Trends in Ecology & Evolution

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Opinion

Animal Social Network Theory Can Help Wildlife Conservation

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Many animals preferentially associate with certain other individuals. This social structuring can influence how populations respond to changes to their environment, thus making network analysis a promising technique for understanding, predicting, and potentially manipulating population dynamics. Various network statistics can correlate with individual fitness components and key population-level processes, yet the logical role and formal application of animal social network theory for conservation and management have not been well articulated. We outline how understanding of direct and indirect relationships between animals can be profitably applied by wildlife managers and conservationists. By doing so, we aim to stimulate the development and implementation of practical tools for wildlife conservation and management and to inspire novel behavioral research in this field.

Trends

Understanding social network structure and position can aid wildlife conservation.

Threatened wildlife populations offer a vital experimental platform for animal SNA.

Linking animal SNA to practice stimulates design of new practical tools and theory.

Introduction

While it is well-recognized that behavioral biology has much to contribute to conservation biology [1–3], the usefulness of animal social network analysis (SNA; Box 1) as a conservation tool has not been addressed. Natural selection can mold received, self-initiated, and indirect social bonds [4–7]. These findings thus imply that animal social network structures might be adapted to the current selective environment, leaving populations vulnerable when these environments rapidly change. Indeed, wildlife population viability strongly depends on the social wiring of a population, and any process that disrupts patterns of social connectivity and stability can have severe consequences [7,8]. Such processes and their consequences for populations urgently need to be better quantified, predicted, and understood. In our opinion, SNA is a valuable tool to assist in this task.

We show the utility of animal social networks in conservation and management by using the conceptual framework introduced by Berger-Tal *et al.* ([9]; see also [3]). The framework focuses on three interconnected themes that we reframe to illustrate the importance of social networks. The features of an animal social network can:

1. Serve as indicators of a society's state, which is valuable for monitoring wild populations. When certain social structures are inherently unstable, they can be used as important indicators of impending group break up or collapse.
2. Aid in identifying how anthropogenic impacts affect group stability and viability. Overharvesting and fragmentation can break apart groups and interfere with demographically important social processes.
3. Help design relationship-based management strategies for animal populations, including threatened as well as 'problem' populations. An understanding of the social structure can

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guide interventions to prevent social transmission of problem behavior and help to plan the most effective reintroductions.

We provide examples for each category while acknowledging that some examples might fit multiple categories. By integrating current knowledge and ideas on animal social networks into this framework, we present a road map that together with existing approaches offers vital tools for evidence-based decision making. This road map can guide researchers toward experimental platforms to test fundamental theories and predictions in animal social network theory as well as benefit wildlife conservation and management. Many of the topics we address are still in dire need of (more) research, a point that is reflected by the unequal lengths of the topics we discuss. With this paper, we hope to encourage researchers to especially target these topics.

Animal Social Networks As Indicators for Nature Conservation

Behavioral indicators can either give information on population status, such as providing an early warning of an impending population crash or social fragmentation, or can be used to evaluate the effectiveness of a management action, such as changes in reserve design [9]. Social network metrics can be used as such indicators, for example, to indicate a stable group structure, since a lack of social stability is known to have a detrimental effect on individual fitness in some species (e.g., horses *Equus caballus* [10]).

Social stability can not only be expressed in terms of long-term stability of group composition, sexual and social partner relationships, family units, coalitions, or otherwise relevant social substructures, but also in terms of the relative quantity and distribution of aggressive and affiliative interactions occurring within the population. Several established social network metrics can be used as analytical tools (Box 2) to monitor and test whether the social dynamics within a population are changing and which individuals or processes are likely to be the cause (Figure 1). For example, changes to subpopulation modularity (community detection, Box 2) or social cohesion in Bechstein's bats *Myotis bechsteinii* and killer whales *Orcinus orca* indicated significant population-level changes [11,12]. In addition, individual-based metrics can serve as important indicators. One example can be seen in white-faced capuchin monkeys *Cebus capucinus imitator*, in which infants from highly social and more central females have higher survival chances in stable periods, yet during alpha male replacements are most likely to fall victim to infanticide [13].

