



Invited Commentaries

Everybody has a social life. Can social network analysis help us understand why not just how? Comment on Pinter-Wollman et al.

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As *Trivers* (1985) noted in the preface to his book on social evolution, everybody has a social life: “Life is intrinsically social and it evolves through a process of natural selection which is itself social...social evolution refers not only to the evolution of social relationships between individuals but also to deeper themes of biological organization stretching from gene to community.” Typically the study of social behavior and evolution has focused more on the characteristics of the socializing individuals rather than the social interactions themselves until recently. It is increasingly being recognized that understanding the processes that lead to the emergence of sociality and other higher order levels of organization requires an understanding of the social interactions themselves (e.g., *Székely et al. 2010*; *McDonald et al. 2013*): It is not necessarily the size of the group that matters but who is in the group and how you interact with them that counts.

Taking a social networks analysis (SNA) approach to studying the behavior of social organisms has many benefits, not least because it allows us to shift the emphasis away from variation in behavior among individuals to how interactions among these individuals shapes variation that natural selection acts on (*Fewell 2003*; *Royle et al. 2012*). However, despite the benefits, applying networks’ approaches to problems in behavioral ecology are not as widespread as perhaps might be expected. This seems surprising given the availability of some excellent books (e.g., *Croft et al. 2008*) and review articles (e.g., *Wey et al. 2008*; *Sih et al. 2009*) that provide clear introductions to SNA and explanations of the potential for new insights to existing problems across a range of topics in behavioral and evolutionary ecology.

One reason for this may be the lack of, or lack of awareness of, the statistical tools needed to be able to test hypotheses. This is the central premise of the review by *Pinter-Wollman et al. (2013)*. The statistical problems associated with analyzing networks data are not inconsiderable, and this has, to some extent, limited the scope for using SNA to test relevant ecological and evolutionary hypotheses. As a result, most studies using SNA are largely descriptive in approach. One of the main messages of this new review is therefore that we need to get beyond the descriptive and use SNA to answer functional questions about sociality. In order to facilitate this, *Pinter-Wollman et al. (2013)* provide an excellent users guide

to some recent advances in statistical techniques and more importantly the available software for running the analyses. In addition, they identify some of the more pressing conceptual challenges involved in applying SNA approaches to problems in behavior, ecology, and evolution and suggest effective ways to reenergize the field (e.g., sharing of databases via digital repositories such as Dryad).

Although the potential wider utility of some of the proposed approaches is not yet clear (e.g., the applicability of motif structure analyses beyond that of studying dominance interactions), without applying these approaches to data to test specific hypotheses we will not know how useful they are. Although the initial effort to get to grips with utilizing SNA to answer questions in behavioral ecology is not inconsiderable, this present review, in conjunction with introductory texts (e.g., *Croft et al. 2008*) and key review articles (e.g., *Wey et al. 2008*; *Sih et al. 2009*), provides an ideal springboard from which to leap. Hopefully, this new review will provide the appropriate encouragement for behavioral ecologists to use SNA to test hypotheses concerning social evolution and not just use it for describing social structure or, for that matter, writing more reviews (although obviously there is nothing wrong with either descriptive studies or reviews per se!). The rewards for doing so are likely to be high; SNA provides a rapidly improving toolbox for unlocking the complexities of social behaviors that can help us understand not just how we have a social life but why.

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The behavioral ecologist's essential social networks cookbook—comment on Pinter-Wollman et al.

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In recent years cross-fertilization with network theory has been one of the more exciting developments in the study of animal behavior. Pinter-Wollman et al. (2013) provide a comprehensive overview of where the study of animal social networks might go in coming years. There is a timely and helpful collection of methods for anyone looking to push this interdisciplinary area forward. Our commentary expands on an area only briefly alluded to in the main review with a view to increasing the breadth of coverage; we then discuss how uncertainty in measuring social networks might lead to caution in adopting new methods.

