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INVITED REVIEW

How demographic processes shape animal social networks

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Abstract

Demographic processes play a key role in shaping the patterns of social relations among individuals in a population. Social network analysis is a powerful quantitative tool for assessing the social structure formed by associations between individuals. However, demographic processes are rarely accounted for in such analyses. Here, we summarize how the structure of animal social networks is shaped by the joint effects of social behavior and turnover of individuals and suggest how a deeper understanding of these processes can open new, exciting avenues for research. Death or dispersal can have the direct effect of removing an individual and all its social connections, and can also have indirect effects, spurring changes in the distribution of social connections between remaining individuals. Recruitment and integration of juveniles and immigrant into existing social networks are critical to the emergence and persistence of social network structure. Together, these behavioral responses to loss and gain of social partners may impact how societies respond to seasonal or catastrophic turnover events. The fitness consequences of social position (e.g., survival and reproductive rates) may also create feedback between the social network structure and

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demography. Understanding how social structure changes in response to turnover of individuals requires further integration between long-term field studies and network modeling methods. These efforts will likely yield new insights into the connections between social networks and life history, ecological change, and evolutionary dynamics.

Keywords: demography, network dynamics, resilience, social evolution, social structure, temporal networks, turnover

Introduction

Populations are more than a collection of individuals—they are complex systems composed not only of individuals but also the ties between them. Each individual interacts and associates with others, and such social connections can in turn affect individual behavior and fitness (Alexander 1974; Hinde 1976). While social structure—that is, the overall pattern of social relations of a population (Hinde 1976)—can be described as the product of social behavior, it is also greatly impacted by the cumulative effects of demographic processes, such as deaths, births, and dispersal. For example, factors such as survival and dispersal (and sex differences thereof) are known to influence the structure and cohesion of kin groups (e.g., Pope 1998), cooperative breeding groups (e.g., Arnold and Owens 1998), and leks (e.g., McDonald 1993). An outstanding challenge in social evolution research is to resolve how the interplay between demographic and behavioral processes generate variation in social structure across time, populations, and species.

One inevitable consequence of demographic processes is *turnover* of individuals—that is, the change in membership of a population as individuals are born, move, and die. These changes in the composition of the population will inevitably influence social structure through the loss of some social connections and the formation of new ones. Moreover, such gains and losses of individuals can further alter social structure by spurring changes in behaviors and patterns of association between remaining (or preexisting) individuals. For example, the death of a dominant individual may drive changes in patterns of associations as the remaining individuals compete for this social position (e.g., Flack et al. 2006). Similarly, the social interactions between

existing individuals and new recruits (i.e., juveniles or immigrants) may influence the size and cohesion of social groups (Ilany and Akçay 2016). Thus, the joint effects of change in population composition and the behavior of new and old individuals as a result of loss and gain of new social connections create a dynamic process that will mold the social structure within a population.

Social network analysis has emerged as a powerful quantitative framework for measuring social structure and understanding the consequences of social relations on ecology, evolution, and culture (Krause et al. 2015). Studies of animal social networks to date have largely lacked an explicit consideration of dynamics resulting from demographic processes, but we suggest that there is great potential to leverage network analysis to provide mechanistic insights into how the change in membership affects societies. The role of demographic processes in the formation and maintenance of measured social network structure is easy to overlook because the process of turnover may occur at time scales longer than the dynamic changes in social relations between existing individuals often measured by social network studies (Cantor et al. 2012). Thus, the impact of demographic processes on social structure will become more evident in *long-term network dynamics*, which we define operationally as changes in network structure that occur over timescales at which demographic processes cause significant change in membership of a population. We suggest that changes in social network structure at this timescale could be the result of the interplay between the cumulative effects of behavioral dynamics and turnover. Equally important is the observation of stability of social structure in the face of turnover, as it poses new questions about how societies maintain structure when membership changes (Shizuka et al. 2014). The impact of demographic processes on social networks may be important to consider even when not explicitly analyzing long-term dynamics because all animal societies in nature will have experienced—and will have been shaped by—these cycles of turnover in the population before being observed. Ultimately, the interplay between demographic processes and social behavior—for example, how the loss and gain of individuals affects social interactions, and how social interactions affect survival, reproduction, or movement—may have a profound impact on social networks in nature.

We argue here that the integration of demographic processes, and the social processes spurred by demographic change, into social network analyses will enrich our understanding of the causes and consequences of variation in social structure across species and populations (**Figure 1**). Investigations of the connections between demography and social networks are rapidly emerging as a frontier in social evolution research. We suggest that resolving the various effects of turnover

