryder et al. (2008)	
Myiopsitta monachus (monk parakeet)			Hobson et al. (2013)			
Zonotrichia quereula (Harris's sparrow)		Chase and Rohwer (1987)	Chase and Rohwer (1987)			
Reptiles						
Egernia stokesii (Gidgee skink)					Godfrey et al. (2009)	
Tiliqua rugosa (sleepy lizard)				Leu et al. (2010)		

Table 2
Continued

Species	Beyond descriptive statistics	Triads	Temporal dynamics	Spatial constraints	Individual variation	Variation among networks
Fish						
Carcharhinus melanopterus (black-tip reef shark)				Mourier et al. (2012)		
Poecilia reticulata (guppy)			Croft et al. (2004)		Croft et al. (2005), Croft et al. (2004)	Croft et al. (2004)
Gasterosteus aculeatus (3-spined stickleback)					Pike et al. (2008)	Croft et al. (2009)
Invertebrates						
Crabs						
Carcinus maenas (European shore crab)			Tanner and Jackson (2012)			
Insects						
Apis mellifera (honey bee)				Naug (2008)	Naug (2008)	
Bombus impatiens (bumble bee)					Otterstatter and Thomson (2007)	
Ropalidia marginata (social wasp)					Naug (2009)	
Odontomachus hastatus			Jeanson (2012)	Jeanson (2012)		
Pogonomyrmex barbatus (red harvester ant)				Pinter-Wollman et al. (2011)	Pinter-Wollman et al. (2011)	
Pogonomyrmex californicus (harvester ant)		Waters and Fewell (2012)				
Temnothorax rugatulus (rock ant)			Blonder and Dornhaus (2011)			
Bolitotherus cornutus (forked fungus beetle)					Formica et al. (2012)	
Summary (N = species)	3	5	17	13	24	9

[a]Examples from studies on humans were brought only for topics that have few nonhuman examples (beyond descriptive statistics and triads). The table primarily focuses on nonhuman examples.

