

Culture, Diffusion, and Networks in Social Animals

JANET MANN and LISA SINGH

Abstract

Long-term studies of social animals provide detailed data on individual attributes, behaviors, and associations that enable us to explore cultural diffusion in networks. In this essay, we describe how network science can be used to improve our understanding of cultural and information transmission. After presenting an operational definition of culture, we discuss methodologies and research questions applicable to unweighted, weighted, and dynamic networks. We then highlight relevant studies and methods for both descriptive and predictive analyses that have been used to identify culture and social learning in animal networks. Applying and extending the techniques presented will improve our understanding of information transmission, social learning, and embedded subcultures in the context of human networks.

INTRODUCTION

Our survival, success, and ability to exploit resources depend on cumulative culture, a ubiquitous feature of human societies. Virtually every facet of our current state was shaped by cultures past; we excel in niche construction, perhaps to a fault (Laland & O'Brien, 2011; Rendell, Fogarty, & Laland, 2011). Cultural processes also shape nonhuman animal phenotypes, albeit to a lesser extent than in humans. Nevertheless, animal societies enable us to study the underlying network properties and processes that are rarely accessible in human research and investigate the relationship between these properties and cultural transmission. For example, long-term studies of social mammals provide multifaceted connections (e.g., interactions, associations, kinship, location/home range, communication) and individual properties (i.e., genotypes and phenotypes) that only a handful of human studies, usually traditional forager societies (e.g., Hadza foragers, Apicella, Marlowe, Fowler, & Christakis, 2012) measure. Although we cannot interview animals, privacy laws do not protect them from frequent monitoring such that real-time behavioral data are often available. This level of detail

allows us to explore the basic properties of cultural diffusion in networks. Here we examine how the application of network science to social animals informs our understanding of culture and information transmission. We highlight relevant studies and methods and then discuss future directions for those studying both human and animal networks. These efforts complement those of social scientists (e.g., see Pachucki & Breiger, 2010) in identifying theoretical and methodological approaches to network science and culture.

Before continuing, a working definition of culture which is applicable or measurable across species is needed. In a recent influential book, Laland and Galef invited social scientists and biologists to discuss *The Question of Animal Culture* (Laland & Galef, 2009). Although definitions are fiercely contested, all contributors agreed on two underlying properties of culture. First, the transmission process involves social learning (learning from the actions or products of others) and second, the socially learned behavior must distinguish between groups (Laland, J. R. Kendal, & R. L. Kendal, 2009). This minimalist definition generally works in describing animal cultures, but the challenge of demonstrating social learning in nonexperimental settings remains.

Owing to this challenge, a number of scientists have tried to eliminate ecological and genetic explanations of behavioral differences between groups as a way to identify social learning and hence leave “culture” as the only remaining explanation (e.g., Krützen *et al.*, 2005; Whiten *et al.*, 1999). This ‘elimination’ method is clearly flawed, since most social phenomena have a combination of ecological, genetic, and epigenetic components that interact with social factors (Kappeler, Barrett, Blumstein, & Clutton-Brock, 2013; Laland & O’Brien, 2011) and one can never prove the null (Laland & Janik, 2006; Sargeant & Mann, 2009). For example, most socially learned traits that have been deemed cultural in animals involve foraging (e.g., pine-cone stripping rats, termite fishing chimpanzees, sponging dolphins), but all of these depend not only on specific ecological conditions, but also on close kin (typically the mother) and necessarily includes association, maternal effects, and biased learning from kin (Aisner & Terkel, 1992; Lonsdorf, Eberly, & Pusey, 2004; Mann *et al.*, 2008; Mann, Stanton, Patterson, Bienenstock, & Singh, 2012). To date, few would doubt that social, ecological, demographic, and genetic factors interact to shape animal social networks and cultural phenomena embedded in those networks. This multitude of intrinsic and extrinsic factors receives less focus in human studies, possibly because we tend to attribute social choice to human networks and biological factors to animal networks. Still, demonstrating social learning among wild animals is difficult. As a consequence, researchers have focused on developmental patterns of a behavior and behavior of associates (e.g., Sargeant & Mann, 2009) or used diffusion models in networks (e.g., Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010) to measure social transmission.

In the last decade, social network studies in the field of animal behavior have accelerated. For example, in three of the mainstream journals, *Animal Behaviour*, *Behavioral Ecology*, and *Behavioral Ecology and Sociobiology*, there were no network studies in 2004 or 2005, one in 2006 and by 2009, 15–21 articles were published cumulatively per year (*Science Citation Index* search with keyword “social network.”) This trend has continued. Along with the increase in animal network research, a plethora of studies began focusing on behavioral traditions and animal culture, with the specific goal of defining culture by its social transmission properties (i.e., social learning), which naturally led to defining the underlying properties of culture using social network analysis.