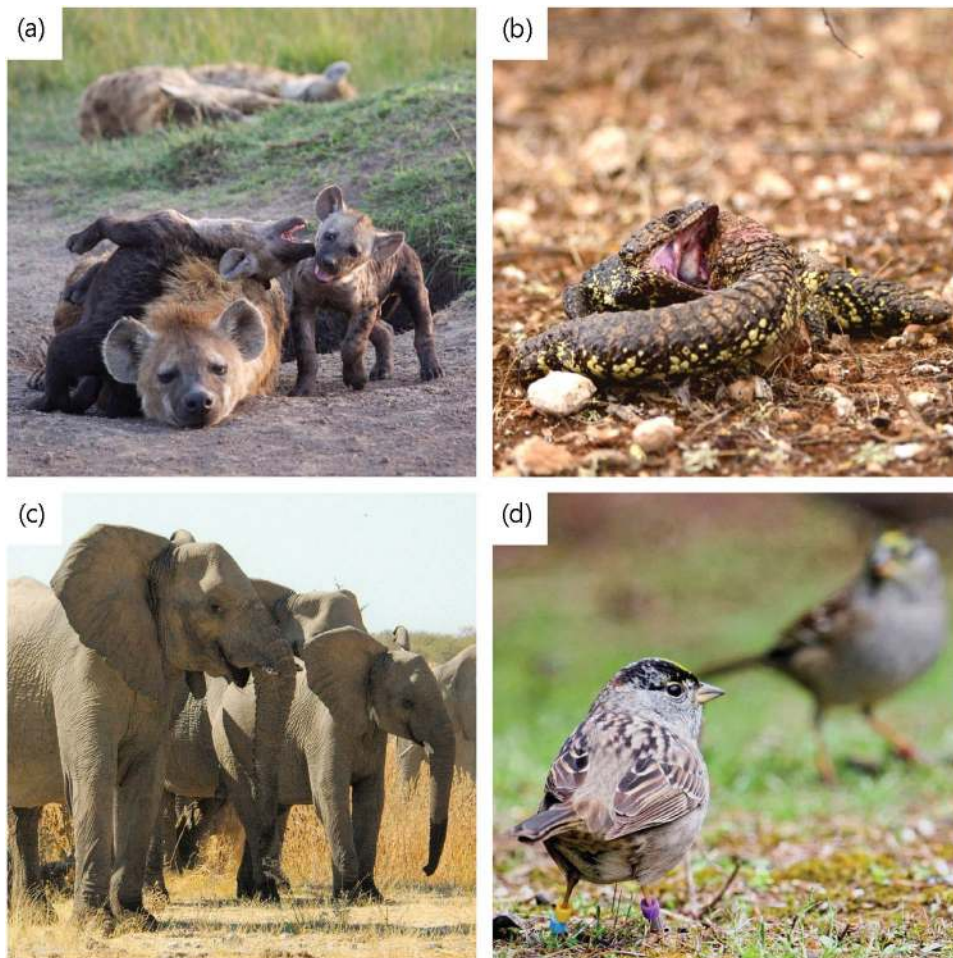


Figure 1 Variation in demographic processes across species contributes to differences in social structure. While individuals lost or gained are often excluded from social network analyses because of the difficulty mismatching networks presents for comparing network structure across time windows, these demographic processes directly impact network structure. One or more demographic processes have been integrated into a handful social network analyses across several different animal systems to better understand how social structure changes over time, including (a) spotted hyena (*Crocuta crocuta*), (b) sleepy lizard (*Tiliqua rugosa*), (c) African elephant (*Loxodonta africana*), (d) golden-crowned sparrow (*Zonotrichia atricapilla*). Photos: T. Montgomery (a), A. E. Johnson (b), K. Powell (c), and B. Lyon (d).

processes on social structure will open the door to further questions that integrate social network theory with life-history theory, ecological change, and evolutionary dynamics. Here, we first describe the key components of long-term social network dynamics in the context of animal social systems. We then review emerging evidence for the interplay between demographic and behavioral processes that influence social structure in the wild and identify some areas ripe for further investigation. Finally, we identify how careful consideration of demographic processes on social networks can open exciting new avenues for integrative research.

Key components of long-term social network dynamics

Animal social networks consist of *nodes*, representing individuals, connected by *edges*, representing social interactions or relations. Edges can be defined using various criteria, such as directly observed interactions or inferred associations using comembership in spatiotemporal groups (Croft et al. 2008; Farine and Whitehead 2015). Networks structure can be approached in multiple ways. Static networks represent the sum of social connections across a given time window creating a snapshot of the social organization. However, real social networks are dynamic systems in which interactions between individuals are constantly shifting. Advances in dynamic network analysis have created new opportunities for analyzing temporal changes of connections between a set of individuals (see Box 1 for a brief description of some statistical methods; Blonder et al. 2012; Hobson et al. 2013; Rubenstein et al. 2015). Our aim is to extend the conceptual framework of dynamic networks to explicitly include the occurrence and consequences of demographic processes.

Social and demographic processes contribute to 3 basic components of change in social networks (**Figure 2**). First, changes in social relations among existing individuals can cause changes over time in how individuals are connected—that is, the distribution of edges in a network (**Box 1**; Figure 2a). Second, death and/or dispersal of individuals away from the population can cause the loss of nodes *and* the edges to which they are connected (Figure 2b). Third, recruitment and social integration of juveniles and/or immigrants to the social network leads to the formation of new edges in the existing network (Figure 2c). In network literature, these 3 processes are often referred to

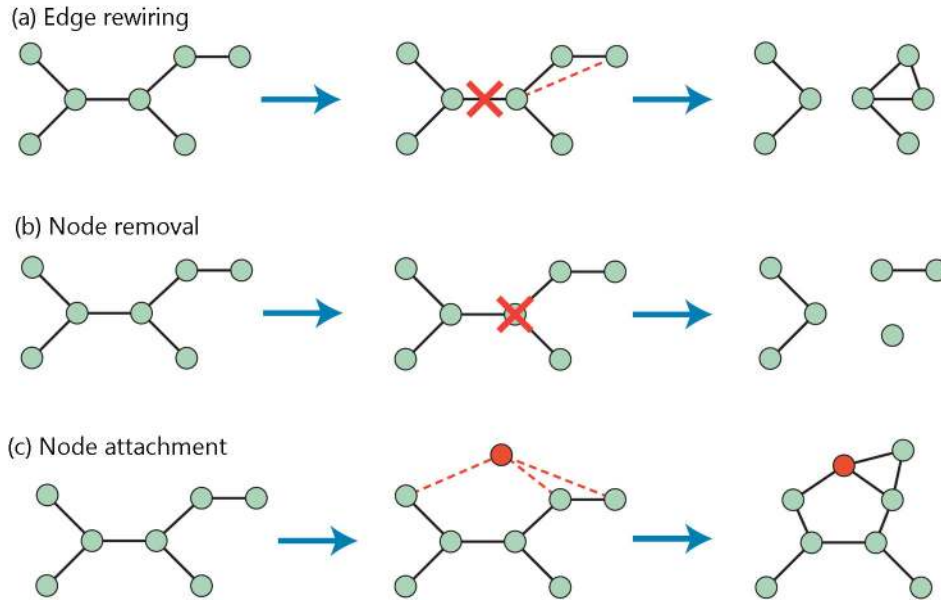


Figure 2 Three forms of change in social network structure. (a) Edge rewiring can occur through the removal and/or addition of social connections among existing nodes. (b) Node removal through death or dispersal of individuals results in the loss of all social connections of that individual. (c) Node attachment following birth or immigration results in the formation of new social connections between the new node and preexisting nodes.

