

Yet, not all node losses and introductions are equal. Individual characteristics of a node can influence how its loss or introduction affects its network. Some individuals are more social than others and these differences are reflected in the presence and the frequency of network connections (Krause et al. 2010). It is plausible that when highly social individuals join a new network, they would initiate multiple connections that influence the network structure. Likewise, loss of a social individual (either by death or dispersal) will disrupt the network more than the loss of a less-social individual. For example, juveniles tend to be more socially active than adults (Turner et al. 2018), and their death or dispersal can result in a significant reduction in network connectivity. Additionally, depending on how social they are, individuals will vary in their responses to the loss of a connection (or to the presence of new conspecifics).

Animals sometimes preferentially connect with successful conspecifics (Kulahci et al. 2018) as doing so provides immediate and future benefits (Kulahci and Quinn 2019). By introducing or removing successful individuals from a group, demographic events can indirectly lead to network changes. For instance, a juvenile might learn a novel behavior (e.g., more efficient way to utilize a resource) in his natal group before dispersing into another group. This successful immigrant, after displaying the novel behavior in the new group, might have a better chance of being integrated into the social network than other immigrants do. Similarly, loss of individuals who possess knowledge that others do not have (McComb et al. 2001) can have striking consequences. Consequently, new nodes can introduce new behaviors and knowledge to the group, while loss of nodes can remove them; and both processes have the potential to feedback on to the network structure by influencing how existing group members respond.

One of the advantages of integrating different fields is borrowing the strengths of each and combining them. Population biology has informed us about species differences in birth, death, and movement. Social network analysis has allowed us to adopt a new way of thinking for linking individual differences to the overall group structure and for gaining insights into transmission processes by capturing both direct and indirect connections (Croft et al. 2008). Now, in their exciting review, Shizuka and Johnson provide a timely encouragement for exploring how demographic events and network dynamics interact with each other. Our ability to predict how demographic events influence networks is likely to be improved by gaining as much information as possible about the species and the individuals we study.

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Density dependence and eco-evolutionary dynamics of animal social networks: a comment on Shizuka and Johnson

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Shizuka and Johnson (2019; hereafter, S&J) highlight the important role of demography in animal social networks. At its simplest, demography is the ecology of births and deaths; a topic covered thoroughly by S&J. Variation in the number of births and deaths will influence network properties (see Figures 2 and 3 from S&J). Classical ecology highlights that births and deaths lead to changes in population size, growth ($\lambda = \frac{N_{t+1}}{N_t}$), and density. Density dependence affects how animals live and die, thus influencing population growth through regulation or limitation (Chitty 1960). The mechanism of this density-dependent feedback has potential to affect the adaptive value of phenotypic traits, including social network traits (Webber and Vander Wal 2018) and their distribution in the population. Some social network traits may also be heritable (Brent et al. 2013). Changes in the distribution of an adaptive phenotype captures an *evolutionary process* with the potential to influence population growth, an *ecological process*, thus spotlighting density dependence as a prospective agent for eco-evolutionary dynamic (Morris 2011).

Identifying the causes and consequences of evolutionary change in the wild is critical for evaluating how changes in phenotypic composition of populations may affect population growth and,