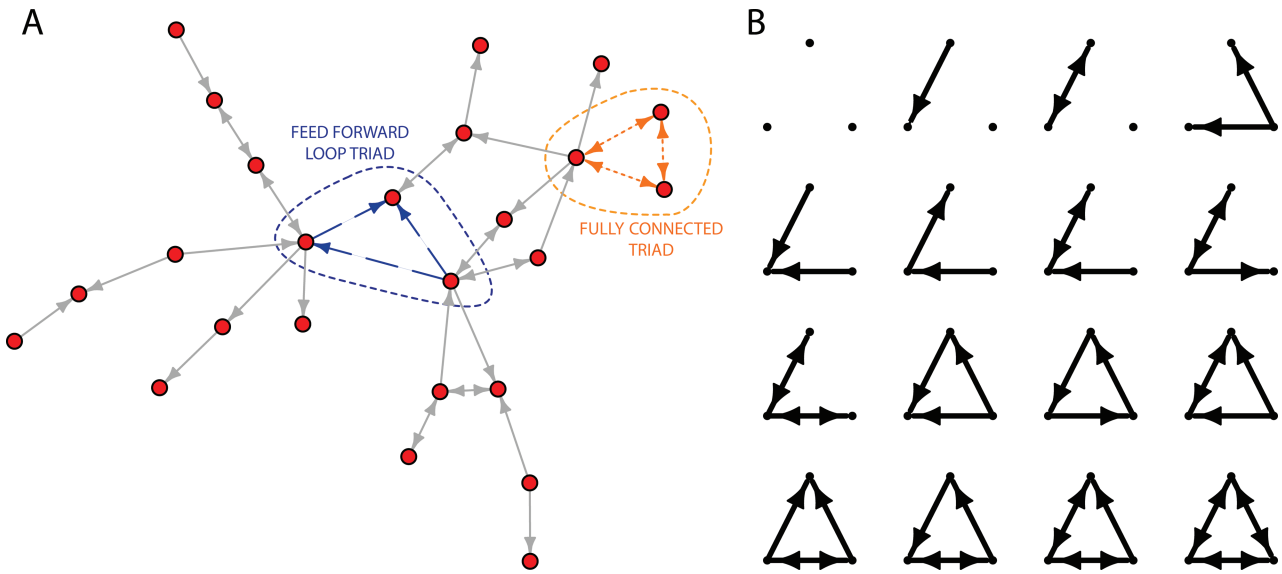

Figure 1
(A) A directed network of 25 individuals linked by 39 interactions. Two triad subgraphs have been highlighted: a feed-forward loop (dashed dark) and a fully connected triad (dotted light). (B) The 16 possible triadic configurations in a directed network. Circles represent individuals and arrows indicate a directed social interaction.

setting. Some of these changes may be caused by the animals themselves as they move across habitats, potentially altering their own social network structure and dynamics. It is therefore important to consider the temporal dynamics and spatial attributes influencing animal social networks to better understand and identify factors affecting sociality. Here, we discuss the temporal and spatial aspects that should be considered when investigating animal social networks and suggest methods for addressing these challenges.

Temporal dynamics

Examining changes to the social structure of animals over time and across ecological settings can elucidate drivers and functions of social organization (Hinde 1976; Whitehead 2008). For example, temporal changes in network structure may affect the dynamics of processes such as the spread of disease within a population (Cross et al. 2004; Naug 2008); social interactions early in life predict later social status (McDonald 2007); and environmental changes may determine emergent properties of animal interactions such as hierarchical group structuring (Wittemyer et al. 2005; de Silva et al. 2011). All of these dynamics shape individual interactions and consequently influence population organization. However, only a few studies examine the temporal dynamics of social networks (Table 2). Here, we summarize 2 main approaches to quantify and test aspects of network temporal dynamics, and highlight tools that can be used to address questions regarding network changes over time. We draw heavily from previous work in the social sciences, where these methods have been developed and extensively applied to the study of human social structure (Snijders and Doreian 2010, 2012).

The first approach to studying the temporal dynamics of networks is the discrete "snapshot" approach. Data collected over time are aggregated within relevant intervals to generate networks. This procedure yields a series of static representations of the social structure (Figure 2A–C). Critically, sampling must be carried out and partitioned at temporal resolutions appropriate for the process of interest. Although there may be some biological (Sundaresan et al. 2007; Whitehead 2008) or ecological (de Silva et al. 2011; Holekamp et al. 2012) basis for choosing suitable time intervals, they depend heavily on the biological questions asked. In addition, species vary in the timescale on which behavior changes, for example, the time interval required to extract meaningful information about ant networks (Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011; Waters and Fewell 2012) is very different from that for elephant networks (Wittemyer et al. 2005; Pinter-Wollman et al. 2009; de Silva et al. 2011). Multiple time frames may be tested to examine which most accurately represents the scale of change relevant to the question being asked (Waters and Fewell 2012).

Tools for longitudinal analyses based on the discrete snapshot approach are relatively well developed. Network dynamics can be visualized graphically using software such as Visone (http://visone.info/), which allows users to create customized movies of temporal changes among static networks (Brandes and Wagner 2004). Social network change detection (SNCD) can be used to identity when network metrics (e.g., betweenness, transitivity) exhibit statistically significant structural change between time periods (McCulloh 2009). SNCD, available through the software program ORA (http://www.casos.cs.cmu.edu/projects/ora/), may be used to determine when events such as breeding, dispersal, and environmental change first begin to impact animal social network structure. Similarly, hidden Markov models can identify structural change points in longitudinally collected behavioral data (Rabiner 1989). Discrete networks can also be analyzed with statistically powerful methods such as stochastic actor-oriented modeling (SAOM, implemented in the R package, RSiena). SAOM examines how individual-based combinations of network processes and covariates influence the probability of animals changing their network links and attributes over time (Burk et al. 2007; Snijders et al. 2010).