as *edge dynamics*, *node removal*, and *node attachment*, respectively. The joint effect of these processes occurring in different sequences, at different temporal scales, or concurrently can cause variation in dynamics of social systems. In addition, variation at the individual level in survival, reproduction, social integration and maintenance of social connections can all affect the resulting social network structure. Finally, ecological factors such as resource distribution and abundance can affect both the behavioral and demographic processes driving edge dynamics, node loss, and node attachment, leading to change in social network structure (e.g., Henzi et al. 2009; St. Clair et al. 2015). Thus, careful consideration of how demographic processes do or do not spur change in social structure may help us better understand the mechanisms that create variation in the structure of societies in nature.

In the following section, we review studies of animal social networks that have explored the consequences of loss and gain of individuals on social structure and discuss various approaches that have employed to explore the interplay between demographic processes and social processes in structuring social networks.

Box 1. A very brief overview of network edge dynamics

While this review focuses primarily on the effects of turnover on social structure, these effects cannot be separated from ongoing short-term changes that occur as a consequence of social dynamics within a population. Addressing temporal change in social connections among existing nodes (edge dynamics) has been a key focus of network theory over the past couple decades (Holme 2015). Edge dynamics encompass edge rewiring—that is, when an individual redirects and edge from one partner to another—as well as edge deletion and edge addition. In natural societies, changes in social relations among individuals may occur on short timescales (hours or days) due to movements of individuals, or may occur on the time scale of seasons through the effects of ecological changes such as resource distribution (e.g., Henzi et al. 2009) or seasonality in social behavior (e.g., Firth and Sheldon 2016). Patterns of social connections among the same set of individuals can also change in response to ecological disturbance in some societies (birds: Lantz and Karubian 2017), while other societies are resilient to changes in ecological condition (lizards: Godfrey et al. 2013). Edge dynamics can be experimentally imposed by changing ecological factors such as resource distribution (e.g., St. Clair et al. 2015) or habitat complexity (Leu et al. 2016). We refer readers to several insightful reviews on the topic (e.g., Blonder et al. 2012; Pinter-Wollman et al. 2014; Holme 2015) for more details on causes and consequences of edge dynamics in social networks.

There are many approaches to analyzing change in patterns of edge distribution over time. Here, we describe just a handful of approaches that are widely used and

particularly pertinent to our discussion of demographic processes in social networks. One simple approach to measuring edge dynamics at the network level is to assess correlations in edges between networks from 2 different time periods using methods such as *Mantel tests* and multiple regression quadratic assignment procedure (*MRQAP*; Dekker and Krackhardt 2003). A complimentary approach is to measure and compare the duration or persistence of social ties using metrics such as *lagged association rates* (LAR; Whitehead 1995). The lagged association rate approach predates the current explosion of interest in network analysis, but effectively accomplishes the goal of measuring edge persistence. A more comprehensive and sophisticated technique is to use *stochastic actor-oriented models* (SAOMs) such as *SIENA* to model how different individual and social behavioral processes can contribute to stability or change in connections between individuals across time (Ilany et al. 2015; Fisher et al. 2017). *Time-ordered networks* provide a way to represent the complete set of information on the sequence, duration and timing of connections between individuals (Blonder et al. 2012). Dynamic network approaches can also be used to uncover temporal layers of specific network-level properties such as community structure (*CommDy*; Berger-Wolf et al. 2010; Rubenstein et al. 2015; *Dynamic Stochastic Block Models*; Matias and Miele 2017). Finally, recent developments in *Multilayer Network* approaches can be applied to investigate changes in networks across time, with different time slices treated as layers (Mucha et al. 2010; Kivelä et al. 2014; Finn et al. 2019). Not all of these approaches have been used to study animal social networks in the wild to date, but they all have potential for revealing different aspects of edge dynamics.

Demographic processes and animal social networks: a review

Direct and indirect effects of death and dispersal on social networks

The death or dispersal of individuals in a network can generate change in network structure through multiple avenues (**Figure 3**). The *direct effect* (Figure 3b) of death and dispersal is the removal of a node as well as the removal of edges connected to the lost individual. This process can change both the connectivity of the individuals that were