Box 1. An Animal Social Networks Primer

Animal SNA is an approach to representing and analyzing the patterns of social connections of a population, and provides descriptive methods for testing a range of hypotheses relating to social structure [53]. In a network, the nodes represent individual animals, while the connections represent social interactions or associations. These connections are often weighted to represent the preference or frequency of association. Examination of direct dyadic interactions between pairs of individuals can tell us about assortment and differential preferences between individuals. However, SNA allows us to go beyond the dyads and examine the importance of patterns of sociality that also consider indirect connections [6]. For example, the SNA approach can be used to examine the flow of information or spread of disease through different social structures [29,54]. Indirect connections can also allow the examination of clusters (e.g., mutual friends might be more likely to be connected), or the social position of different types of individuals.

Networks are often analyzed as static snapshots over a given time interval, but we are starting to move in the direction of more dynamic analyses of how social structure changes over time. Thus, rather than merely studying the presence of social ties over a given period, the changes in these ties in time become the targets of analyses [52,55]. Dynamic SNA will be key to understand how wildlife populations might socially adapt to human-induced spatiotemporal fluctuations in the environment, even more so when species are characterized by living in fission–fusion societies. Next to more traditional observation methods, new and advanced technologies (Figure IA) allow efficient collection of vast amounts of animal movement and proximity data [18], enabling and easing the quantification of animal social networks, their dynamics, and their consequences for groups as well as populations. In some systems, observing or tracking just 10% of the population can be sufficient to obtain a reasonable indication of the specific network metrics [25].

SNA has been used across a wide range of taxa, both in captivity and in the wild; although studies on cetaceans and primates are perhaps best known, ungulates, birds, carnivores, rodents, bats, reptiles, fish, and invertebrates have also been studied [55] (Figure IB). SNA can be especially useful in populations in which the preferred (or avoided) social partners (i.e., the social ties) are not immediately evident (e.g., fission–fusion), but its relevance is certainly not restricted to highly social populations [28,29,56].

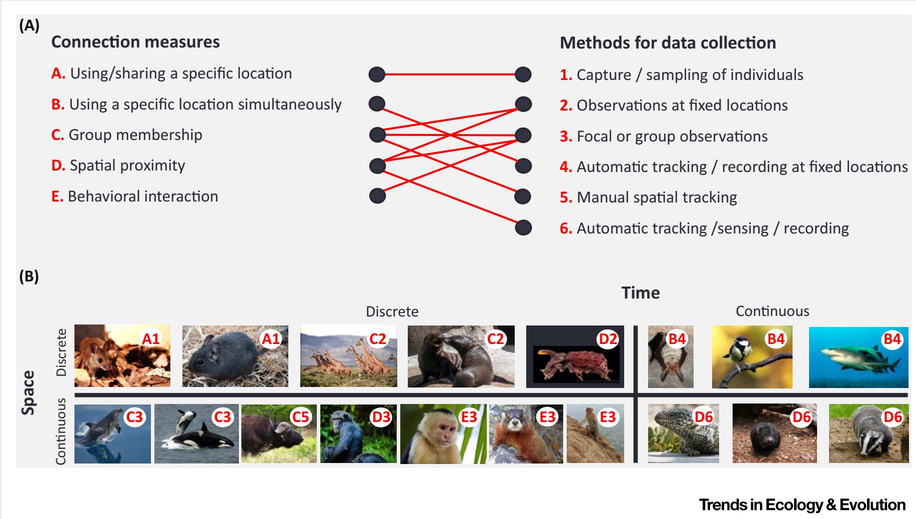

Figure I. Measures and Methods for Documenting Social Networks of Animals in the Wild. (A) A number of measures and methods are currently used to quantify social links between animals in the wild. The measures and methods mentioned here have all been used in the studies we refer to throughout this paper. This is, however, not meant to be an exhaustive list for animal social network analysis. Moreover, not all methods allow for all types of measures to be used and vice versa (red links were used by the wildlife studies we discuss). Ideally, one quantifies behavioral interactions between individuals to infer social links, but since this is often practically challenging other measures are used as proxies. Some of these measures (e.g., simultaneous use of location) have the advantage that they can be gathered via technologies that allow for the collection of large data sets (e.g., location-dependent automatic tracking). However, the rapid development of accelerometers and animal-borne cameras is likely to soon make this possible for behavioral interactions. (B) The social network studies discussed here have gathered social network data for 18 different species in the wild. The associated principal measure and method for each species are mentioned in the white balloon of the picture. We have categorized these species by whether the methods allowed discrete or continuous data collection in time and space. Please note that in reality there is no hard line, there is a continuum between discrete and continuous data collection in both space and time. For example, spatial data collection ranges from using fixed locations to transects to locally or globally tracking the animals. Categorization was thus purely done for visualization purposes. Species examined, starting top left corner and going clockwise: yellow-necked mouse *Apodemus flavicollis*, degu, giraffe *Giraffa camelopardalis*, California sea lion, forked fungus beetle *Bolitotherus cornutus*, Bechstein's bat, great tit *Parus major,* lemon shark *Negaprion brevirostris*, Eurasian badger, Tasmanian devil, sleepy lizard, rhesus macaque *Macaca mulatta*, yellow-bellied marmot *Marmota flaviventer*, white-faced capuchin monkey, chimpanzee, African buffalo *Syncerus caffer*, killer whale, and bottlenose dolphin *Tursiops* spp. (credit fungus beetle, Macroscopic solutions; lemon shark, Albert Kok CC BY-SA 3.0; Pixabay).