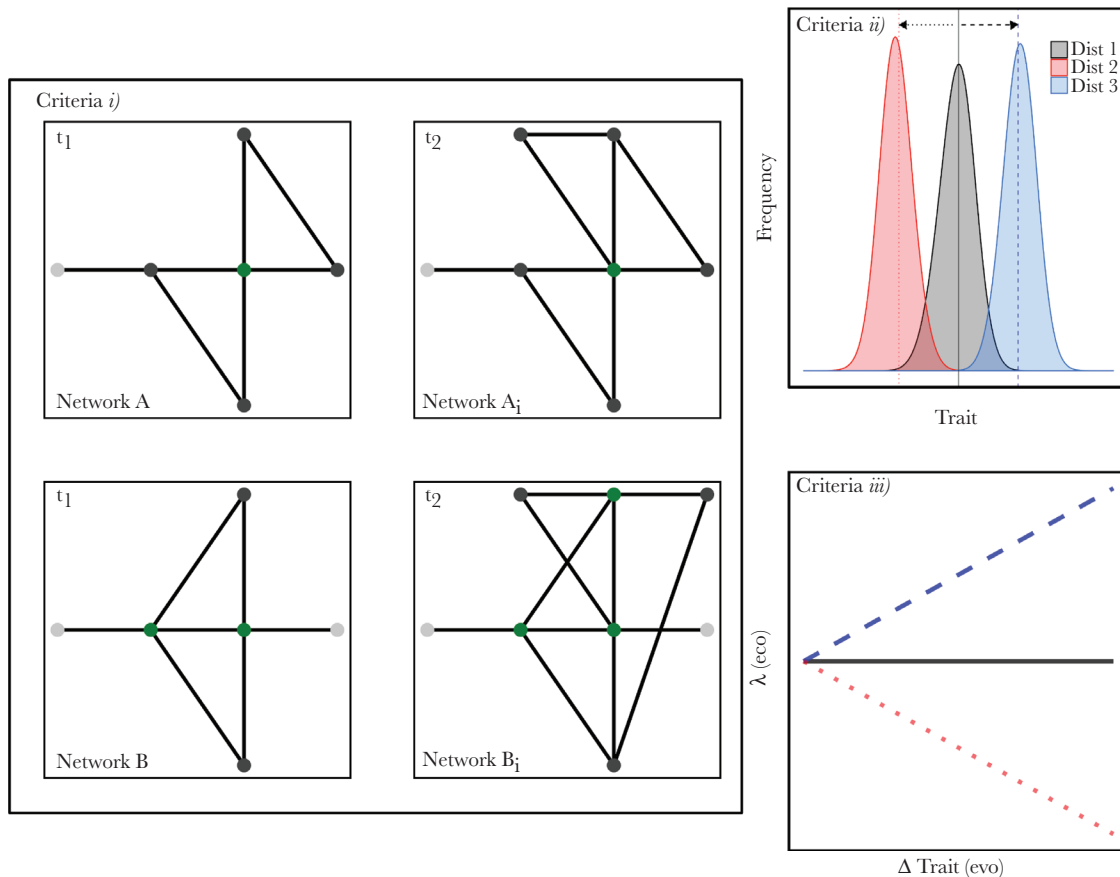


Figure 1

One of many possible hypothetical scenarios outlining potential for social eco-evolutionary dynamics. Individuals in networks *A* and *B* vary in their social position at t_1 , but population density is the same. Green nodes represent individuals with four social connections and, in this example, only individuals with four or more connections can reproduce (one green individual in Network *A* and two green individuals in Network *B*). Networks A_i and B_i represent a subsequent generation (t_2), or time-step and, in Network A_i , there is one new individual recruited by the green individual in Network *A*, while, in Network B_i , there are two new individuals recruited by the two green individuals in Network *B*. Recruited individuals from Networks *A* and *B* to A_i and B_i are assumed to inherit qualities of their parents centrality, where only the most central individuals reproduce (Fussmann's criteria 1). As the frequency of central individuals increases over time, the difference in the average phenotype (centrality in this case) can be calculated using, for example, selection differentials or gradients (Fussmann's criteria 2). In our hypothetical example of criteria 2, the difference between the gray and blue distributions represents an increase in centrality, while the difference between gray and red histograms represents a decrease. Changes in the distribution of a trait mark an evolutionary process. If the difference in the distribution of a trait over time changes *and* this change influences population growth (λ), this is a plausible mechanistic link between ecological and evolutionary dynamics (Fussmann's criteria 3). In our example, the solid black line represents no change in λ as a function of evolution, whereas the blue-dashed line represents a scenario where the positive change in the mean value of a trait (Δ Trait) increases population growth, while the red-dashed line represents a scenario where the negative change in the mean value of a trait (Δ Trait) reduces population growth. Taken together, this hypothetical scenario highlights the potential for density-dependent social eco-evolutionary dynamics.

therefore, population density. The criteria suggested by Fussmann et al. (2007) to demonstrate an eco-evolutionary feedback include: 1) documented change of abundance over several generations, that is, changes in population density; 2) a record of genetic or phenotypic frequencies and their changes over time; and 3) a plausible mechanistic link between ecological and evolutionary dynamics.

Most animal populations fluctuate in abundance over time, thus inherently changing social network structure as individuals are born into a network and/or are removed from a network by death or dispersal. S&J highlight the proximate consequences of removing key individuals from networks, but it is also important to consider when new individuals are recruited into a population, the social position obtained, and how is their social position related to their parents social position (i.e., heritability). Assuming centrality is adaptive, and S&J deftly outline the influence of social network traits on

fitness, there is room to expand more precisely how this relationship subsequently alters population density and the eco-evolutionary consequences of this phenomenon.

Figure 1 presents one possible example. Assuming centrality is repeatable, heritable, and adaptive (Brent et al. 2013; Vander Wal et al. 2015), central individuals will yield central offspring (Figure 1, criteria 1). This is an example of behavior influencing λ and, thus, population density. As selective pressure for centrality occurs, the distribution of centrality in a population may change through time. When heritable and adaptive phenotypes influence fitness, there may be selection for more central individuals over time (Figure 1, criteria 2). Importantly, social network traits influence fitness (S&J and references therein). However, the role of population density as a mediator between social traits and fitness remains largely untested. As populations grow, changing density may influence how social network traits affect

reproduction and survival, that is, the adaptive value of the behavior (see Figure 1 in Webber and Vander Wal 2018). Mechanistic links between ecological and evolutionary dynamics occur when the change in distribution of a network trait over time (i.e., evolution) is correlated with λ (i.e., ecology). Central to the notion of eco-evolutionary dynamics is that the selection driven change in the distribution of a trait in a population correlates, or creates a feedback, with an ecological process (Smallegange and Coulson 2013). For social network traits, this means positive selection where average centrality increases due to higher population density and more individuals are recruited into the population, thus increasing λ (Figure 1, criteria 3).

Here, we rely on three notions tied to density dependence: density affects population growth; density affects network structure; and density may affect the adaptive value of social network traits. Coupling density dependence with animal social networks extends the notion of social eco-evolutionary dynamics, excellently highlighted in S&J, more precisely to the principles outlined by Fussmann et al. (2007). The field of eco-evolutionary dynamics is rapidly growing. The synergy between population density and network structure in populations that cycle or fluctuate provides a compelling framework for testing, and reasonable expectation to discover, an eco-evolutionary dynamic between the likely density-dependent adaptive value of social position and population growth (Figure 1).

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On assessing the importance of demographic change for social structure: a comment on Shizuka and Johnson

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The review by Shizuka and Johnson (2019) 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.

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, personal observations). 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 Figure 3e. Because kinship is not typically 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 depends on similarity of female reproductive state. When females are nursing young foals and come into postpartum 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