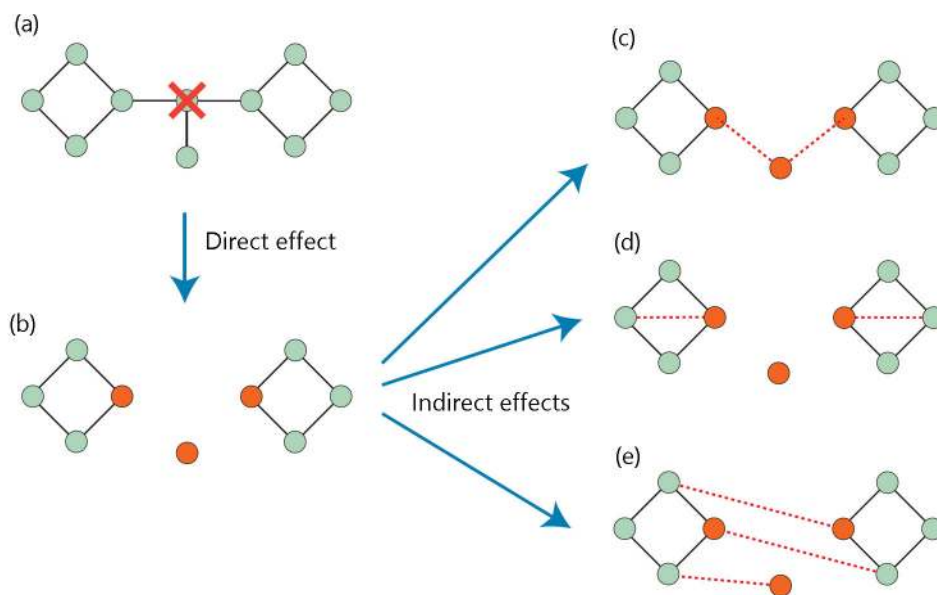


Figure 3 Simplified example of direct and indirect effects of node removal. The loss of a individual in a network (a) results in the removal of social connections that involved that individual—that is, the direct effect of node removal (b). In this case, the loss of a “bridge” individual leads to a fragmented social network. This can have further cascading indirect effects of node removal, depending on how the remaining individuals change their behavior—in particular, the individuals that were connected to the individual that was lost (orange nodes). For example, an individual may “fill” the social position of the lost individual (c), thus reestablishing the former network structure—that is, 2 clusters of nodes connected by a “bridge” individual. Alternatively, the remaining individuals may preferentially redirect their social connections toward “friends of friends” (d). This would maintain a fragmented social network, but with increased cohesion within separate clusters. Another possibility is that individuals redirect lost social connections toward random members of the population (e). This could lead to dramatically different social network structure—in this case, the collapse of distinct social clusters.

associated with the lost individual, as well as network-level properties, such as density and modularity. In some cases, loss of one individual may have drastically different consequences relative to the loss of another depending on the shape of the network and their position within it. For example, the loss of “keystone” individuals—individuals which are highly connected, dominant, and/or perform important social functions—may have a more significant effect on network structure than the loss of a random individual (Modlmeier et al. 2014). However, the direct effect of node and edge removals on network structure or function may be mitigated or exacerbated by *indirect effects*, that is, changes in behaviors or connections among remaining individuals (edge rewiring), prompted by the loss of relationships. Depending on the behavioral responses of the remaining individuals, network structure may be more or less prone to change as a consequence of the loss of individuals due to deaths and dispersal (Figure 3c–e). Different approaches—1) simulated node removals, 2) experimental removals, and 3) observations of natural mortality events—have been utilized to examine effects of removing individuals from social networks, and these approaches differ in the degree to which they capture the indirect effects of deaths and dispersal.

Simulated node removal studies only capture the direct effects of node and edge removal. (**Table 1**, part 1). In such studies, the structure of an empirical network is compared before and after simulated removal of random or targeted sets of individuals. These simulations are easy to perform computationally and have been used widely in animal social networks (Table 1, part 1). However, simulated node removals should be interpreted with caution because they assume no indirect effects of deaths and dispersal on remaining individuals—an assumption that is often violated (Blonder et al. 2012).

Experimental removals of individuals from existing social networks (Table 1, part 2), while more logistically challenging than simulated removals, have the potential to reveal both direct and indirect effects of the loss of individuals. Loss of individuals may impact the behavior of remaining individuals in several ways, leading to changes in network structure. For example, Annagiri et al. (2017) studied the effects of removing individuals from colonies of Indian queenless ant (*Diacamma indicum*) and found that experimental removals led to smaller changes in social network structure compared with simulated removals. This retention of social function and network structure was

Table 1 Examples of studies examining effects of node removal, node attachment, and turnover in animal social networks

Citation	System (population type)	Individuals removed or recruited	Main topological effects observed
1. Simulated removal only			
Fedurek and Lehmann (2017)	Olive baboon (<i>Papio anubis</i> ; wild)	Removal by age classes and at random	Removing by adult vs. juvenile has opposing effects on density, clustering, and centralization
Lusseau (2003)	Bottlenose dolphin (<i>Tursiops</i> sp.; wild)	Removal of central nodes and at random	Removal of central nodes, but not random nodes, increases diameter of network. Cluster size resilient to node removals.
Manno (2008)	Columbian ground squirrel (<i>Urocitellus columbianus</i> ; wild)	Removal of central nodes and at random	Network diameter and cluster size are more resilient to random removal than to targeted removal of central individuals
Mourier et al. (2017)	Blacktip reef shark (<i>Carcharhinidae melanopterus</i> ; wild)	Removal by centrality and by capture probability	Number of nodes in largest component is resilient to reasonable fishing pressure (<25% of individuals)
Williams and Lusseau (2006)	Killer whale (<i>Orcinus orca</i> ; wild)	Removal following fishery strategy and at random	Number of nodes in largest component is resilient to random removal but vulnerable to targeted removal
2. Experimental removal (sometimes coupled with simulated removal)			
Annagiri et al. (2017)	Indian queenless ant (<i>Diacamma indicum</i> ; captive)	Removal of central nodes	Network is resilient to experimental, but not simulated, loss of single leader
Firth et al. (2017)	Pigtailed macaque (<i>Macaca nemestrina</i> ; captive)	Random removal	Individuals that experience the loss of stronger social associates exhibited greater increase in node degree and strength compared with control individuals
Flack et al. (2006)	Great tit (<i>Parus major</i> ; wild)	Removal of policing males	Experimental removal affects mean degree, reach, degree assortativity in grooming and play networks, and clustering in proximity network
Naug (2009)	Social wasp (<i>Ropalidia marginata</i> ; captive)	Random removal	Density increased in experimental but not simulated removals
Beisner et al. (2015)	Rhesus macaque (<i>Macaca mulatta</i> ; captive)	Removal of high-ranking natal male	No change or only temporary change in aggression patterns
3. Natural removal (death and dispersal)			
Franz et al. (2015)	Yellow baboon (<i>Papio cynocephalus</i> ; wild)	Natural mortality of alpha and beta males	Little change in mean degree or clustering coefficient, and minor changes rebounded after a month
Barrett et al. (2012)	Hamadryas baboon (<i>Papio hamadryas</i> ; wild)	Natural mortality	Loss of high-ranking individual changes clustering coefficient in agonistic interactions but not grooming network. Drop in joint entropy due to removals.
Carter et al. (2009)	Eastern gray kangaroo (<i>Macropus giganteus</i> ; wild)	Natural mortality by predation	No major change in pattern of connectivity after elevated predation, but positive effect of social association on grazing disappears after member loss