Connectivity is likely to be an important predictor of population resilience [14] and is regarded as a guiding principle in conservation planning. Specific sites and areas such as fish passages, dens, roost trees, or migratory stopover sites can connect subpopulations [15,16]. Habitat network analysis, incorporating species-specific habitat use and local and long-distance movement data, has proved to be a powerful tool to identify important stepping stones for connectivity [15,17]. However, the next important step would be to investigate whether these habitat network analyses, which focus primarily on estimated spatial connectivity, can be complemented by SNA, which focuses specifically on social connectivity. Continuous spatial tracking in combination with SNA [18] might allow us to identify both locations and individuals

Box 2. Why Use Animal SNA in Wildlife Conservation and Management?

Managers and conservationists can use animal SNA to inform themselves about important changes in social systems, and can potentially identify warning signs of impending detrimental change. Such changes are less detectable using methods purely based on population size or dyadic relationships, because these alone do not provide an understanding of the overall societal structure. Often, the majority of connections that hold together a population network is indirect. There are many different network statistics that can be used to assess potentially unfavorable changes in the structure of dynamic networks (Table I). All statistics are best used on weighted networks where connections are based on relative frequency or strength rather than binary presence/absence.

To give an example, resident killer whales of the Salish Sea face what conservationists say is their biggest threat to date: 1000 km of new pipeline from Alberta to Vancouver's coastline, which will increase tanker traffic. A network approach would show whether the increased tanker traffic negatively impacts their social structure by, for example, increasing social fragmentation measured through density, components, and community structure (Table I). Closer inspection of the community structure could reveal fragmentation of extended family groups on which they are dependent for protection and successful foraging [22].

Table I. Relevant Social Network Statistics for Wildlife Conservation and Management

Statistic	What does it do?	What do changes indicate?
Density	Measures the number of connections in a network as a proportion of the number of possible connections.	The network is becoming more connected (more socially integrated) or less connected (more socially fragmented).
Community detection	Measures the number of communities in a population (along with their membership). Communities are closely connected clusters of individuals that are less well connected outside of the community.	The population is becoming more socially integrated as the number of components increases, and more group oriented as it decreases. Some communities will become components (see below) as the network fragments or becomes more socially differentiated.
Component detection	Measures the number of communities that are entirely disconnected from the rest of the network.	Similar to community detection, but more severe. As the number of components that include more than one individual increases, the network will have subgroups that are not connected to the rest of the population.
Betweenness centrality	Indicates the potential for flow of (for example) information or disease, through each individual or group in the network.	Certain individuals become more, or less, important for network flow.
Time-lagged association rate	Measures the stability of associations over time by correlating future connections between pairs of individuals with past connections.	As the measure decreases, the social structure is becoming less stable over time. As the measure increases, associations are becoming more stable (and potentially more socially differentiated).

that form crucial social bridges between subpopulations. Incorporating social connectivity will therefore contribute more fine-scale information on effective connectivity.

Although effects of the social structure on total population viability are to be expected [19], concrete evidence is still mostly lacking. Individual fitness effects of social network position have been revealed [4,5,13,20], but these might cancel each other out in large populations. Small populations, however, will be much more sensitive to fluctuations in individual fitness that are a consequence of social structuring. Especially, but not exclusively, species that occur in unnaturally small populations or social groups, have a high reliance on (rigidly structured) sociality and have a low reproduction rate, can be vulnerable to sudden population crashes resulting from changes in social structure. Social network monitoring to verify social cohesion for such species is likely to be important, particularly if by doing so interventions can maintain or restore cohesion.

