



Invited Commentary

Placing the effects of demography on networks in ecological context: a comment on Shizuka and Johnson

Orr Spiegel^{a,⊙} and Noa Pinter-Wollman^{b,⊙}

^aSchool of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel and ^bDepartment of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095, USA

The generative processes that determine the structure of animal social networks (SNs) are understudied and may differ from processes that generate other networks. Shizuka and Johnson (2019; hereafter S&J) provide a comprehensive review of how demographic processes shape animal SNs. In our opinion, this well-crafted manuscript presents an important step toward improving the study of the dynamics of animal SNs.

We would like to add to S&J's review by placing the links and feedbacks between SNs and demography in a broader framework that explicitly integrates the influence of ecology and behavior on SNs. While some processes we highlight are mentioned briefly by S&J, our framework (Figure 1) aims to integrate multiple generative pathways of animal SNs to broaden the discussion and offer a more inclusive view. Our perspective emphasizes the importance of behavior as a central pillar in many of these processes and the global ecological pressures on SN formation. First, as briefly mentioned by S&J, ecology can affect the nature of social interactions (arrow #1). For example, plentiful resources can promote affiliative interactions, while scant resources may lead to hungry individuals that are agonistic. Second, are the effects of demography that S&J detail (arrows #2a–2c). A third pathway, which is overlooked by S&J, (arrow #3) is the effect of ecology and spatial constraints on the movement of animals, which affect the formation of social interactions and probability of encounters (Pinter-Wollman et al. 2017). For example, clumped and ephemeral resources affect foraging movements which can force encounters (Pinter-Wollman et al. 2014; Spiegel et al. 2016), thus serving as a generative mechanism of SNs that adds to social preferences or tendencies. Furthermore, in many cases, movement behaviors can affect demographic processes (arrow #4). For instance, individual variation in tendency to disperse and in movement distances during dispersal (Cote et al. 2010; Spiegel et al. 2017), may impact with whom the dispersing individuals form new social links. Finally, SN structure can feedback onto ecology, independent of demographic processes (arrow #5), for example, via group foraging that depletes resources and forces animals to move to new places and interact with new individuals.

This feedback, which is overlooked by S&J, would affect all the different generative processes.

We especially appreciate S&J's discussion of the importance of time scales on SN generation. Temporal dynamics of demographic changes, and synchrony among individuals can profoundly impact social structures. For example, singletons dispersing gradually would have different impacts on SNs than abrupt departures of large subgroups. Furthermore, it is important to note that many studies of animal social behavior focus on processes, such as disease and information transfer, that occur on much shorter timescales than demographic processes like births and deaths. These short-term social dynamics are overlaid on networks that are formed by slower processes (e.g., arrow #2a–2c). Therefore, any advancement in the way we study the formation of SNs will advance our studies of the processes that occur on the SNs.

Together, the different timescales of network dynamics, spatial constraints on SNs, and feedback between ecology, demography, and SNs highlight methodological challenges for obtaining data on both life-long social networks and demographic events. SNs are mostly studied in long-lived animals (Webber and Vander Wal 2019), requiring long-term research programs that track both demographic events and social ties of individually identified animals. These programs are expensive, and often suffer from incomplete data, especially about social interactions. Furthermore, it is not always possible to study an individual throughout their entire life or to distinguish between mortality and dispersal events. Varying tracking durations can bias results (e.g., shorter tracking for dispersers compared with residents, or variation in tagging reliability). For example, such biases can place certain individuals in central positions of a SN, not because they are truly central, but because they have been tracked for the longest time. Rapid technological development of bio-telemetry and image analysis tools may provide solutions to these challenges (Krause et al. 2013; Valletta et al. 2017).

To conclude, we would like to reiterate our excitement of incorporating a demographic perspective into the study of animal social networks when it is applicable and possible. We suggest that placing the demographic processes, nicely introduced by S&J, within the broad ecological processes that impact animal interactions can lead to a better understanding of the behavioral, ecological, and evolutionary processes that govern animal sociality.

Address correspondence to N. Pinter-Wollman. Email: nmpinter@ucla.edu; O. Spiegel. Email: orrspiegel@tauex.tau.ac.il

Received 7 June 2019; editorial decision 11 June 2019; accepted 12 June 2019.