4. Natural recruitment and attachment (i.e., birth or immigration)

Ilany et al. (2013)	Rock hyrax (<i>Procapra capensis</i> ; wild)	Immigration	Tendency for triads including new individuals to be unbalanced (+++)
Jarrett et al. (2018)	Vervet monkey (<i>Chlorocebus pygerythrus</i> ; wild)	Recruitment of natal juveniles	No social inheritance. Social inheritance model does not fit the data well.
Kawazoe and Sosa (2019)	Japanese Macaque (<i>Macaca fuscata</i> ; wild)	Immigration	High eigenvector centrality predicts integration success among male immigrants

5. Turnover (both removal and recruitment/attachment)

Boucherie et al. (2017)	Rook (<i>Corvus frugilegus</i> ; captive)	Natural mortality/escape; new individuals	Triadic closure and negative degree preference, but no strong effect of membership turnover
Cantor et al. (2012)	Guiana dolphin (<i>Sotalia guianensis</i> ; wild)	Emigration and immigration	Turnover of individual creates modularity in longterm networks due to associations driven by temporal overlap
Elliser and Herzing (2011)	Atlantic bottlenose dolphins (<i>Tursiops truncatus</i> ; wild)	Natural mortality or emigration and immigration	Network split into 2 communities following major turnover after hurricane. Immigrants associate with residents and integrate into network.
Farine and Sheldon (2016)	Great tits (<i>Parus major</i>), Blue tits (<i>Cyanistes caeruleus</i>), Marsh tits (<i>Poecile palustris</i>), Coal tits (<i>Periparus ater</i>), Nuthatches (<i>Sitta europaea</i>)	Natural mortality and recruitment of natal juveniles	Consistent community structure across years. Movement patterns replicated across years due to habitat geometry.
Goldenberg et al. (2016)	African elephants (<i>Loxodonta africana</i> ; wild)	Poaching older females and recruitment of natal juveniles	Oldest available individual fill central roles; social inheritance of juveniles. Social structure maintained under turnover
Ilany et al. (2015)	Spotted hyena (<i>Crocuta crocuta</i> ; wild)	Natural mortality and recruitment of natal juveniles, immigrants	Immigrant males form stronger bonds than natal males and associate more with other immigrants
Shizuka et al. (2014)	Golden-crowned sparrows (<i>Zonotrichia atricapilla</i> ; wild)	Natural mortality and immigration	Consistent community structure across years. Returning individuals form communities with same individuals as previous year, newer individuals join those communities.

attributed to changes in individual behavior following removals: individuals expressing leadership at low levels prior to removals increased their leading behavior, replacing the function of the lost individuals through network rewiring (i.e., Figure 3c). Similar dynamics have been shown in other systems such as social spiders, *Stegodyphus dumicola*, where removing and replacing shy individuals (but not bold individuals) have large effects on collective prey capture rate (Pinter-Wollman et al. 2017). While network structure was not measured explicitly, this functional change likely reflects network dynamics similar to what is seen in ants (Annagiri et al. 2017). Removal of individuals may also specifically affect the behavior of those individuals that experience the loss of social partners. For example, Firth et al. (2017) used temporary removals of individuals in great tits (*Parus major*) to show that individuals who lost their strong associates responded by increasing social associations with new individuals and strengthening existing ties. Thus, variations between systems in individual responses to partner loss could generate differences in how network structure responds to demographic change across time.

While experimental removals can reveal how the sudden disappearance of a member affects remaining social connections, it may still fail to adequately capture social network dynamics that occur under natural loss due to mortality or dispersal (Table 1, part 3). For example, Franz et al. (2015) showed that natural mortality of high-ranking males did not lead to dramatic changes in network structure in baboons (*Papio cynocephalus*). This stands in contrast to findings of the experimental study of pigtailed macaques (*Macaca nemestrina*) by Flack et al. (2006) in which the network structure changed drastically after the removal of socially important individuals. One explanation for discrepancies between experimental and natural node removals is that the timeline of experimental studies may be too short, such that a reaction to a perturbation may not represent the long-term effects node loss (Franz et al. 2015). Another confounding effect is that group members in natural populations may be able to anticipate the looming death or dispersal of other members, for example, when these forms of individual loss are driven by observable traits such as condition or disease. Senescence may induce changes in network position, such that when a formerly central or keystone individual dies it has already moved to the periphery of the network. Thus,

large, dramatic changes in network structure from one time step to another may only occur very rarely in nature, when certain members die unexpectedly while they are occupying a functionally important social position, or when demographic or environmental stochasticity causes the death of a critical number of members (Hannon et al. 1985; Lazaro-Perea et al. 2000). Long-term studies may thus be critical for adequately addressing the how social network structure responds to the removal or loss of individuals in long-lived systems.

Recruitment and integration of new individuals into an existing social network

Network theoreticians have long considered how the addition of new nodes impacts network structure. A number of models have been developed to explore how different network patterns emerge from the processes governing how a new individual establishes connections to an existing social network (such as homophily or preferential attachment: Barabási and Albert 1999; Jackson and Rogers 2007). However, such network growth models typically do not reflect natural population dynamics in which both gains and losses of individuals occur due to demographic processes.