The second approach for studying network dynamics is the continuous approach that maintains data in streams of time-stamped observations (Bender-deMoll and McFarland 2006; Berger-Wolf and Saia 2006; Palla et al. 2007; Tantipathananandh and Berger-Wolf 2009; Blonder and Dornhaus 2011; Blonder et al. 2012). Rather than aggregating data to consider structural changes

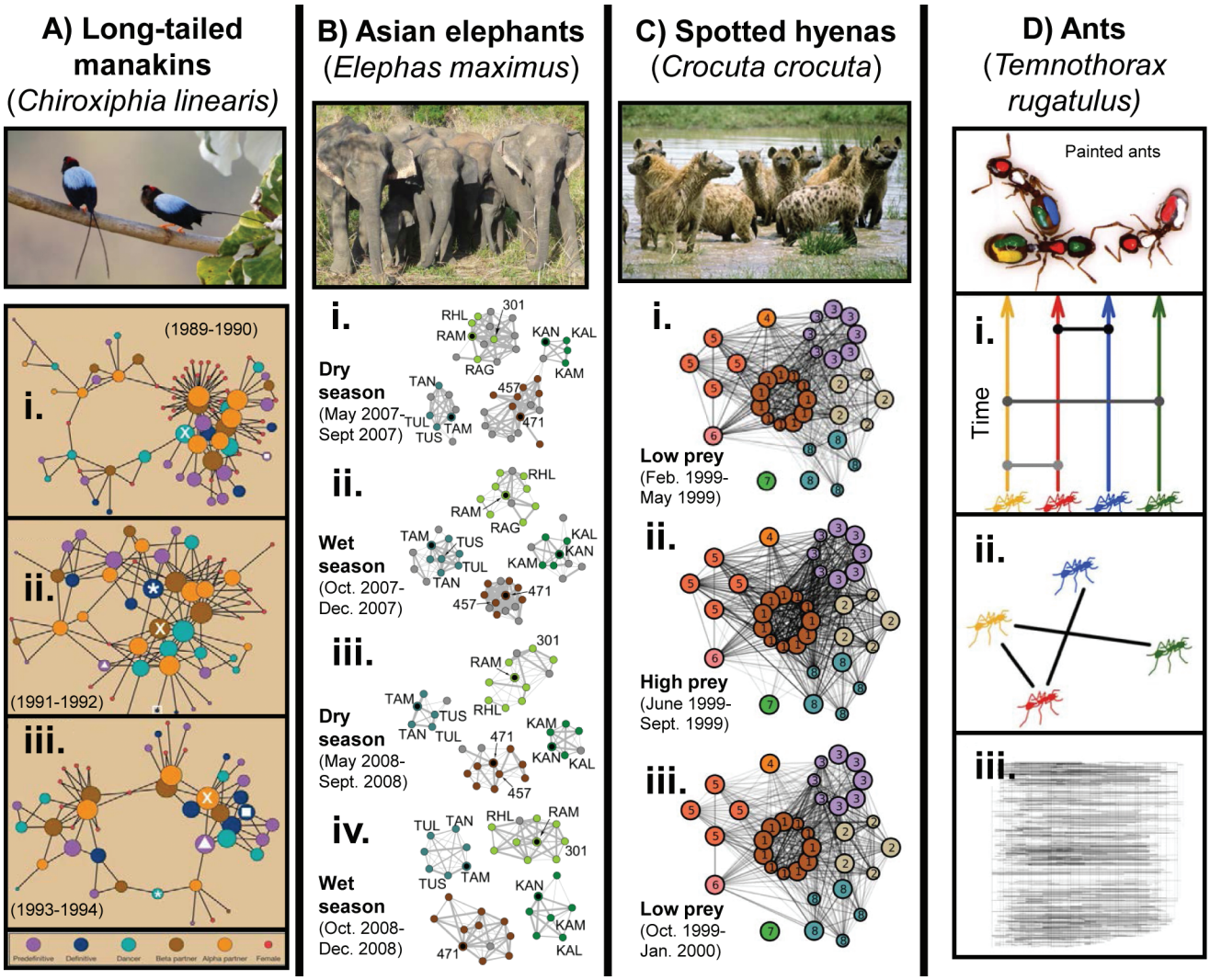

Figure 2

Examples of temporal dynamics across animal social networks. (A) Networks in successive 2-year timeblocks of long-tailed manakins (*Chiroxiphia linearis*). Permission from the National Academy of Science, McDonald DB. 2007. Predicting fate from early connectivity in a social network. Proc Nat Acad Sci USA. 104:10910–10914. Photo by Christine Fisher. (B). Network dynamics among adult female Asian elephants (*Elephas maximus*) in the dry and wet seasons. Originally published by BioMed Central, "de Silva S, Ranjeewa ADG, Kryazhimskiy S. 2011. The dynamics of social networks among female Asian elephants. BMC Ecol. 11:17." Photo by Uda Walawe Elephant Research Project. (C) Network dynamics among adult and subadult spotted hyenas (*Crocuta crocuta*) during periods of low and high prey abundance. Permission from Wiley, "Holekamp KE, Smith JE, Strelioff CC, Van Horn RC, Watts HE. 2012. Society, demography and genetics in the spotted hyena. Mol Ecol. 21:613–632." Photo by Kay E. Holekamp. (D) Information flow among ants (*Temnothorax rugatulus*) represented as (i) links over time, (ii) time-aggregated networks, and (iii) time-ordered networks. Permission from PLOS, "Blonder B, Dornhaus A. 2011. Time-ordered networks reveal limitations to information flow in ant colonies. PLoS One. 6:e20298."

between time frames, these techniques focus on the order and timing of changes in relationships between nodes (Bender-deMoll and McFarland 2006). The continuous approach can provide detailed insight into situations where the timing and order of interactions is critical, such as diffusion of behaviors (Boogert et al. 2008) or information flow (Blonder and Dornhaus 2011; Figure 2D). Currently, the tools based on the continuous approach