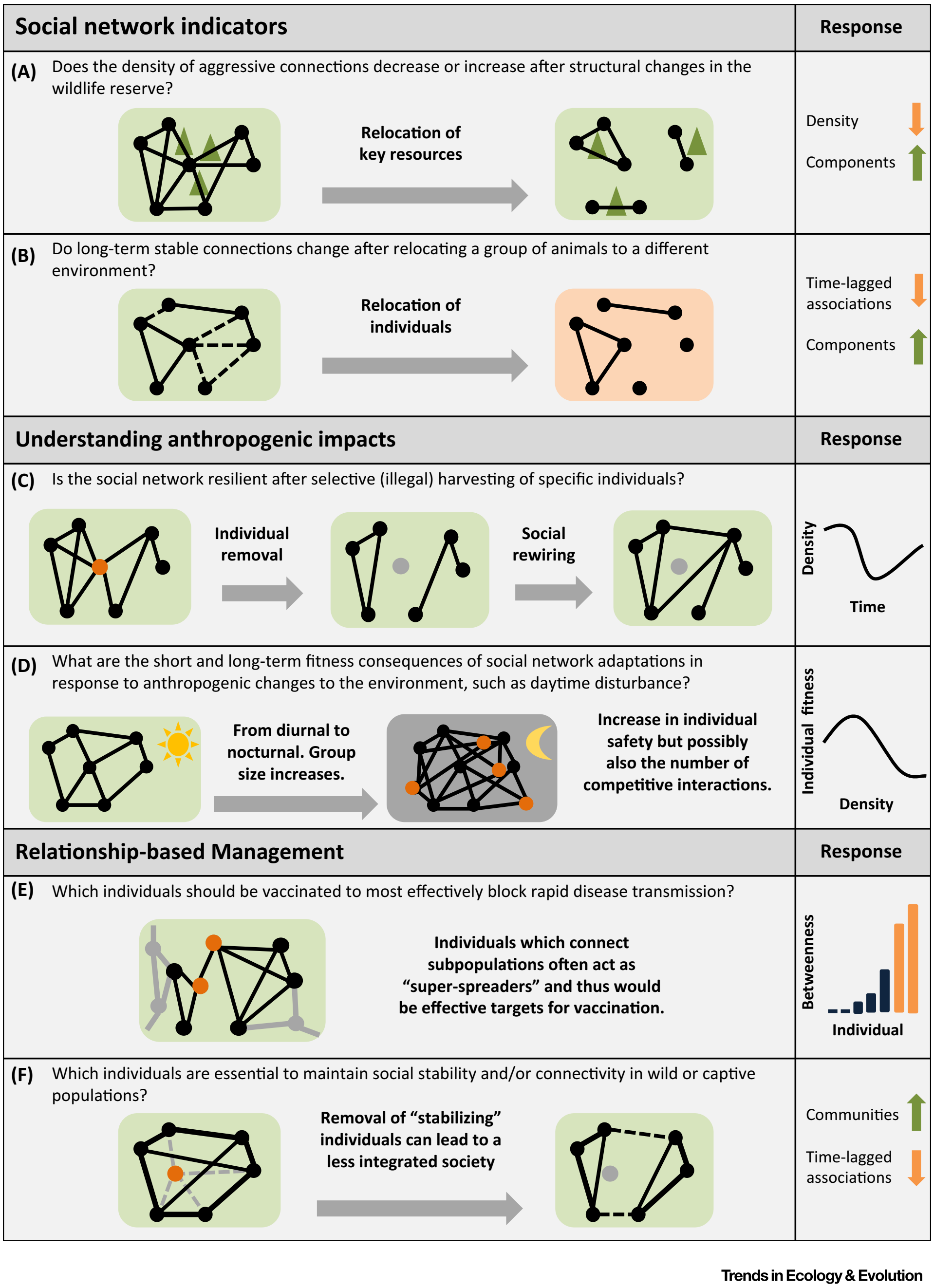

Figure 1. Linking Wildlife Conservation Questions with Animal Social Network Dynamics Can Aid Wildlife Conservation and Management. The left column shows a social network representation of relevant wildlife conservation and management questions. The right column shows how answers to such questions could be quantified using social network statistics. (A) Animals which form territories around essential resources might show a high density of agonistic interactions when these resources are clumped. SNA could indicate whether redistributing resources is an effective management intervention to decrease the density of aggressive interactions. (B) Groups of animals are regularly relocated to aid conservation projects. SNA can reveal the social structure before relocation and might be used to evaluate if the structure remains intact. (C) When individuals with specific traits and associated social roles are favored by (illegal) harvesters, social groups might fragment. SNA can be employed to understand if this fragmentation will be temporary or permanent. These data might even help predict impending collapse of specific populations when certain individuals are expected to disappear soon. (D) Many animals adjust their behavior in response to anthropogenic disturbance. For example, some social foragers are known to be flexible in the time of day they forage. When they change to nocturnal