A simulation model proposed by Ilany and Akçay (2016) provides a good starting point for understanding how the interplay between the process of social integration and turnover of individuals affect social network dynamics. In this model, a random individual dies and an offspring is born to a randomly chosen mother in each time step. Two parameters govern the subsequent social integration process: offspring inherit the social relations of their mother with some probability (P_n) and establishes a novel connection with random individuals with probability (P_r). Large values of P_n represents the social inheritance of affiliates (Figure 4a). Ilany and Akçay (2016) show that differences in these 2 parameters alone are sufficient to generate large variations in network structural properties such as community structure and trait assortment and cause network structure to deviate substantially from a random network (**Figure 4**). Cantor and Farine (2018) use a similar approach to model how foraging rules, combined with social inheritance of network ties, can promote the emergence of stable social groups that are maintained over generations. In this model, initially

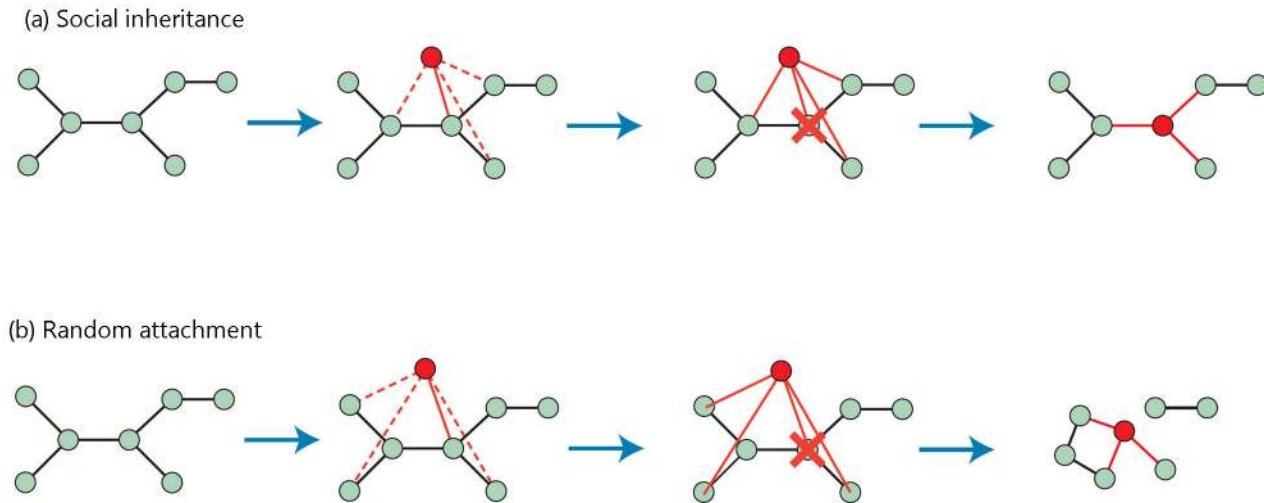


Figure 4 Social process of node attachment affects outcome of turnover. (a) Under social inheritance, the new recruit (red node) is initially attached to the parent (solid red line), as well as the associates of its parent (dashed red line). If the parent node dies, then the new recruit ends up replacing its position, maintaining robustness in social network structure. (b) When new recruits form random connections to existing nodes, then the network structure may change substantially.

inherited ties can persist or be broken based on success in group foraging. Thus, this model begins to incorporate the effects of dispersal in cross-generational dynamics of social networks. This framework for modeling opens new avenues for asking how social networks assemble and change (or not) in response to turnover of members and promises to elucidate how demography and social processes interact to shape social networks. This type of modeling approach also sets the stage for further exploration on the *relative* effects of social and demographic dynamics on social structure. For example, under what conditions do the effects of short-term social dynamics within populations obscure the effects of turnover on social structure? What is needed now is a deeper empirical understanding of the social processes that govern node attachment in natural systems that can then be incorporated into future network models.

To date, a small number of empirical studies have directly addressed how new individuals integrate into existing social networks of animals in the wild. In African elephants (*Loxodonta africana*), juvenile females explore and develop social ties in part by associating with their mother's associates, leading to vertical transmission of social

hierarchy (Goldenberg et al. 2016). Such vertical transmission of social connections could occur by very simple mechanisms such as the similarity of spatial movement patterns of parents and offspring or through social processes akin to “social introductions” that occur in humans (Jackson and Rogers 2007). In contrast, grooming networks of free-living adult vervet monkeys are not stable over time, and the grooming networks for young females are not predicted by that of their mother (Jarrett et al. 2018). While young females are similar to their mothers in amount of grooming received and given, young females associate more with their own age cohort rather than maternal associates, a pattern of behavior which may promote network change as the population ages and turns over. Less is known about how immigrants integrate into an existing social network, perhaps due in part to the logistical difficulty of studying new, unmarked individuals during the immigration process. However, one recent study on wild Japanese macaques (*Macaca fuscata*) identified centrality in male–male affiliative relationships as a key parameter predicting successful social integration of immigrants (Kawazoe and Sosa 2019). In contrast, immigrant males in spotted hyenas tend to form associations with other immigrants (Ilany et al. 2015). We anticipate that the study of social integration of both juveniles and immigrants will continue to be an important area of exploration for understanding long-term social network dynamics.

Responses of social networks to different turnover rates

We posit that variations in social processes underlying the responses of individuals to loss of partners as well as the integration of new individuals may result in variations in responses of social networks to different rates of turnover. To date, theoretical studies have explored social structure at an equilibrium state emerging from gradual turnover of individuals (i.e., loss of one individual succeeded by gain of one individual: e.g., Jackson and Rogers 2007; Ilany and Akçay 2016). While some animal systems may experience such gradual rates of turnover, other systems experience turnover in large pulses—i.e., if there are discrete reproductive seasons, periods of high mortality, or increased rates of turnover due to catastrophic events. How might social networks vary in their response to high rates of turnover?