are less accessible, less widely developed, and more limited in their utility than those based on the discrete approach. One exception is the R package "timeordered" developed by and for behavioral ecologists (Blonder and Dornhaus 2011). Despite current limited availability of analysis packages, continuous analyses offer exciting new opportunities because they allow behavioral ecologists to model networks in a truly dynamic fashion. The importance of temporal dynamics in animal social networks may encourage behavioral ecologists to further develop analytical approaches and tools that facilitate rigorous hypothesis testing concerning patterns of temporal change.

Spatial constraints

Animal social networks operate and evolve within spatial contexts (Barrat et al. 2005; Ohtsuki et al. 2006). The link between spatial and social dynamics has long been fundamental in the study of geography (Hägerstrand 1970) and is an emerging theme in the study of human networks (Barrat et al. 2005; Lauw et al. 2005; Crandall et al. 2010; Barthelemy 2011; Expert et al. 2011). Spatial dynamics are important to consider when examining animal sociality because of the changes in spatial behavior during an animal's life, for example, during natal dispersal or migration, that

potentially affect its social associates. Furthermore, when individuals hold exclusive territories, space use may play a crucial role in defining social units, and by extension, network clusters or modules. Spatial proximity is important for maintaining cooperation (Nowak et al. 1994), and fission-fusion dynamics are defined by the spatiotemporal cohesion of individuals (Aureli et al. 2008). Recent technological innovations in tracking devices are revolutionizing the way we collect social association data, providing detailed information on the location of individual animals at high spatial and temporal resolution (Pinter-Wollman and Mabry 2010; Haddadi et al. 2011; Aplin et al. 2012; Psorakis et al. 2012; Rutz et al. 2012). However, integrative studies of space use and social interactions are still fledgling topics in the empirical studies of behavioral ecology (Table 2).