CULTURAL ANALYSIS USING SOCIAL NETWORKS

Network science is an emerging discipline that studies network representations and predictive models as a way to both explain and predict various physical, social and biological phenomena (Easley & Kleinberg, 2010; Newman, 2010). In cultural analysis, networks are advantageous for investigating questions at different scales from the individual (ego networks) to groups and the network structure as a whole, where the size of the network may range from a few to billions of individuals. Network analysis and graph theory can be used to help explain the connection between the functionality of a group and the behavior of different members of the group (Pinter-Wollman *et al.*, 2014). Further, patterns of information flow both depend on network structure and influence network structure. Unraveling this relationship is necessary to understand the relationship between information dissemination and social learning, that is, cultural processes. However, network structure is not *equivalent* to social transmission. To understand those processes, behavioral sampling of individuals in the network is needed. This is an area where behavioral ecologists excel.

At the basic level, networks are just a collection of points (typically referred to as *nodes*, *actors*, or *vertices*) connected by lines (typically referred to as *edges*, *ties*, *links*, or *arcs*). For simple analyses, we may consider only a simple network in which the nodes are all the same type, for example, people, animals, organizations, proteins, or computer systems, and the edges connect two nodes based on a relationship between the two nodes. Example relationships include kinship, friendship, alliance partner, professional affiliation, and email correspondence. Social network analysis allows for multiple granularities of analysis and can be beneficial for answering macro-, meso- and micro-level questions. Examples of the macro-level questions might concern network density, the number of individuals and paths in the network, and the distribution of connections. Connectivity can follow a range of

distributions, such as random, small-world (high clustering), regular lattice (no clustering, low heterogeneity, low randomness, and high path lengths), or scale-free (moderate heterogeneity and randomness—many small world networks are also scale-free). Meso-level features include distinctiveness of clusters, community composition, centrality or isolation of communities, and whether local neighborhoods are tightly connected. At the micro-level, we might be interested in identifying the information brokers, hubs or highly connected individuals or isolates. Answering such questions can inform descriptive and predictive models on cultural processes across micro, meso, and macro network structures. Still, node and edge attributes (i.e., cultural behaviors) are needed to identify, quantify and model social transmission.

In a simple network model, the edges do not show the direction of the relationship, the type of relationship or the strength of the relationship. Depending on the analysis, adding one or more of these features can improve the depth of the analysis and remove potential bias (Singh, Bienenstock, & Mann, 2010). For example, the strength of a relationship can be shown in a network by adding weights to each edge (Wasserman & Faust, 1994). Generally, for social networks, weights are values between zero and one. However, negative weights can be used to represent different levels of animosity between individuals (Newman, 2004). Weighted networks inform on strong and weak relationships and communities, including channels of high information flow, that is, likely paths for social information transmission. Finally, adding direction to relationships enables researchers to pose questions related to relationship reciprocity and dominance (Carrington, Scott, & Wasserman, 2005). As social systems become more complex, network analysis becomes more useful because of its ability to accommodate features of social complexity such as motif analysis, hierarchies, individual recognition, and the exponential “cognitive load” faced with an increasing number of social relationships (e.g., Dunbar, 2012).

Figure 1 shows a small example of two networks, a simple unweighted, binary, uni-mode on the left, and a richer weighted, directed, uni-mode network on the right. Colors are used to show clusters in the networks. The unweighted network is sparsely connected (reducing the possible number of paths for information flow) and has two clusters with a single edge (in red) between the clusters. Even though this network is simple, we can still see that the composition of the two clusters is different. The blue one has a central individual that controls information flow, while the yellow one contains a clique within it, potentially allowing for more rapid flow of information. Because there is only one edge between the two clusters, the potential for information flow between clusters is reduced. The weighted, directed network is also sparse. However, because of the directionality of the edges, we

