Behavioral Ecology

Invited Commentary

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

Luke Rendell and Shane Gero

Centre for Social Learning and Cognitive Evolution and Sea Mammal Research Unit, School of Biology, University of St. Andrews, St. Andrews, KY16 9TS, UK

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. Theirs 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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