NETWORKS AND THE DIFFUSION OF BEHAVIOR

Pinter-Wollman et al. (2013) mention the link between social networks and the spread of behavior or information. This application of network analysis is termed “social influence theory” in social sciences, where it has been a major topic for some time (e.g., Robins et al., 2001; Shoham et al., 2012). In animal behavior, related methods have been developed to integrate data on the spread of behavior or knowledge through social networks. Collectively termed “Network-based Diffusion Analysis”, this is a set of techniques that fit data on the time or order of acquisition of the behavior in questions to an adapted Cox proportional hazards model (Franz and Nunn, 2009; Hoppitt et al., 2010). The model is adapted to include a parameter by which the summed strength of association between a given individual and other individuals that have already acquired the knowledge or behavior modifies the rate of acquisition (in conventional Cox terms, the “hazard rate”) of that individual. The models can work with precise time-of-acquisition data, discrete time-of-acquisition data (e.g., the sampling period an animal was first seen performing the behavior of interest) or simply the order of acquisition (i.e., individual B was first observed, then A, then C) and can include individual and time-varying factors that might influence underlying learning rates. These methods have already proved valuable in several contexts (Kendal et al., 2010; Aplin et al., 2012; Atton et al., 2012; Allen et al., 2013).

ANALYZING SOCIAL NETWORKS IN NOISY BIOLOGICAL SYSTEMS

Just as with all biological data, measuring social networks is rife with uncertainty (Lusseau et al., 2008). Much network theory has originated in fields—computer science for example—that do not always

have to deal with the kind of noise that characterizes biological systems. As a result, caution is advisable in adopting these methods. Does our knowledge of the study system meet the requirements of these techniques? Are we really as omniscient as a computer network administrator in how we can characterize the networks we are studying? How sensitive are these methods to measurement error or bias in the underlying behavioral data? Such questions outline the basis both for caution and opportunity for statistically minded behavioral ecologists to make a contribution that might end up having implications beyond our own field.

Pinter-Wollman et al. (2013) show their awareness of these points in their critique of existing methods for quantifying associations based on spatial and temporal co-ordination. However, analytical methods with assumptions that are explicit and have been validated are not inherently weaker than more complex methods that carry fewer assumptions. The relationship between spatial ecology and social structure is complex. It is difficult to envisage a situation where social structure would ever exist independently of spatial ecology—the former evolves within the constraints of the latter—so in the absence of observing directed behavioral interactions, the “gambit of the group” should not be seen as inherently faulty if its assumptions can be justified. Although existing approaches have their limits, it is perhaps easy to be overcritical when, as Pinter-Wollman et al. acknowledge, “a general procedure that incorporates spatial and temporal variability in space use at the population level has not yet emerged.” That particular cake has yet to rise, and biologists who think hard about the limitations of their data and collection protocols are unlikely to wait while it does.

More generally, when methods are introduced from other fields, it is still vital to keep in mind that every analysis will bring with it some kind of assumptions. Just because we can *run* an analysis does not necessarily mean we can *interpret* it correctly. Matthiopoulos and Aarts (2010) have expressed the dilemma of practitioners faced with new methods as “retrain or delegate,” but an alternative in this case is “collaborate.” We feel that the most exciting advances are likely to be made in collaborations between experts who work directly on these analytical methods and experts who have a deep understanding of their study system and the limits of the data they are collecting. Naïveté in either of these areas is likely to lead to problems.

Lest we be misinterpreted as overly negative however, it is clear that Pinter-Wollman et al. (2013) have done us a great service in collating a wide and exceptionally up-to-date overview and opening doors to a powerful set of new methods by creating an accessible cookbook of statistical recipes. Advances in social network analysis, like the ones described and envisioned, have an enormous potential to extract maximum information from long-term studies and at the same time powerfully illustrate the inherent value of those studies. The cake has every chance of being delicious.

