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Invited Commentary

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 *on* 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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