Behavioral Ecology Advance Access published January 23, 2014
1989 - 2014 25 YEARS BEHAVIORAL ECOLOGY
Behavioral Ecology
The official journal of the ISBE International Society for Behavioral Ecology

# Invited Commentary

## Response to comments on the dynamics of network dynamics

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 Drive, 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]Department of Biology, 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, Arizona State University, PO Box 874601, 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

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 cooperative acts, disease prevalence, and information flow.

## 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 interspecific 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.

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

Received 5 January 2014; accepted 7 January 2014.

doi:10.1093/beheco/aru004

**Forum editor:** Sue Healy

## REFERENCES

Borgatti SP, Halgin DS. 2011. On network theory. Organ Sci. 22:1168–1181.

Farine DR. 2013. Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol Evol. 4:1187–1194.

Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S, Rutz C. 2013. Reality mining of animal social systems. Trends Ecol Evol. 28:541–551.

Mersch DP, Crespi A, Keller L. 2013. Tracking individuals shows spatial fidelity is a key regulator of ant social organization. Science. 340:1090–1093.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, de Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, et al. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav Ecol. Advance Access published June 14, 2013, doi:10.1093/beheco/art047.

Rands SA. 2013. We must consider dynamic changes in behavior in social networks, and conduct manipulations. Behav Ecol. Advance Access published January 17, 2014, doi:10.1093/beheco/art129.

Rendell L, Gero S. 2013. The behavioral ecologist's essential social networks cookbook. Behav Ecol. Advance Access published October30, 2013, doi:10.1093/beheco/art099.

Royal NJ. 2013. Everybody has a social life. Can social network analysis help us understand why not just how? Behav Ecol. Advance Access published July 3, 2013, doi:10.1093/beheco/art055.

Sih A, Wey TW. 2013. Dynamic feedbacks on dynamic networks: on the importance of considering realtime rewiring. Behav Ecol. Advance Access published November 4, 2013, doi:10.1093/beheco/art081.

Strandburg-Peshkin A, Twomey CR, Bode NW, Kao AB, Katz Y, Ioannou CC, Rosenthal SB, Torney CJ, Wu HS, Levin SA, et al. 2013. Visual sensory networks and effective information transfer in animal groups. Curr Biol. 23:R709–R711.