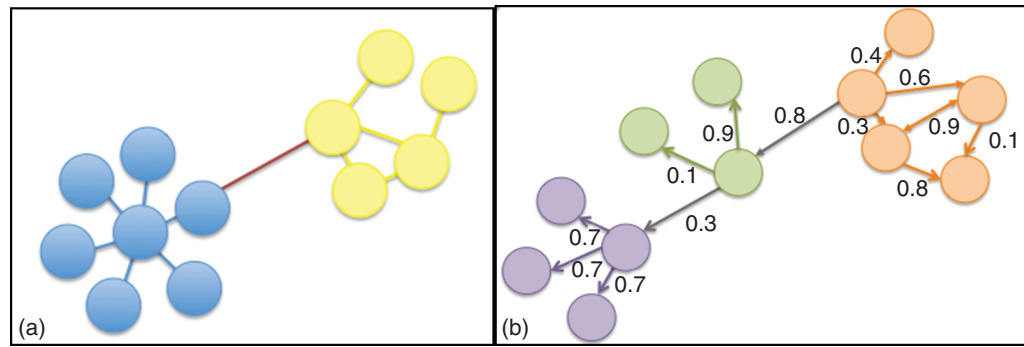


Figure 1 Example networks: (a) unweighted and undirected; (b) weighted and directed.

can see that information flows from the orange nodes to the green and purple. In addition, as weights are used to capture relationship strength, we also see that there is a mix of strong and weak relationships through the network, and while information flow is possible, a message or a piece of information is unlikely to travel to all the nodes. While both types of networks are informative, relationship strength and reciprocity are important factors in cultural diffusion.

In a recent paper, Pinter-Wollman *et al.* (2014) provoked behavioral ecologists to think about moving beyond descriptive analyses of observed patterns, to testing specific hypotheses and predictions regarding the function of network structures. For example, even though patterns of behavior might correlate with associations in a network, suggestive of social learning, that does not explain what drives the behavior or the association. Most literature, to date has focused on descriptive analysis because of the limited number of techniques available for predictive analysis, particularly in the context of more complex, dynamic networks. We now highlight descriptive and predictive approaches used in the literature for identifying and modeling structures and groups in these different types of networks.

DESCRIPTIVE SOCIAL NETWORK ANALYSIS

Presumably, social transmission predominates in local or embedded communities in a network. Literature from physics and computer science focuses on measures of cohesion and clustering to identify communities or subsets of individuals that are more densely connected to each other than expected (Girvan & Newman, 2002; Newman, 2006; Palla, Barabasi, & Vicsek, 2005, 2007, Shen, Cheng, Cai, & Hu, 2009). Different measures are used to identify communities. For example, Girvan and Newman (2002) remove edges with high betweenness (the fraction of shortest paths that traverse an edge) to

identify communities. Another approach proposed by Newman (2006) partitions a network into one with high modularity (the fraction of edges in a group minus the expected fraction if the network was random) to identify communities. While these two methods propose algorithms that identify nonoverlapping communities, Palla *et al.* (2005) propose using a clique percolation method that finds maximal cliques to identify overlapping communities. If social transmission is taking place, then these communities that are based on network topology would also exhibit similar behavior (potential subcultures).

While these works focused on static, binary networks, recent techniques have begun considering how communities change and evolve over time (Backstrom, Huttenlocher, Kleinberg, & Lan, 2006; Caravelli, Wei, Subak, Singh, & Mann, 2013; Gorke, Hartmann, & Wagner, 2009; Tantipathananandh, Berger-Wolf, & Kempe, 2007) and how users behave in these groups (Sharara, Singh, Getoor, & Mann, 2011, 2012). Looking at these dynamic groups in the context of social transmission, we can measure if “self-selection” is taking place and individuals are attracted to each other based on socially learned traits. That is, modularity has a reciprocal nature in networks, increasing cohesion and social transmission at the same time. In animal networks, killer whales exhibit similar “dialects” and calls within matrilineal units (subcommunities), clearly via shared association with kin (e.g., Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Similarly, sperm whale matrilineal units use distinct codas that also appear to be socially learned (Rendell & Whitehead, 2003). In both cases, the communication system is used for cohesion. It is rare in animal societies however, that there is high behavioral heterogeneity such that subcultural units within a larger network can be readily identified. Typically, *all* members of a community engage in the socially learned behavior (e.g., termite fishing, Whiten *et al.*, 1999).

