

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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