Editor-in-Chief: Leigh Simmons

doi: 10.1093/beheco/arz113

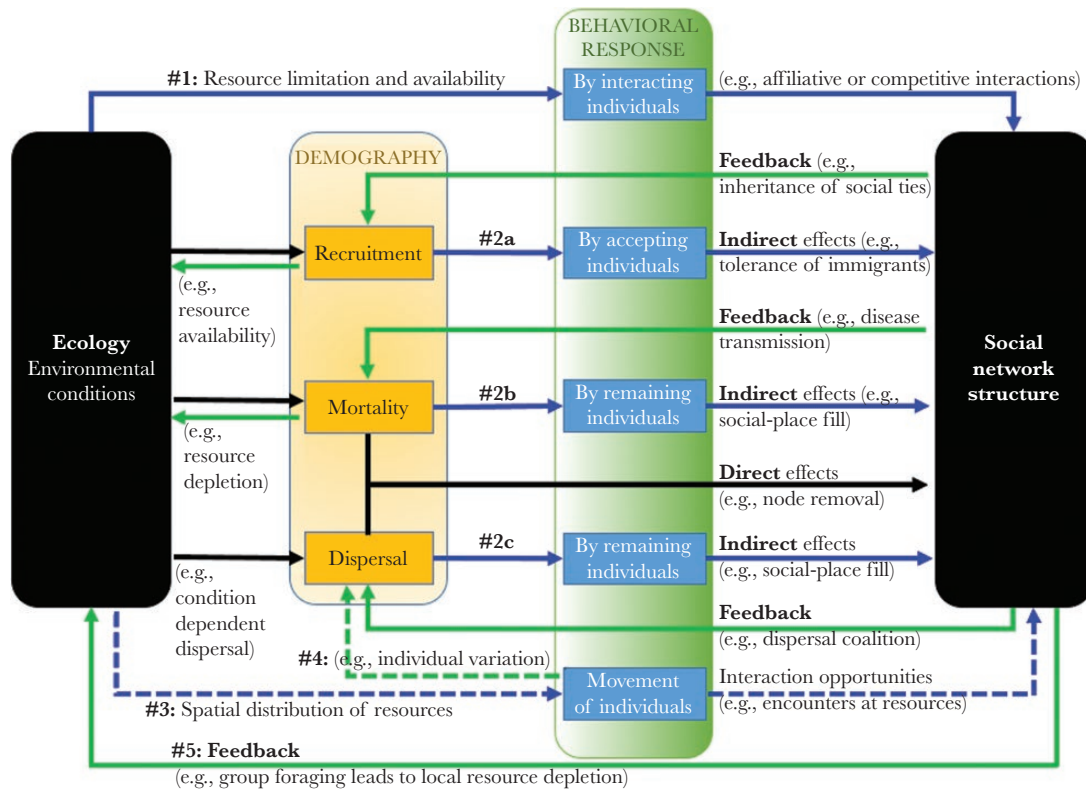


Figure 1

A conceptual framework that places demographic effects within other generative processes of animal social networks. Environmental conditions can affect social networks directly through social behavior (arrow #1), through demography, as detailed in Shizuka and Johnson (2019); (arrows #2a-c), or through effecting movement and space use (arrow #3). Blue arrows are indirect effects, black are direct effects, and green are feedbacks, the dashed arrows (#4 and #5) were not included in Shizuka and Johnson's (2019) article.

REFERENCES

- Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical transactions of the Royal Society of London. Series B Biol. Sci.* 365:4065–4076. <https://royalsocietypublishing.org/doi/full/10.1098/rstb.2010.0176>
- 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.
- Pinter-Wollman N, Fiore SM, Theraulaz G. 2017. The impact of architecture on collective behaviour. *Nat Ecol Evol.* 1:111.
- Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, de Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, et al. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav Ecol.* 25:242–255.
- Shizuka D, Johnson AE. 2019. How demographic processes shape animal social networks. *Behav Ecol.* doi:10.1093/beheco/arz083.
- Spiegel O, Leu ST, Bull CM, Sih A. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol Lett.* 20:3–18.
- Spiegel O, Leu ST, Sih A, Bull M. 2016. Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods Ecol Evol.* 7:971–979.
- Valletta JJ, Torney C, Kings M, Thornton A, Madden J. 2017. Applications of machine learning in animal behaviour studies. *Anim Behav.* 124:203–220.
- Webber QMR, Vander Wal E. 2019. Trends and perspectives on the use of social network analysis in behavioural ecology: a bibliometric approach. *Anim Behav.* 149:77–87.