Community structures have been analyzed to identify probable cases of social learning and culture in animal societies (Cantor & Whitehead, 2013). A few have used dynamic approaches to investigate cultural transmission in animal networks, such as lobtail foraging in humpback whales in the North Atlantic (Allen, Weinrich, Hoppitt, & Rendell, 2013). In this case, they used an order of acquisition analysis (see Hoppitt *et al.*, 2010) to examine diffusion in humpback whale networks over time. The detail on dynamic interactions between naïve and knowledgeable individuals was weak, although the pattern over decades was strongly suggestive of social transmission. Dynamic approaches are particularly valuable for investigation of group structure evolution and the changing dynamics of group membership. For example, Caravelli *et al.* (2013) adjust static community detection algorithms to dynamic ones to better understand the evolution of communities over time. The authors also develop metrics related to frequency of appearance of

individuals in groups over time to better understand the longevity of social relationships. Dynamic measures such as stability and diversity in group participation, where stable actors are those who participate in the same group over time, while diverse actors are those who consistently participate across a number of different groups over time (Sharara *et al.*, 2012) can also serve as a tool for understanding cultural change and stability. A variety of studies (e.g., Allen *et al.*, 2013; Blonder, Wey, Dornhaus, James, & Sih, 2012; Boogert, Reader, Hoppitt, & Laland, 2008) have used dynamic methods for unveiling social transmission in networks.

Binary networks have received far more attention in human networks than animal networks, possibly because of the view that weighted networks provide similar information as binary in terms of topology (Garlaschelli & Lofredo, 2009; Mastrandrea, Squartini, Fagiolo, & Garlaschelli, 2013; although see Rankin *et al.* submitted), but also because, except in social media and phone networks, we rarely have weighted information in human networks. Behavioral ecologists typically collect weighted data on their subjects such as time together or rates of interaction. Such weights are considered critical components of information transmission (e.g., Whitehead & Lusseau, 2012) and are presumably relevant in human societies where social relationships span a continuum based on such factors as frequency, closeness/intimacy, strength, importance, and valence.

A common approach for computing weights in animal social networks is the social affinity or association indices (Whitehead, 2008). These measures account for the number of times each individual is “sighted” alone and with every other individual to create a ratio for each pair of individuals ranging from 0 to 1 where 1 indicates that the pair is always together. The strength of social affinity is that it is an asymmetric weight that maintains relationship direction, capturing individual’s relative sociability and sighting rate independently of other individuals in the network. In other literatures, traditional community detection algorithms are adjusted to consider weights (Newman, 2004; Opsahl & Panzarasa, 2009). For example, Newman calculates the betweenness of edges as if weights do not exist, and then divides the betweenness by the weight of the edge before partitioning the network into communities. Opsahl and Panzarasa propose using a generalized global clustering coefficient as a measure to identify members of the same community. The strength of such methods depends on how the weights are initially computed.

Another direction considers identifying key individuals involved in information transmission processes. Several studies have identified key individuals in information transmission. Some of these approaches involve actual or modeled targeted removals to determine how information flow might

be disrupted or other social changes take place. In the study by Flack, Girvan, de Waal, and Krakauer (2006), removal of specific pigtail macaques that served as “peacemakers” or “police-monkeys” in captive groups disrupted the social structure and would presumably impact social transmission. In a different approach, Williams and Lusseau (2006) simulated the consequences of targeted versus random removals of killer whales in a wild population and demonstrated that targeted removals fragmented social units and would likely disrupt social transmission. Actual removals from culling or poaching among African elephants can have social impacts that last for decades largely because cultural information is lost (Archie & Chiyo, 2012; Shannon *et al.*, 2013).

At the heart of information transmission is determining how to model the transmission of ideas. One direction of research investigates ways to model the flow through a network. Similar to disease transmission, we can model nodes in a network as active, for example, informed or influenced, or inactive. Active nodes can then use the edges of the network to spread the contagion (e.g. information). For example, Domingos and Richardson (2001) used a global, probabilistic model that employed the joint distribution of the behavior over all the nodes to find influential ones. Kempe, Kleinberg, & Tardos (2003) used a diffusion process that begins with an initial set of active nodes and used different weighting schemes to determine whether or not a neighbor should be activated.

PREDICTIVE SOCIAL NETWORK ANALYSIS

Traditional statistical methods can be difficult to use with relational data because by definition, the members of the network are not independent from each other. In fact, it is the relationship between individuals that is typically of interest in the analysis. This lack of independence makes it difficult to interpret with traditional statistical tests. However, there are some methods that are particularly exciting for hypothesis testing about the function and role of different interaction patterns and relationships.

Relational variables tend to be central for predictive analyses that involve networks. Two approaches that have been widely used to model dependencies between relational variables are multiple regression quadratic assignment procedure (MRQAP) (Dekker, Krackhardt, & Snijders, 2007; Krackhardt, 1988) and exponential random graph models (ERGM) (Snijders, 2002; Snijders, Pattison, Robins, & Handcock, 2006). Instead of variables that are vectors of values, both methods have variables that are entries in an adjacency matrix to capture the relational aspect of the data. Both methods are meant for cross sectional network data analysis, however, they

are designed to answer slightly different questions. (The discussion below is based on the ones presented in Dekker *et al.*, (2007) and Snijders (2002).)