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Dynamic feedbacks on dynamic networks: on the importance of considering real-time rewiring—comment on Pinter-Wollman et al.

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Pinter-Wollman et al. (2013) highlight modern issues and advances in the study of animal social networks (SNs). We particularly appreciate their tips on useful, accessible software that can help SN practitioners incorporate the new advances into their own analyses. Our comment jumps off from the title of their paper, “the dynamics of animal social networks.” We highlight some critical issues about temporal network dynamics that deserve more attention.

WHAT DO WE MEAN BY DYNAMICS OF SNS?

We first suggest that clarifying the meaning of “SN dynamics” will help organize our conceptual approaches. Blonder et al. (2012) note that this terminology can refer to two distinct types of phenomena: flow processes that occur within a particular network structure versus changes in the topology of the network itself, that is, dynamics of the network and dynamics of the network, respectively. Understanding dynamics of flow on or through the network focuses on how

information, disease, resources, contacts, and so on move from individual to individual through their network contacts. In contrast, understanding changes in the network itself focuses on factors that influence how, why, or when links between individuals get stronger or weaker—why an existing social link might be broken, and why a new one might form. Most interesting is the possibility that these two types of SN dynamics might often be linked via reciprocal feedbacks on similar timescales. This yields the potential for dynamic feedbacks with complex outcomes (Sih et al. 2009; Blonder et al. 2012).

DYNAMICS FEEDBACKS

Many studies implicitly assume that social network structure (SNS) affects flow of or access to an entity (e.g., information or disease) through a network, at both the individual and group levels (Newman 2003; Wey et al. 2008). When that entity affects the individual’s state (e.g., energy reserves, information state, and disease state), and its state affects fitness, then an individual’s SN position and the group’s SNS influence individual and group fitness. At the same time, individual traits (e.g., age, sex, condition, or behavioral type) are expected to influence its SN position and the outcomes of this position (Croft et al. 2009; Godfrey et al. 2012). Importantly, as Pinter-Wollman et al. (2013) note, “Animals may modify their social interactions in response to changes in external conditions... potentially altering their own social network structure and dynamics.” We focus on this exciting idea—that individuals not only can but should change their SNS in response to that very SNS, thus creating feedbacks. For example, if an individual changes its social behavior in response to getting sick or learning new information (a reasonable scenario), then it changes its potential for spreading the disease or information. A key point is whether these feedbacks are negative or positive. If individuals that get sick (or learn something new) tend to become less active or avoid social interactions, this is a negative feedback that clearly should reduce further spread. If, however, individuals that get infected with illness or knowledge tend to become more socially active (form new and/or stronger network links), then this positive feedback loop should clearly enhance spread. That there should be network “rewiring” with ongoing feedbacks in response to change (Flack et al. 2006) is an obvious point but surprisingly understudied.

Theory that incorporates dynamic network feedbacks should better match processes in real systems, thus providing more accurate and realistic insights than approaches that ignore feedbacks. Relevant dynamic phenomena that should benefit from this include the 1) development of SNS, including the substructuring or divergence of networks into separate communities (Newman 2003); 2) the stability of SNS (e.g., effects of perturbations on changes or not in SNS), including the possibility of alternative stable SNS; 3) nonlinear shifts in flow processes (e.g., epidemiological thresholds); and 4) effects of these complex dynamics on the fitness of individuals with different traits and SN positions, and on group fitness, especially where mixes of individuals may lead to emergent network phenomena.

