

Invited Commentary

Demographic processes in animal networks are a question of time: a comment on Shizuka and Johnson

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Shizuka and Johnson (2019) highlight that demographic processes, such as birth, dispersal, and death, represent an important set of open questions in the ecology and evolutionary biology of social systems. The authors make the case that the impacts of demographic processes shape animal social structure. For example, the death of a group member corresponds to the loss of a node from the social network. From empirical studies, we know that even short-term perturbations to a social system (e.g., splitting a group for just 2 days) can have clear effects on network structure and subsequent group function that extend beyond the immediate gain or loss of a node (Maldonado-Chaparro et al. 2018). A pertinent first set of questions to address on this topic are 1) when will demographic processes perturb social network dynamics, 2) what is our ability to detect such perturbations, and 3) whether selection can promote behaviors that mitigate the effects of perturbations arising from demographic processes.

One reason why demographic processes may not have impact on social dynamics in the same way that social instability has is because of the time frame over which they occur. Here, context might matter. For example, the death of individuals can arise from different sources: a death can be age related or can be predator induced. These two contexts are unlikely to have the same impact. Older individuals that occupy high ranks in societies, and therefore are more likely to have an important role, often drop down the hierarchy before they die (Strauss and Holekamp 2019). Thus, the impact of removing an individual from the population through age-related causes could be anticipated by the system. By contrast, predation can induce very rapid changes to the membership of social groups. Effects of predation are likely to be more representative of the results of experimental studies involving the temporary

removal of individuals (Flack et al. 2006). Thus, not all demographic changes are the same, and the impact of the perturbation they induce could be context (and system) dependent.

Addressing the question of demographic effects on the formation and maintenance of social structure in animal societies is timely. However, a challenge is that protracted events (such as the death of an important individual) might have a weak signal, whereas sudden events might have a strong signal but correspond to very rapid changes in the network. Both situations would make the impact of perturbations arising from demographic processes difficult to detect. For example, perturbations can be difficult to disentangle from the underlying fluidity in social dynamics (Franz and Alberts 2015) or from the uncertainty caused by measurement error or lack of precision in the observational data (Davis et al. 2018). Thus, although many long-term studies have proven valuable for addressing questions about changes in populations over time, these may not have the necessary temporal resolution in their data to investigate demographic effects on social structure. But, the future is promising. Recent technological and analytical advances now allow us to collect fine-scale data on social behavior spanning over long time periods (e.g., Alarcon-Nieto et al. 2018). The implementation of such approaches will allow us to construct the finely resolved long-term data sets needed to acquire a deeper understanding of the potential effects that Shizuka and Johnson highlight. Thus, we propose that overcoming this new research horizon will most likely require investing in collecting new data rather than revisiting older studies.

Shizuka and Johnson make a call for having greater consideration of demographic processes in studies of social behavior. We support their view that more explicit emphasis is needed on how life-history processes, ecological change, and social instability can shape patterns of selection operating via social structure. However, we propose that doing so requires moving beyond classical approaches for collecting data. Alongside collecting fine-scale long-term data, we need to continue developing the statistical tools necessary to overcome the challenges of analyzing social data in a temporal domain (Farine 2018). These will be necessary to, for example, identify the processes that take place when demographic changes induce a perturbation on a group or population. We are confident that the research community is already starting to overcome these challenges, which will soon allow us to address the new frontier highlighted by Shizuka and Johnson.

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