MRQAP was designed to investigate factors affecting pairwise associations. Given two different square matrices, is there an association between the same entries in these different matrices? MRQAP is a relational version of a standard regression analysis that can be used on weighted or binary networks. The procedure itself is a set of permutation tests for multiple linear regression model coefficients. The determinants are at the relationship or dyad level and the dependencies generated by the network structure as a whole are controlled for. Questions of interest are typically of the form—How do different factors (age, gender, etc.) influence the strength of association in undirected, directed, weighted or binary dependent variables?

We recently applied the MRQAP to investigate whether individuals group because they share a cultural trait—in contrast to animals sharing a cultural trait because they group (e.g., killer whale dialects, Yurk *et al.*, 2002). We study sponge tool use in wild bottlenose dolphins where the dolphins (spongers) use basket shaped marine sponges to ferret prey from the seafloor (Mann *et al.*, 2008; Patterson & Mann, 2011). Only about 5% of community members use sponges in this way (Mann & Patterson, 2013), but spongers associate regularly with nonspongers (Mann *et al.*, 2012). Our recent work demonstrated that a subset of the community preferentially associate based on their tool-using status, when sex, location, and maternal kinship are controlled for (Mann *et al.*, 2012). Because dolphins learn “sponging” from their mothers and tend to be solitary while hunting with their sponge tools (Mann *et al.*, 2008), we were able to show homophily based on tool-using status, going a step beyond others have shown to date. That is, spongers appear to prefer to be with each other, suggesting that they identify with others similar to themselves (Mann *et al.*, 2012). This is similar to patterns found in human social groups (McPherson, Smith-Lovin, & Cook, 2001). Homophily based on similar age, sex, reproductive state or other factors is common in animals, but they usually share the cultural trait because they group, not group based on shared cultural traits (Mann *et al.*, 2012).

In contrast, ERGM is designed to model networks as a whole, considering dependencies between different relational variables jointly. This allows one to model structural dependencies in the network. ERGM can still be used to model dependencies between relational variables while controlling for network structure, but it is well suited for modeling structural dependencies of the network. In an ERGM analysis, relationships can be directed or undirected, but the relationships must be binary. An ERGM analysis uses stochastic modeling to determine the probability that a connection exists between individuals based on some set of predictor variables. The explanatory variables may be attributes of the individuals, dyadic, or network

features. Questions of interest are typically of the form—How do various factors influence the structure of binary networks? Henrich and Broesch (2011) used ERGM to study transmission processes of critical cultural information on medicinal plants, fishing, and yam farming among Fijian villagers and had fascinating results. They found, for example, that social learning biases were stronger towards those who demonstrated success at a given behavior (fishing and farming) than knowledge per se (Henrich & Broesch, 2011). ERGM is used extensively in the social sciences, but has recently been applied to animal networks although not in the domain of culture (Pinter-Wollman *et al.*, 2014; Ilany, Barocas, Koren, Kam, & Geffen, 2013). One limitation with ERGM is that weighted approaches have only recently been developed (Krivitsky, 2012).

SUMMARY AND NEW DIRECTIONS

As more people share behavioral information online publicly, researchers will have the opportunity to better understand human behavior and the influence of social relationships on this behavior. This essay presented different studies and methods that have been proposed for identifying culture in animal societies. Applying and extending both the descriptive and predictive technique presented will improve our understanding of information transmission and social learning in the context of human networks. This in turn may help researchers identify subcultures that are embedded in human networks.

As mentioned previously, many of the methods for descriptive analysis do not consider complex networks that contain multiple node types, multiple edge types, weights, reciprocity, and attributes. Including all of these network features is important for more complete descriptive analysis. Similar extensions are needed for inference models as well. Without them, our ability to answer questions related to culture and social learning will remain limited.

Acknowledgments: We are grateful to our colleagues on The Shark Bay Dolphin Research Project and our funding sources: NSF, 0941487, 0918308, ONR 10230702, the National Geographic Society Committee for Research and Exploration and Georgetown University.

REFERENCES

- Aisner, R., & Terkel, J. (1992). Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. *Animal Behaviour*, *44*, 327–336.
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131), 485–488.