TIME-ORDERED NETWORKS

To study network dynamics, both how flow on the network results in changes in the SNS and how those changes feedback to influence subsequent flow, it is critical to pay close attention to the shifting temporal pattern of interactions. The common method of aggregating interactions across time to form a snapshot representing a static SN can be quite misleading. For example, the transmission of disease from A to B to C (and so on) depends not just on whether or not the 3 individuals interacted, but on whether A interacted with B before as opposed to after A got sick. If illness has time lags (e.g., individuals

are often infective only during a particular period after interacting with an infected partner), the temporal details of the interactions clearly matter. Pinter-Wollman et al. (2013) discuss key issues and some recent advances in quantifying and analyzing time-ordered networks. Blonder et al. (2012) provide further detailed discussion of parallel recent advances in other fields. Overall, further study of SN dynamics with feedbacks strikes us as one of the most important future directions for this field. As detailed, time-ordered data and computational ability become less limiting, studying these feedbacks on continuous networks should provide novel understanding of feedbacks on relevant timescales of great interest to behavioral ecologists.

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We must consider dynamic changes in behavior in social networks and conduct manipulations: comment on Pinter-Wollman et al.

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Discovering a new set of relevant tools and concepts always brings excitement and discovery to a field, and the recognition of network theory and social analysis techniques by ecologists (not just behavioral ecologists—there have been similar flurries of activity in other allied fields in ecological and evolutionary biology, as detailed by Proulx et al. 2005) has led to an explosion of both empirical and theoretical activity. Pinter-Wollman et al. (2013) give an excellent snapshot of the current

state and direction of the field. The computationally intense nature of the questions asked require good tools to attack them, and both Pinter-Wollman et al. (2013) and Whitehead (2008) give some excellent signposts for available software. We should perhaps remember during this gold-rush period that many of these tools are designed for use in other disciplines and aren't necessarily designed to address the exact questions posed within the field. There is nothing wrong with embracing ideas from other disciplines, but attention should be paid to making sure that the logic behind the assumptions made is appropriate to the sorts of questions being asked within behavioral ecology.

Understanding how groups and societies form, behave, and are shaped by evolutionary processes are difficult problems and are made more difficult by the potential need to consider the actions of multiple individuals at the same moments in time. Much field behavioral ecology is limited by the degree of attention an observer can give to observing and recording interactions between individuals, and this may have consequences for how useful these techniques are within some species. Here, I touch on 2 problems that we should be mindful of when we intend to use social analysis tools.

THE RELATIONSHIPS BETWEEN INDIVIDUALS CAN CHANGE OVER TIME

It is likely that a typical behavioral dataset will consist of a relatively sparse set of observations of dyadic interactions, taken over a long period of time. Given datasets like this, it is tempting to look at the full set of interactions presented and attempt to identify a static picture of the composition of the group. However, both the observed individuals and the groups that they form are dynamic entities, and it is possible that their structure and behavior are changing over the course of the observations.

For example, if we take a state-dependent perspective of how the behavior of an individual is influenced by (and has impact on) factors such as its own physiology and the external environment (Houston and McNamara 1999), we could demonstrate that the optimal behavior of individual could potentially change rapidly in response to changes in external factors. These could include changes in response to altered behavior of other members of the group, which again could be caused by multiple factors. The influence of group members on each other may therefore be extremely labile and may change too rapidly to be detectable by the methodology used to collect social data. For example, in groups where decision making is related to physiological state rather than (or in complement to) dominance (Rands et al. 2008; Rands 2011), certain individuals may become temporary “leaders” for short periods of time simply due to their energetic requirements (see Fischhoff et al. 2007 for an example of this occurring in lactating zebra). Here, “leadership” is a short-term role and is maintained only as long as the physiological state of a key individual is at an appropriate level. This suggests that any analysis conducted of social structure should be mindful of structural changes that may be occurring within the timeframe being observed. This adds an extra layer of complexity to the understanding of the dynamic changes in the network described by Pinter-Wollman et al. (2013).