One hindrance to the advancement of studying the spatial constraints on social networks is the difficulty in separating the two. Except when networks are constructed based on direct behavioral interactions (Figure 2A,D), characterizations of a social network often rely on the assumption that spatial proximity implies social affiliation (Whitehead 2008; Figure 2B,C). This widely applied technique, termed "the gambit of the group" (Whitehead and Dufault 1999), is derived from the realistic expectation that among nonhuman animals, individuals must be in close physical proximity to interact. Nevertheless, this assumption suffers from recognized weaknesses in that it ignores the nonsocial spatial factors affecting animal movements and co-habitation, which bring individuals to the same location (e.g., a resting site) without necessitating interactions. Furthermore, this approach suffers from observer biases originating from the need for real-time "judgment calls" about what constitutes a group (Whitehead and Dufault 1999; Whitehead 2008).

These issues in data collection are carried forward in statistical frameworks meant to test for the presence of social structure. Null models derived from permutation approaches are commonly used to assess whether individuals interact with one another more than expected at random (Bejder et al. 1998; Whitehead et al. 2005; Whitehead 2008; Sundaresan et al. 2009). However, such permutation tests assume that any two individuals in the population can co-occur in the same group, without accounting for spatial factors, such as the presence of resources, movement corridors, and so on. Such geographical attributes may attract individuals to the same location or prevent them from ever meeting, regardless of social preference, rendering results from a naive null model difficult to interpret. More stringent null hypotheses should take into account the probability that 2 randomly drawn individuals encounter one another relative to their spatial configuration (as in Pinter-Wollman et al. 2009). Furthermore, testing social affiliation data against spatially explicit null models that account for patterns of space use could reveal associations that arise simply because individuals are attracted to similar geographical features. A general procedure that incorporates spatial and temporal variability in space use at the population level has not yet emerged but is an area ripe for exploration (Psorakis et al. 2012).

Algorithms for detecting communities provide some basis for distinguishing space use from social preference at levels of organization larger than a dyad. There are now numerous methods for partitioning networks into subcomponents (reviewed by Porter et al. 2009 and Fortunato 2010), many of which rely on the topological features of the network itself, such as denser connections within communities than among communities. Such algorithms have been successfully used to discriminate social units in populations with considerable spatial overlap that might have otherwise been considered a single large social unit (Oh and Badyaev 2010; de Silva et al. 2011; Kerth et al. 2011; Mourier et al. 2012). However, for behavioral ecologists, many standard community-detection algorithms still provide an incomplete understanding of spatial drivers because they do not use spatiotemporal data per se. Recent approaches that do incorporate spatial data explicitly in defining social structure (such as those used by Lauw et al. 2005; Crandall et al. 2010; Expert et al. 2011; Psorakis et al. 2012) deserve greater attention from behavioral ecologists. By incorporating data on the distributions and dynamics of ecological variables, these methods can provide a more complete understanding of how putatively "social" networks depend on, or can be distinguished from, these underlying ecological factors.

In parallel, the branch of network analysis involving statistical modeling, such as SAOM and ERGM (Snijders et al. 2010), offers a promising approach to determining whether individuals in the network are responding to spatial and/or social preferences. For example, ERGM and SAOM can include both spatial (e.g., distance between individuals, habitat attributes, and so on) and nonspatial covariates in the statistical model (see above for more information on these techniques). Frameworks for evaluating the effect of social preference together with other factors governing contact patterns are also independently emerging from the study of collective movement in humans and animals (Couzin and Krause 2003; Getz and Saltz 2008; Bode et al. 2011a, 2011b). As the popularity of social network analyses grows, the consideration of explicit spatial information when generating networks and testing hypotheses is an area in need of further development in the study of nonhuman animals.