- Apicella, C. L., Marlowe, F. W., Fowler, J. H., & Christakis, N. A. (2012). Social networks and cooperation in hunter-gatherers. *Nature*, *481*(7382), 497–501.
- Archie, E. A., & Chiyo, P. I. (2012). Elephant behaviour and conservation: Social relationships, the effects of poaching, and genetic tools for management. *Molecular Ecology*, *21*(3), 765–778.
- Bacher, K., Allen, S., Lindholm, A. K., Bejder, L., & Krützen, M. (2010). Genes or culture: Are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.)? *Behavior Genetics*, *40*(5), 706–714.
- Backstrom, L., Huttenlocher, D., Kleinberg, J., & Lan, X. (2006). Group formation in large social networks: Membership, growth, and evolution. International Conference for Knowledge Discovery and Database (KDD), pp. 44–54.
- Blonder, B., Wey, T., Dornhaus, A., James, R., & Sih, A. (2012). Temporal dynamics and network analysis. *Methods in Ecology and Evolution*, *3*, 958–972.
- Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origin and spread of innovations in starlings. *Animal Behaviour*, *75*(4), 1509–1518.
- Cantor, M., & Whitehead, H. (2013). The interplay between social networks and culture: Theoretically and among whales and dolphins. *Philosophical Transactions of the Royal Society B*, *368*, 20120340.
- Caravelli, P., Wei, Y., Subak, D., Singh, L., & Mann, J. (2013). Understanding evolving group structures in time-varying network. *Advances in Social Networks Analysis and Mining*, 142–148.
- Carrington, P., Scott, J., & Wasserman, S. (2005). *Models and methods in social network analysis*. New York, NY: Cambridge University Press.
- Dekker, D., Krackhardt, D., & Snijders, T. A. (2007). Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika*, *72*, 563–581.
- Domingos, P. & Richardson, M. (2001). Mining the network value of customers. ACM International Conference on Knowledge Discovery and Data Mining.
- Dunbar, R. I. (2012). The social brain meets neuroimaging. *Trends in Cognitive Sciences*, *16*(2), 101–102.
- Easley, D., & Kleinberg, J. (2010). *Networks, crowds, and markets: Reasoning about a highly connected world*. New York, NY: Cambridge University Press.
- Flack, J. C., Girvan, M., de Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, *439*, 426–429.
- Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 1829–1836.
- Garlaschelli, D., & Loffredo, M. I. (2009). Generalized bose-fermi statistics and structural correlations in weighted networks. *Physical Review Letters*, *102*(3), 038701.
- Girvan, M., & Newman, M. E. J. (2002). Community structure in social and biological networks. *Proceedings of the National Academy of Sciences*, *99*(2), 7821–7826.
- Gorke, R., Hartmann, T., & Wagner, D. (2009). Dynamic graph clustering using minimum-cut trees. Proceedings of the 11th International Symposium on Algorithms and Data Structures (WADS '09), pp. 339–350.

- Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: Evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1139–1148.
- Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, 263(4), 544–555.
- Ilany, A., Barocas, A., Koren, L., Kam, M., & Geffen, E. (2013). Structural balance in the social networks of a wild mammal. *Animal Behaviour*, 85(6), 1397–1405.
- Kappeler, P. M., Barrett, L., Blumstein, D. T., & Clutton-Brock, T. H. (2013). Constraints and flexibility in mammalian social behaviour: Introduction and synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618), 20120337.
- Kempe, D., Kleinberg, J., & Tardos, E. (2003). Maximizing the spread of influence through a social network. *ACM International Conference on Knowledge Discovery and Data Mining*, pp. 137–146.
- Krackhardt, D. (1988). Predicting with networks—Nonparametric multiple-regression analysis of dyadic data. *Social Networks*, 10(4), 359–381.
- Krivitsky, P. N. (2012). Exponential-family random graph models for valued networks. *Electronic Journal of Statistics*, 6, 1100–1128.
- 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(25), 8939–8943.
- Laland, K. N., & Galef, B. G. (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 & Evolution*, 21, 542.
- Laland, K. N., Kendal, J. R., & Kendal, R. L. (2009). Animal culture: Problems and solutions. In K. N. Laland & B. G. Galef Jr., (Eds.), *The question of animal culture* (pp. 174–197). Cambridge, MA: Harvard University Press.
- Laland, K. N., & O’Brien, M. J. (2011). Cultural niche construction: An introduction. *Biological Theory*, 6(3), 191–202.
- Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, 428(6984), 715–716.
- Mann, J., & Patterson, E. M. (2013). Tool use by aquatic animals. *Philosophical Transactions of the Royal Society*, 368, 20120424.
- Mann, J., Sargeant, B. L., Watson-Capps, J., Gibson, Q., Heithaus, M. R., Connor, R. C., & Patterson, E. (2008). Why do dolphins carry sponges? *PLoS One*, 3(12), e3868.
- Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications*, 3, 980.
- Mastrandrea, R., Squartini, T., Fagiolo, G., & Garlaschelli, D. (2013). Enhanced network reconstruction from irreducible local information. arXiv preprint arXiv: 1307.2104.
- McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a feather: Homophily in social networks. *Annual Review of Sociology*, 27, 415–444.