PASSIVE OBSERVATIONS AND EXPERIMENTAL PERTURBATIONS

Social network analysis can give us many useful insights into how individuals interact and has implications for our understanding of many aspects of behavioral ecology (Sih et al. 2009). Although they give a new means of exploring the structure of interactions within groups and societies, we must remember that these techniques should not be used in isolation from other techniques within

our arsenal. Much social network analysis is essentially passive and aims to make predictions about the structure of a group based on a series of observations, where some analytical hypothesis-testing is possible through techniques such as knockouts of behavioral interactions (as detailed by Pinter-Wollman et al. 2013). We must not forget that if we do not conduct any experimental manipulations on the groups being observed, then we will be unable to expose any hypotheses we form about social structure to the scrutiny possible with a well-controlled experiment. Only when we are able to compare the structure of a series of experimentally manipulated groups with a series of valid controls can we truly embrace these techniques within the framework of behavioral ecology.

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The positive commentaries to our review paper on the advances in social network analysis raise a number of important points that merit summation and elaboration: 1) The problems that uncertainty and imperfect sampling create for understanding social network structures and the advantages of experimental manipulation; 2) The need for careful and judicious application of new statistical methods; 3) The importance of incorporating temporal dynamics; and 4) The potential benefits of collaboration.

UNCERTAINTY, IMPERFECT SAMPLING, AND VALUE OF EXPERIMENTS

Rendell and Gero (2013) raise a key point that our understanding of animal social networks is largely based on imperfect sampling of associations and interactions. Therefore, we must be careful in how we apply methods from other fields, such as computer science and physics, which are able to obtain complete sampling of the networks they study. New technologies such as automated tracking systems and proximity data loggers (Mersch et al. 2013; Strandburg-Peshkin et al. 2013) as well as the promise of “reality mining” (Krause et al., 2013) have the potential to close this sampling gap, should it exist, but until then, we must account for imperfect sampling in statistical analyses.

In some cases, however, behavioral ecologists do possess full knowledge of animal social networks. For example, the full network is often known in closed experimental settings for which all individuals may be adequately monitored over time by use of tracking or video technologies. Experiments in captive or seminatural settings are particularly amenable to such advantages. In this regard, we agree with commentator Rands (2013) who calls for a move from passive observation-based studies to more actively manipulated experimental designs. Although experimental manipulation is not feasible in some cases, it is a powerful method for testing hypotheses about the underlying causes of social dynamics, selection pressures, and evolutionary processes.

Notably, studies on nonhuman animals benefit from the rich history of sampling techniques established by behavioral ecologists to quantify the behaviors of animals. Ties in animal social networks benefit from an objectivity that is more challenging to achieve in the social sciences. Studies on network ties among humans are often based on surveys or self-reported data that vary in their degree of reliability. Thus, behavioral ecologists studying nonhuman animals are able to capitalize on a rich tool kit for quantifying natural variation in key variables such as cooperative acts, disease prevalence, and information flow.

Response to comments on the dynamics of network dynamics

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APPLICATION OF NEW STATISTICAL METHODS

Both Royal (2013) and Rands (2013) reiterate one of the main points of our review—the need to move beyond utilizing social network analysis for describing social structures to testing hypotheses, using appropriate statistical tools. By aggregating a set of analytical tools (Table 1 in Pinter-Wollman et al. 2013), our goal is to facilitate this move from description to testing ecological and evolutionary relevant hypotheses.

These statistical tools are especially important when attempting to elucidate the effects of the environment and of intra- and inter-specific interactions on social patterns. As we move toward the next phase of using social network analysis to study behavioral ecology, it is critical to forge approaches and applications that are structured by the idiosyncrasies of natural systems. Indeed, we fully agree with Rendell and Gero (2013) that approaches developed in other fields should not be blindly applied to our complex systems. Instead, the goal of our

review is to help behavioral ecologists identify, modify, and develop approaches that are important for moving forward the application of social network analysis to the study of animal social behavior.