Some systems consistently experience high levels of turnover without massive reorganization of the social network. For example, Shizuka et al. (2014) and Farine and Sheldon (2016) both found that winter social networks of songbirds (migrant golden-crowned sparrows, *Zonotrichia atricapilla*, and resident species including tits and nuthatches) had consistent structure across years despite 30–50% turnover of individuals annually (typical for small birds). In these cases, the stability of social networks may be due to high levels of consistency in social connections among surviving birds, combined with predictable patterns of social integration of new individuals each year. Similarly, Goldenberg et al. (2016) found that some aspects of hierarchical community structure of African elephant social networks were preserved despite high turnover during years of high poaching intensity. In this case, the details of how young females initiate and develop social connections starting with their mother's associates may contribute to the stability of social structure across generations.

Other systems exhibit large-scale reorganization of social networks following a period of elevated turnover rate of individuals. For example, Elliser and Herzing (2011) observed the social network of Atlantic bottlenose dolphins (*Tursiops truncatus*) before and after a hurricane that led to 50% loss of adults (due to either mortality or emigration). They found that immigrant individuals integrated into the existing network (rather than forming a separate community). Nevertheless, the social network fissioned into 2 communities following the turnover event. Presumably, the massive loss of individuals during the hurricane removed key individuals that had kept the population in one cohesive unit, and immigrants failed to replace the social roles of these individuals. Thus, animal social networks exhibit differing levels of change in response to turnover. Uncovering the causes of such variation requires a deeper understanding of the behavioral responses to deaths, births, and dispersals in the population.

The potential for feedback between network structure and fitness consequences of social position

We have thus far considered the effects of loss and gain of individuals on social network structure. However, there are also effects of network structure on fitness, that is, when variation in social position

causes differential survival, reproductive success, or dispersal. Thus, there may be scope for social eco-evolutionary dynamics (Pelletier et al. 2009) to emerge in animal social networks. For example, systems in which highly central individuals suffer lower survival may have much more dynamic social structure than systems in which peripheral individuals are more likely to die off (Modlmeier et al. 2014). The resulting variation in social network dynamics could also result in differences in how selection operates on traits and behaviors that affect centrality and the duration of tenure of animals in central network positions. Similarly, societies with increased reproduction by central individuals, coupled with social inheritance of social networks, could generate vastly different social networks than systems in which reproduction does not depend on network position.

Emerging work illustrates that survival can be linked to social network position in a variety of ways, depending on the system. Social network analysis of mammalian societies have shown that survival may be positively correlated with centrality of individuals (Barbary macaques: Lehmann et al. 2015; feral horse: Nuñez et al. 2015), negatively correlated with centrality (Bottlenose dolphins: Stanton and Mann 2012), negatively correlated with variance in edge weights (Rock hyrax: Barocas et al. 2011), or positively associated with stability or quality of social connections (Chacma baboons: Silk et al. 2010; Barbary macaques: McFarland and Majolo 2013; Blue monkeys: Thompson and Cords 2018). Such variation observed across systems makes sense when you consider the dramatic differences in social/ breeding systems observed across species: for example, in some systems rank can increase longevity, while in others high rank may come at the cost of reduced survival (Sapolsky 2005).

Just as survival may be correlated with network position, the production of offspring is often influenced by social position. Rank is often found to have a positive impact on a female's ability to produce surviving young (e.g., Pusey et al. 1997). Only a handful of studies have specifically addressed how position in a social network relates to reproductive success, but these studies also illustrate the wide variety of ways social interactions can impact reproductive success. For example, social conflict (heterogeneity of association strengths) negatively impacts female fitness in degus (*Octodon degus*; Wey et al. 2013), female yellow-bellied marmots with lower affiliation strengths have

higher reproductive success (Wey and Blumstein 2012), and greater social lability in house finches during the nonbreeding season is correlated with greater pairing success in the breeding season (Oh and Badyaev 2010).

Here, we only briefly address how network position may impact survival and reproduction, but an individual's position within a social group and their patterns of association may also impact the sex of offspring they produce, the likelihood of dispersal away from the group, and their potential to integrate into a new society following dispersal. An exciting prospect is to extend these studies to investigate how such fitness consequences of social position influence the long-term dynamics of social network structure. This is a ripe area for both empirical and theoretical exploration.

Opportunities for future research

Integration of demography and social behavior in studies of animal societies presents some exciting opportunities for future avenues to connect the study of social networks with larger fields within ecology and evolution. Here, we identify a few key opportunities for linking network dynamics to life history theory, population dynamics, evolutionary dynamics, and mining long-term datasets.

Towards a life history theory of social networks

An integrative view of long-term social network dynamics highlights the potential importance of life history traits on social network structure. If deaths, births, and dispersal matter for social network structure, then variation across species and populations in overlap of generations, survivorship patterns, life span, senescence, reproductive strategies, dispersal strategies, etc., ought to contribute to variation in social network structure. For example, the life-history hypothesis for the evolution of cooperative breeding posits that low adult mortality predisposes some avian species toward the formation of cooperative social groups (Arnold and Owens 1998). Another example for the connection between life history and social networks is found in killer whales (*Orcinus orca*), where there is a strong correlation between prolonged postreproductive lifespan and position in a

leadership network—postreproductive females lead groups, and the presence of such leaders influences the survival of other members of the group (Brent et al. 2015). Other connections between life history and social networks have yet to be explored. For example, deaths of associates may have a relatively larger impact on the behavior of survivors when most individuals live to older age (i.e., Type I survivorship curve) compared with populations where most individuals die young (i.e., Type III survivorship curve) because of the longer duration (and perhaps fitness consequence) of social connections. In another example, if the sex of individuals influences their patterns of associations, then patterns of sex-biased dispersal will also influence the process of node attachment when an immigrant joins a population. There are myriad ways in which consideration of the life history of the system will impact how a social network is assembled and is changed through the turnover of individuals. We feel this is a very rich area of research that is ripe for exploration. Gaining a more cohesive understanding of how the process of turnover of individuals impacts social networks is one of the first steps toward developing this framework.