- Newman, M. E. J. (2004). Analysis of weighted networks. *Physics Review E*, 70(5), 056131.
- Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, 103(22), 8577–8582.
- Newman, M. E. J. (2010). *Networks: An introduction*. New York, NY: Oxford University Press, Inc.
- Opsahl, T., & Panzarasa, P. (2009). Clustering in weighted networks. *Social Networks*, 31(2), 155–163.
- Pachucki, M. A., & Breiger, R. L. (2010). Cultural holes: Beyond relationality in social networks and culture. *Annual Review of Sociology*, 36, 205–224.
- Palla, G., Barabasi, A.-L., & Vicsek, T. (2007). Quantifying social group evolution. *Nature*, 446(7136), 664–667.
- Palla, G., Derenyi, I., Farkas, I., & Vicsek, T. (2005). Uncovering the overlapping community structure of complex networks in nature and society. *Nature*, 435, 814.
- Patterson, E. M., & Mann, J. (2011). The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops* sp.). *PloS One*, 6(7), e22243.
- Pinter-Wollman, N., Hobson, E.A. Smith, J.E., Edelman, A.J. Shizuka, D., de Silva, S., ... , McDonald, D.B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology*, 25(2), 242–255.
- Rankin, R., Mann, J., Singh, L. O., Patterson, E. M., Krzyszczyk, E. B., & Bejder, L. (in review). Dolphin social structure driven by weighted and topological information: A null model approach. *Animal Behaviour*.
- Rendell, L., Fogarty, L., & Laland, K. N. (2011). Runaway cultural niche construction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1566), 823–835.
- Rendell, L. E., & Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1512), 225–231.
- Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour*, 78(3), 715–721.
- Shannon, G., Slotow, R., Durant, S. M., Sayialel, K. N., Poole, J., Moss, C., & McComb, K. (2013). Effects of social disruption in elephants persist decades after culling. *Frontiers in Zoology*, 10(1), 62.
- Sharara, H., Singh, L., Getoor, L., & Mann, J. (2011). Understanding actor loyalty to event-based groups in affiliation networks. *Social Network Analysis and Mining*, 1, 115–126.
- Sharara, H., Singh, L., Getoor, L., & Mann, J. (2012). Finding prominent actors in dynamic affiliation networks. *Human Journal*, 1(1), 1–14.
- Shen, H., Cheng, X., Cai, K., & Hu, M.-B. (2009). Detect overlapping and hierarchical community structure in networks. *Physica A: Statistical Mechanics and its Applications*, 388(8), 1706–1712.
- Singh, L. O., Bienenstock, E. J., & Mann, J. (2010). What are we missing? Perspectives on social network analysis for observational scientific data. In B. Furht (Ed.), *Handbook of social networks: Technologies and applications* (pp. 147–168). New York, NY: Springer Science & Business Media, LLC, Chapter 7.

- Snijders, T. A. B. (2002). Markov chain Monte Carlo estimation of exponential random graph models. *Journal of Social Structure*, 3, 2.
- Snijders, T. A. B., Pattison, P., Robins, G. L., & Handcock, M. (2006). New specifications for exponential random graph models. *Sociological Methodology*, 36(1), 99–153.
- Tantipathananandh, C., Berger-Wolf, T., & Kempe, D. (2007). A framework for community identification in dynamic social networks. International Conference for Knowledge Discovery and Database (KDD), pp. 717–726.
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications* (Vol. 24). Cambridge, England: Cambridge University Press.
- Waters, J. S., & Fewell, J. H. (2012). Information processing in social insect networks. *PLoS One*, 7, e40337.
- Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.
- Whitehead, H., & Lusseau, D. (2012). Animal social networks as substrate for cultural behavioural diversity. *Journal of Theoretical Biology*, 294, 19–28.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ... , Boesch, C. (1999). Cultures in chimpanzees. *Nature*. 399(6737), 682–685.
- Williams, R., & Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. *Biology Letters*, 2(4), 497–500.
- Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63(6), 1103–1119.