VARIATION WITHIN AND AMONG NETWORKS: EVOLUTION AND ECOLOGY OF SOCIAL NETWORKS

Evolution acts on variation. When studying how natural selection acts on social network structure, variation is important at multiple levels, both within and among networks. Variation in connectivity or other centrality measures among individuals comprising a network influences how it operates (Williams and Lusseau 2006; Pinter-Wollman et al. 2011). Variation in network structure and function among social groups within a population influences how those groups adjust to various environments (Gordon et al. 2011), potentially affecting the survival and reproductive success of individuals within the group and the relative success of each group within the population (Royle et al. 2012). Species differences in network structures and dynamics likely reflect the selective pressures under which they evolved. Thus, network structure and function may be targets of selection in ways often overlooked by evolutionary models. To realistically explore the evolutionary drivers of social systems and understand the various levels of selection acting on these systems, intraspecific comparisons within and across populations and interspecific comparisons of social networks are needed.

Variation among individuals within a network

The notion that key players, such as dominant individuals (Rowell 1974) or leaders (Couzin et al. 2005), may have disproportional effects on social structure has long been a hallmark concept in behavioral ecology. Traditional computational tools focus primarily on the outcomes of dyadic interactions between key players and other members of the group. However, the use of social network theory extends these traditional approaches by allowing

behavioral ecologists to examine the role of key individuals, or key subgroups of individuals, on the emergent structure and function of the groups in which they reside. The implementation of new network approaches in the study of animal behavior highlights the important role that individual variation plays in network processes such as information flow (Lusseau and Newman 2004; Flack et al. 2006; Smith et al. 2010; Pinter-Wollman et al. 2011). Furthermore, studies that examine how variation among individuals in attributes such as age and sex affect their position in the network (Table 2) are beginning to shed light on how group composition may influence its success. However, further work is needed to understand how variation and group structure influence evolutionary processes.

Exploring the mechanisms that underlie individual variation within a network will advance our understanding of how social groups operate. However, only little is known about the mechanisms that produce variation in social networks or even whether individuals persist in their social roles over time and across situations (Sih et al. 2009; Wilson et al. 2013). Although genetic and developmental processes may cause individuals to occupy persistent roles within a network, network structure must also respond to changes in the physical environment. Thus, ecological and social changes may act in concert to affect which individuals occupy central or dominant roles within the group. For example, when certain individuals are removed from a group, others may take their social role (Robson and Traniello 1999).

One fruitful way in which behavioral ecologists may examine the effects of variation among individuals on network processes is by using "knockout experiments." In such experiments, certain individuals or interactions are removed from the network to examine how they affect network processes (Flack et al. 2006). These experiments allow for the investigation of the differential effects of removing various system components on the robustness and functionality of the social network. However, removals are not always feasible, for example, in field studies, when working with vulnerable species, or when networks change rapidly. In such cases, computer simulations of removals or natural removals, such as those attributed to natural mortality or dispersal events, offer opportunities to understand the additive and nonadditive effects of certain individuals on group-level structure and function. Although the results of such simulated removals must be interpreted with care, these tools have been underutilized by behavioral ecologists aiming to conserve species. Application of network theory could inform management decisions through inferences about the resilience of natural populations to anthropogenic effects (as in Williams and Lusseau 2006). What determines whether removed central individuals are replaced and which individuals step in as replacements are still open questions.