A key point brought forward by [Rendell and Gero \(2013\)](#) is the importance of recognizing, defining, and testing the assumptions underlying network analysis and its interpretations. In many cases, we assume our sampling is not influenced by population structure, spatial dynamics, or temporal dynamics during the study period. Selecting null hypotheses that ignore underlying structure (spatial or behavioral) that limits or facilitates random interactions, or misappropriate the scale of analysis relative to temporal dynamics, can lead to erroneous conclusions. A recently developed R package, *asnipe*, ([Farine 2013](#)) now provides a useful tool for incorporating time and space in permutation analyses of networks, producing biologically meaningful null hypotheses. Understanding one's study species, particularly its natural history and ecological interactions, is critical for formulating questions, developing powerful research designs and appropriately structuring analyses.

TEMPORAL DYNAMICS

Three of the 4 responses to our paper highlight the importance of temporal dynamics when analyzing social networks and point out further aspects to consider.

[Sih and Wey \(2013\)](#) highlight the important distinction between the dynamics of processes that flow on an existing interaction network and processes that change the network structure, which they succinctly summarize as dynamics on the network versus dynamics of the network. They further elaborate on the positive and negative feedbacks between network structure and the information that travels on it. We would like to echo their insightful call for integrating these feedbacks in both theoretical and empirical studies of animal social dynamics. Along with the time-ordered analysis method both we and [Sih and Wey \(2013\)](#) discuss, recent advances in animal tracking ([Krause et al. 2013](#); [Mersch et al. 2013](#); [Strandburg-Peshkin et al. 2013](#)) will provide the data needed for examining the complex relationship between network structure and function.

[Rendell and Gero \(2013\)](#) further emphasize the importance of examining processes that occur on networks, such as information flow, and provide quantitative tools for studying these dynamics. We recognize that our review of tools to study network dynamics focused on changes to the structure of the network and are delighted with the additional analysis tools provided by [Rendell and Gero \(2013\)](#) for studying the dynamics of processes that diffuse on the network. Understanding such dynamics is crucial for the study of communication, disease spread, collective decision making, establishment of dominance hierarchies, and many other social processes.

However, it is worth noting that not all changes to an individual's behavior results from information flow on the network. [Borgatti and Halgin \(2011\)](#) discuss the possibility that individuals that are not connected with one another, but whose networks are similarly structured, will exhibit the same behavior not because they influence one another but because the structure of their connections has the same affect on them (i.e., bond models). Thus, structural changes could affect the behavior of individuals without affecting the flow of information on the network. Animal societies with long-term stable relations may be best analyzed using a structural (bond model) approach rather than a flow approach.

[Rands \(2013\)](#) thoughtfully raises the potential problem that relationships among individuals may change between observations. This returns to the idea we focus on in our review of changes to network structure over time. We believe that time-ordered analysis, which examines the dynamics of networks not by creating snapshots

or aggregating data but by stringing the observed interactions in a sequential manner, addresses the concerns of changes to relationships between observations. In addition to potential social changes that may happen between observations, we would like to highlight the environmental changes that can occur between observations, further obviating the importance of considering the complex interaction between time and space on social network structure.

COLLABORATIONS

Finally, we reiterate the observation of [Rendell and Gero \(2013\)](#) that “the most exciting advances are likely to be made in collaborations between experts who work directly on these analytical methods and experts who have a deep understanding of their study system.” Interdisciplinary partnerships between behavioral ecologists and computational biologists, mathematicians, or computer scientists have the potential to be fruitful, as long as new approaches are firmly grounded in biological relevancy. In addition to such collaborative undertakings on single systems, we hope our review will facilitate broader comparative work both by pushing our field toward greater standardization of data collection (as required by many of the approaches reviewed) and by inspiring data reposition and sharing. Such endeavors can facilitate future examination of network data using new statistical tools as they evolve as well as collaborative macro ecological/evolutionary studies that may offer the power to resolve some of the more intractable questions about drivers of various social properties. We hope our discussion here will facilitate and encourage future interdisciplinary collaborations and look forward to seeing the fruits of such synergistic activities.

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