FURTHER READING

- Cantor M, Whitehead H. (2013). The interplay between social networks and culture: Theoretically and among whales and dolphins. *Philosophical Transactions of the Royal Society B* 368: 20120340. <http://dx.doi.org/10.1098/rstb.2012.0340>
- Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, 263(4), 544–555.
- Laland, K. N., & Galef, B. G. (Eds.) (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.
- Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. de Silva, ... , McDonald, D. B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances *Behavioral Ecology*, 25(2), 242–255. doi:10.1093/beheco/art047

JANET MANN SHORT BIOGRAPHY

Janet Mann, Professor of Biology and Psychology and Vice Provost for Research at Georgetown University, earned her PhD at The University of Michigan with expertise in the field of animal behavior. Since 1988 her

work has focused on social networks, female reproduction, calf development, life history, conservation, tool-use, social learning and culture among bottlenose dolphins in Shark Bay, Australia. Her long-term study “The Shark Bay Dolphin Research Project,” tracks over 1600 dolphins throughout their lives. Mann has published over 80 scientific papers in journals such as *Nature Communications*, *Philosophical Transactions of the Royal Society*, *Proceedings of the National Academy of Sciences*, *Proceedings of the Royal Society*, *Biological Conservation*, and *Animal Behaviour* and in books such as *The Question Animal Culture*, *The Biology of Traditions*, *Rational Animals*, and *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies*. Her edited volume, *Cetacean Societies* (University of Chicago Press, 2000), received several awards. Twice she was a fellow at *The Center for Advanced Study in the Behavioral Sciences* at Stanford University. Dr. Mann’s research has received considerable media attention worldwide, including a BBC Documentary “The Dolphins of Shark Bay” focusing on her work in 2011. In 2013, Pamela Turner published a children’s book “The Dolphins of Shark Bay” (Houghton Mifflin) about Dr. Mann’s research.

<http://explore.georgetown.edu/people/mannj2/>

LISA SINGH SHORT BIOGRAPHY

Lisa Singh, Associate Professor in Computer Science at Georgetown University, is an expert in large-scale data mining. She received her PhD from Northwestern University in 1999. Her research interests include: mining social networks, data science and analytics, privacy preserving data mining, anomaly detection, graph databases, and sampling and bias in social networks. Her research is supported by the National Science Foundation and the Office of Naval Research. Dr. Singh has worked extensively with animal data sets and social media data sets. She has collaborated with researchers across disciplines at Georgetown University (biology, anthropology, medicine, linguistics, foreign serve, etc.), as well as the University of Maryland, the University of California—Santa Cruz, Hewlett Packard, the Census Bureau, and Oak Ridge National Labs. Dr. Singh also serves on organizing and program committees of the major data mining and database conferences, including KDD, ICDM, SIGMOD, PVLDB, and ICDE. She is also heavily involved in initiatives involving women in computer science and computer science in K-12 education. More information about her work can be found at: <http://cs.georgetown.edu/~singh>.

RELATED ESSAYS

- Mediation in International Conflicts (*Political Science*), Kyle Beardsley and Nathan Danneman
- Kin-Directed Behavior in Primates (*Anthropology*), Carol M. Berman
- The Sexual Division of Labor (*Anthropology*), Rebecca Bliege Bird and Brian F. Codding
- Culture and Cognition (*Sociology*), Karen A. Cerulo
- Adaptation for Culture (*Anthropology*), Jill M. Church
- Sexual Behavior (*Anthropology*), Melissa Emery Thompson
- Culture and Social Networks (*Sociology*), Jan A. Fuhse
- Food Sharing (*Anthropology*), Michael Gurven and Adrian V. Jaeggi
- Herd Behavior (*Psychology*), Tatsuya Kameda and Reid Hastie
- Emerging Trends in Social Network Analysis of Terrorism and Counterterrorism (*Sociology*), David Knoke
- Reconciliation and Peace-Making: Insights from Studies on Nonhuman Animals (*Anthropology*), Sonja E. Koski
- Cooperative Breeding and Human Evolution (*Anthropology*), Karen L. Kramer
- Implications for Human Sciences (*Anthropology*), Kevin N. Laland and Michael O'Brien
- Cultural Conflict (*Sociology*), Ian Mullins
- Gestural Communication in Nonhuman Species (*Anthropology*), Simone Pika
- Economics and Culture (*Economics*), Gerard Roland
- Production of Culture (*Sociology*), Vaughn Schmutz and Candace N. Miller
- Vocal Communication in Primates (*Anthropology*), Katie E. Slocombe
- Primate Allomaternal Care (*Anthropology*), Stacey Tecot and Andrea Baden