Variation among populations and species

As the study of animal social networks expands, broad-scale comparisons of network structure within and across species will become possible. Comparing the similarities and differences among animal networks provides a framework for studying the diversity of system-level functionality. We are not the first to call for comparing network measures across species and populations (Krause et al. 2007). Indeed, studies comparing the social networks of similar species that live in different environments have revealed adaptive social structures shaped to the environment in which each species live (Sundaresan et al. 2007; Kasper and Voelkl 2009; de Silva and Wittemyer 2012). As the field of animal social networks matures, more opportunities for comparative studies across taxa will arise (Table 2). As more studies of closely related species become available, we suggest comparing metrics of social structure across phylogenies to increase the breadth of questions about the evolution of sociality. To facilitate comparisons of social networks across populations and species, it is critical to standardize sampling methods and to facilitate data sharing. Other fields have already made great strides that allow researchers to use large-scale, collaboratively maintained, databases for comparative work (e.g., microarray data (Brazma et al. 2001) and speech corpora (LDC corpus catalogue, http://www.ldc.upenn.edu/) while some fields utilize universal measures (e.g., physiological studies of scaling laws). It is time that behavioral ecologists who examine animal social networks establish standards for collecting and storing social network data to enable large-scale comparisons across systems that are necessary for advancing our understanding of the structure and function of these networks.

Standardizing network data is not straightforward and will require the consideration of many factors. For example, the frequency and time frame of data collection, network size, and even what constitutes a link among individuals are all factors that may vary among studies and will affect the ability to compare among them. Furthermore, the function of the group in each species will determine which biological questions may be answered using a comparative approach. To allow for comparison among networks, we emphasize the need to record individual-based data in a spatially and temporally explicit manner. So, instead of storing data as interactions or as group affiliation, each individual observed should be recorded separately, with a time stamp and location from which network data can later be constructed using various spatiotemporal filters to define an interaction. Moving forward toward collaborations and comparative studies, one useful tool may be sharing social network data in centralized repositories such as the Dryad Digital Repository (http://datadryad.org/) (e.g., Holekamp et al. 2012). If these databases include proper documentation of collection methods, and assumptions made by the observer, each user will then be able to choose only those networks that are relevant to the biological question at hand. These are only some suggestions to begin the process of standardizing network data. Further work is needed to develop and establish tools that will facilitate comparative studies on the evolution of social behavior.

CONCLUSIONS

The study of animal social networks is rapidly expanding. Social network analysis is being applied to a wide variety of taxa, and many new analysis methods are constantly being developed, adopted, and adapted to advance our understanding of animal sociality. Although novel descriptions of social structure in species that are as yet unstudied will continue to expand the foundations of the field, behavioral ecologists have now accumulated a vast body of data with which more general hypotheses about networks can be tested. In this review, we have summarized recent methodological and conceptual advancements that we believe will be useful for furthering our understanding of animal social structure. We aggregated the analytical tools reviewed in Table 1 and a sample of studies that incorporate these methodological and conceptual advancements in Table 2. We found that many studies already consider individual variation, in one form or another, and to a lesser extent, temporal dynamics, and spatial constraints. There is a striking paucity of studies utilizing statistical network modeling and triadic motifs to examine animal social networks and very few cross-species comparisons (Table 2).

Broader use of the advancements we describe will allow us to test complex hypotheses about the function, mechanism, development, and evolution of animal sociality. In summarizing these advances and identifying areas in need of attention, we hope to provide researchers with a toolbox of up-to-date methods that can be used to spur new research programs, further development of network analysis methods, and progress our understanding of the proximate and ultimate processes that shape animal sociality.

FUNDING

Colonel Rogers Excellence Fund at the University of Wyoming to A.J.E. and D.B.M.; San Diego Center for Systems Biology (NIH #GM085764) to N.P.-W.; National Science Foundation GK-12 (DGE-0947465) DISSECT Fellowship at New Mexico State University to E.A.H.; National Science Foundation Biological Informatics Postdoctoral Fellowship to A.J.E.; Chicago Fellows Postdoctoral Fellowship to D.S.; NSF Postdoctoral Research Fellowship in Biology to S.dS.

We thank the social network group at the University of Wyoming for organizing the Symposium on "Network Science in Biological, Social, and Geographic Systems" that catalyzed the formation and formulation of the ideas we presented.

Forum editor: Sue Healy

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