that when territorial males temporarily leave in search of other actively reproductive females, the females with demanding young foals will remain united to amortize vigilance costs of avoiding harassing males as well as predators.

What is interesting about fission–fusion societies is that there is usually some resilience built into the system that can dampen the potential harm associated with some of the indirect network rearrangements posited by Shizuka and Johnson's (2019) simulations. In a recent study on a population of the fission–fission bottle-nosed dolphin in Sarasota Bay, FL in which dolphins were temporarily removed from the population for rehabilitation after being damaged in boating accidents, Greenfield and colleagues (in review) showed that removed individuals when returned to the population had fewer strong associations than before they were harmed. Yet, the strongest bonds usually remained. Typically, these were between mothers and young or between male allies since male coalitions are essential for mating success and they take a long time to develop. Moreover, within 2 years, damaged individuals had increased to predamage levels their number of strong associates even if the identity of the partners had changed. Clearly, not all bonds are equally important and those that are do not always permanently dissolve even though an individual's protracted absence could be construed as death.

Temporary adjustments to losses and the subsequent rewirings of the kinds shown by the dolphins when reappearances occur are not depicted in Shizuka and Johnson's (2019) figures 2 or 3, but are likely to be common. It is hard to predict "what ifs" using static network graphs as employed in this review. We need to explore the important role of demographic perturbations on social structure and their consequences for inherent social relationships using dynamic graphs and their temporally constructed metrics that are more sensitive to the time scale of change, because dynamic graphs do not average data over long periods (Rubenstein et al. 2015).

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The long view on demographic effects on social networks: a response to comments on Shizuka and Johnson

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Births, deaths, and dispersal are universal processes in animal populations. In our review (Shizuka and Johnson 2019), we illustrate how these fundamental demographic processes must play a role in shaping animal social networks. As Ilany (2019) elegantly put it, these are simple processes that can generate complex societies. Spiegel and Pinter-Wollman (2019) take this thinking a step further and present an integrative framework embedding these demographic effects within other ecological factors that shape animal societies. Vander Wal and Webber's (2019) comment on the role of social networks on density dependence and eco-evolutionary dynamics exemplify the type of extensions that we hope this review will instigate. Here, we wish to highlight two key themes that emerge from the various commentaries: causes of variation in responses to demographic effects, and the promise of technological advances in addressing some key questions about the effects of demography on social networks.

Maldonado-Chaparro and Farine (2019) point out that demographic processes do not always lead to detectable changes in social structure and dynamics. For example, age-related death of individuals may not have the same effect as the loss of that individual due to predation. In the former case, other individuals may be able to anticipate the eventual demise of one of their members, and the resulting social dynamics may reduce the impact of the loss of those individuals (Shizuka and Johnson 2019). But a larger question worth asking is whether demographic processes are important only in cases where they result in detectable changes to social structure dynamics. Because the turnover of individuals is a universal feature of societies, our challenge is to find out why societies vary in their responses to demographic change (Rubenstein 2019). From this viewpoint, understanding what promotes stability and dynamism of social structure in the face of demographic change becomes just as important as the ability to detect change when it happens. Taking the hypothetical example of an individual's death, what might be the social dynamics that mitigate network change when the death of that individual can be anticipated? Are such social behaviors under selection to promote social stability, and if so, how do individuals (and which individuals) gain fitness benefits from social stability? Alternatively, as both Kulahci (2019) and Rubenstein (2019) point out, stability or resilience may be an underlying feature of certain societies such as those with fission–fusion dynamics.

Many commentaries also highlighted the potential for new technologies for collecting behavioral data to transform our understanding of how demographic processes shape animal societies. Specifically, fine-resolution data on social interactions may be necessary for disentangling when demographic effects perturb social dynamics beyond their natural fluctuations (Maldonado-Chaparro and Farine 2019). Collecting data at fine temporal resolution over long time periods may also help us address whether or not short-term processes build up to long-term effects (Ilany 2019; Spiegel and Pinter-Wollman 2019). We agree that these are critical questions and we are equally excited about the promise of new tracking and data logging technologies to transform our understanding of long-term social dynamics. But we also emphasize that our aim should be to complement direct observations with autonomous data collection strategies, rather than substitute one for the other. Even with the rapid progress in the collection of fine-scale behavioral data, we will still need to collect this data over the timescale of generations to study the impact of demographic processes. In the meantime, retrospective analysis of existing long-term research efforts is an important potential avenue for address pressing questions about demographic effects of social networks. Moreover, we should also acknowledge that new technology cannot substitute the accumulated natural history knowledge gleaned from repeated observations of known individuals over their lifetimes (Ilany 2019). For example, without long-term direct observations, we may not be able to track the cultural transmission of novel foraging behaviors (e.g., Allen et al. 2013) because data-logging technology to track such behaviors could not be designed without first identifying the behavior. Moreover, the design and implementation of new technologies should be based on natural history knowledge about the ecology of social interactions based on direct observations. There is a reason that many, if not most, successful applications of new technologies to study animal social networks have leveraged existing long-term study populations.

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