

On assessing the importance of demographic change on social structure

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The study by Shizuka and Johnson on “How demographic processes shape animal social networks” identifies an important overlooked fact that demographic changes associated with death, emigration or immigration can perturb social systems by disrupting existing social relationships. Since social networks have become a powerful way of quantitatively characterizing social relationship using various social metrics such as degree, weighted degree, betweenness and cliquishness (cluster coefficient), the authors argue that the typologies created by these graphs and their associated metrics can provide insights into not only the direct consequences of demographic changes, but also the indirect ones that occur via rewiring.

The many hypothetical and real-world examples in their excellent review along with simulations involving removals and additions, show that demographic changes sometimes lead to large direct and indirect changes, but not always. I suspect that much of this variation depends on the species’ social structure itself. In particular, societies constructed of strongly bonded closed membership groups are likely to respond to changing composition differently from fission-fusion societies where individual comings and goings are common and frequent. For example, in feral horses where female bond to males forming harem groups to avoid sexual harassment (Rubenstein 1986; Rubenstein 1994 and Rubenstein and Hack 2004), the disappearance of the breeding male is likely to create social instabilities even if the death of such a male does not immediately lead to the disintegration of the group (Rubenstein, pers. obs.). In the short run, links among females strengthen, increasing the network metrics of weighted degree and cliquishness, much like the example illustrated in the review’s figure 3d. Eventually, however, without the presence of the long-term bonded male to fend off nearby sexually harassing stallions and bachelor males, these males eventually break the bonds among the females, integrating some of them in their existing groups much like the graph in the review’s figures 3e. Because kinship is not involved in shaping the bonds among equids females (Tong, et. al 2015), continual male pressure erodes the bonds among females making it unlikely that the entire clique, or module, will be incorporated as a unit in the new male’s group.

In fission-fusion societies individuals regularly break and reform bonds. In the horse’s close kin, the Grevy’s zebra, females spend time with many males even though they show preferences for some over others. Similarly, females show varying degrees of associations with particular females and the strength of these bonds often depend on similarity of female reproductive state. When females are nursing young foals and come into post-partum heat, the presence of a male can provide important protection from marauding and harassing males (Rubenstein and Hack 2004). It is also common for these females to strengthen bonds among themselves. Weighted degree and cluster coefficients among these females increase during this critical developmental period and help insure that when territorial male 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's and Johnson's simulations. In a recent study on a population of the fission-fusion bottlenose 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 two years, damaged individuals had increased to pre-damage 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 the review's figures 2 or 3, but are likely to be common. The fact that it is hard to predict 'what ifs' using static network graphs as employed in this review highlights the need to explore the important role of demographic perturbations on social structure and their consequences on inherent social relationships using dynamic graphs and their temporally constructed metrics that are more sensitive to the time scale of change because they do not average data over long periods (Rubenstein et. al. 2015).

References

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