Predicting the responses of animal social systems to ecological change

Social networks are influenced by ecological change, but how exactly does ecology impact societies? We suggest that there are 2 potential pathways by which ecological change could affect social networks: 1) environmental effects on social dynamics, and 2) ecological effects on demographic (turnover) rates. Emerging evidence suggests both effects occur in nature. Changes in connectivity between existing individuals (i.e., edge dynamics) occur in response to changes in resource distribution and habitat complexity (Ansmann et al. 2012; St Clair et al. 2015; Leu et al. 2016; He et al. 2019), seasonal fluctuations in resource abundance (e.g., Henzi et al. 2009), and ecological disturbance such as fires (Lantz and Karubian 2017). Fine-scale measurements of social interactions using new data-logging techniques can provide particularly clear pictures of how environment affects social dynamics. For example, St Clair et al. (2015) coupled wireless sensor technology with an experimental resource pulse to pinpoint the temporal scale of edge dynamics such as the duration of altered association patterns as well as diurnal patterns of change.

Meanwhile, large-scale ecological change can alter population dynamics, which will likely affect social networks through demographic processes. These demographic effects that regulate and shape social network structures should not be ignored. We suggest that adopting an integrative view of how ecology affects both behavioral and demographic processes will help us resolve how and when social systems will respond to ecological change. Are some systems more stable despite shrinking population sizes because certain behavioral processes such as social inheritance maintain social structure in the face of turnover (Ilany and Akçay 2016)? Are there thresholds of ecological change that leads to the breakdown or shifts in social network structure (e.g., dolphin populations before and after a hurricane: Ellisler and Herzing 2011), and if so, how might ongoing anthropogenic change affect social systems? The potential causes of robustness and resilience have been a source of debate in ecological systems and socioecological systems (Gunderson 2000; Folke 2006). We suggest that such links between social and ecological resilience may be important for animal societies as well. This may become a more pressing question as large-scale ecological change and population decline become increasingly severe with ongoing anthropogenic change.

Evolutionary implications of turnover and social structure

The evolution of social behavior, socially selected traits, and cultural traits are influenced by social structure. Accordingly, turnover of individuals and fluctuations in social structure have the potential to cause fluctuations in selection on social behavior as well as traits that mediate social interactions. For example, network structure affects the dynamics of selection on cooperative behavior (e.g., Ohtsuki et al. 2006). More recent evidence suggests that dynamic social networks with births and deaths can substantially affect the spread of cooperation across time (Akçay 2018). The dynamics of social selection can also be influenced by patterns of clustering and assortment of traits within the social network (Farine et al. 2015). As such, long-term fluctuations in social network structure could relate to fluctuations in selection on socially selected traits (e.g., Chaine and Lyon 2008). A more explicit understanding of how demographic change relates to social structure could help reveal whether long-term dynamics of social networks translate into long-term dynamics of social evolution.

Integration of long-term field studies with network models

One implication of this perspective is that long-term field research is indispensable to understanding how behavioral and demographic processes interact to shape animal societies (Clutton-Brock and Sheldon 2010). Observing the assembly and resilience of natural social networks often requires long-term research on social interactions within populations and coupling these data with demography. Mining existing data from long-term studies may be one avenue for exploring some of the interplay between behavior and demography. In fact, we have already highlighted here several key examples of success in using long-term field data to elucidate important social processes underlying social network resilience (e.g., Ilany et al. 2015; Goldenberg et al. 2016). There is vast potential to dig further into existing long-term datasets to uncover the interplay between behavior and demography that contributes to social network structure. For example, it may also be feasible in some systems to measure how the loss of an individual(s) spurs change in social behavior and connections of remaining individuals. As highlighted above, experimental studies have already demonstrated that removal of individuals can change the behavior of survivors to whom they were associated (Flack et al. 2006; Firth et al. 2017), and there is evidence that loss of key individuals can change social dynamics within cooperative breeding groups (e.g., Hannon et al. 1985; Lazaro-Perea et al. 2000). Social primate literature illustrates the substantial impact mortality can have on patterns of association in natural populations (Engh et al. 2006; Seyfarth and Cheney 2013). Similarly, long-term population studies will be critical in documenting the process of social integration of juveniles and immigrants. An intriguing possibility would be to leverage recent innovations in automated technologies (e.g., miniature and long-lasting animal tracking devices, proximity sensors, etc.; Krause et al. 2013) with ongoing long-term studies to detect fine-scale behavioral responses to demographic change. This may also enable us to ask whether the relative importance of the cumulative effects of short-term social dynamics and demographic processes in shaping social structure. Finally, long-term research has the potential to reveal rare events of dramatic change in social network structure within a population. These events could help reveal the processes governing the response of social networks

to ecological or demographic change (see "*Predicting the responses of animal social systems to ecological change*").

Conclusion

Social network theory has brought many new insights into the patterns of social organization in animal systems. However, to fully leverage network approaches to understand the processes underlying the structure and resilience of animal societies, we will need to embrace the demographic processes that affect all populations of organisms. This will require merging the rapid progress in quantitative approaches from network theory, particularly temporal/ dynamic network approaches, with careful natural history observations of animal populations over multiple generations. Long-term field studies are required because the natural process of turnover of the social network occurs over generations, and experimental manipulation alone is insufficient to understand how animals respond to network changes. Application of network analysis approaches to long-term empirical data can help reveal the interplay between demographic events (e.g., deaths and births) with its ripple effects on the rest of the network through rewiring of social connections. Network models can help us understand how node loss and attachment, combined with even simple social processes (e.g., social inheritance) can generate complexity and variation in social systems (Ilany and Akçay 2016; Cantor and Farine 2018).

We believe this integrative approach towards longitudinal social network dynamics will provide valuable insights into the causes and consequences of social stability. Considering the interplay of demography and social processes can provide a life history perspective on variations in social networks and help us predict ecological resilience of social systems. Moreover, long-term dynamics of social networks will likely influence all social evolution. As we uncover more implications of animal social networks in the wild, we should work to consider how those implications play out over generations as the population, and the social network, undergoes the inevitable processes of death, birth, and dispersal of its members.

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