(Figure legend continued on the bottom of the next page.)

Understanding Anthropogenic Impact through Animal Social Networks

Quantification of social structures can help predict how populations will respond to certain disturbances that could cause a population to fragment or crash. To be stable, social networks will require a degree of flexibility to withstand deviations in social bond strength, for example, those that are occurring due to predictable seasonal changes in the distribution or availability of resources [21]. A baseline social structure will be necessary to detect such deviations and to estimate what level of deviation is considered normal. Because determining what is normal in a currently rapidly changing world is challenging, long-term monitoring schemes and data on past social structure (such as population density, demographics, average group size) are very useful for this (e.g., [20,22–25]). Unfortunately, for many species this baseline information is still unavailable, and for severely threatened species it is now no longer possible to collect. This underscores the potential conservation value of studying species while they are common.

Depending on the variety of social systems for which long-term social data are available, SNA can be applied to identify some general warning signs of population fragmentation or collapse and to investigate whether certain social structures enhance resilience (e.g., what might be referred to as social shock absorbers). For instance, social network–based simulations showed that the stability of the network (characterized by a lack of network fragmentation) in populations of Northeastern Pacific killer whales was robust to random removals but not to simulated targeted removals that mimicked real-life capture events of socially central juvenile females [23]. The removal of individuals with distinct social roles can thus destabilize entire social groups [23,26]. Yet, sometimes, social groups and populations might prove to be resilient to such perturbations [24,26].

When connectivity among individuals is disrupted, it could have serious consequences for population viability. For example, when fragmented habitats reduce encounter rates, there will likely be changes in social interactions, mate choice options, and antipredator behavior, all of which can influence individual fitness [8]. Fragmentation might decrease encounter rates due to an overall decrease in resources, or it might increase encounter rates because individuals clump together in the remaining small patches of suitable habitat [7,8]. In Eurasian badgers *Meles meles*, increases in population density led to more aggressive encounters [27]. In sleepy lizards *Tiliqua rugosa*, in which intrasexual associations are rare, structural changes to the complexity of the environment increased social connectivity and stability, but likewise increased the number of aggressive interactions [28]. An increase in aggressive interactions can consequently lead to higher stress levels, higher injury rates, and might facilitate the spread of contagious diseases [29]. However, social network modifications in response to human-induced changes in environmental conditions need not be detrimental. Adjusting the social structure could be an adaptive way to cope with changed predation pressures or stress levels [30]. How plastic animal social networks actually are in response to anthropogenic impacts, and the effects of this social plasticity on reproduction and survival, are important questions that require study.

Relationship-Based Management

Relationship-Sensitive Disease Control

Individuals regularly differ in the social roles they play in their population and a small number of individuals can thus have a disproportionate effect on the population's social dynamics.

foraging, to avoid daytime disturbance and/or compensate for lost foraging opportunities, group size is likely to increase, consequently resulting in increased safety but potentially also more social conflict. On the short-term, the social network change might therefore seem adaptive while resulting in a decrease in mean fitness on the long term. (E) SNA can identify which individuals best connect the others in a population. Individuals with high 'betweenness' are likely effective targets for vaccines. (F) Especially when directional interactions are quantified, central individuals can be identified via SNA. SNA, social network analysis.

Particularly striking examples come from studies tracking the flow of microbe, parasite, and pathogen transmission [31], such as in the group-living giraffe *Giraffa camelopardalis*. In giraffes, the flow of *Escherichia coli* more closely followed the links within the social network than the overlaps of individual home ranges [32]. Further, in badgers, the spread of tuberculosis is thought to be mitigated by the distinctive social position of infected individuals [33] and similarly, centrality measures accurately predicted the risk of *Mycobacterium bovis* transmission during den sharing in the common brushtail possum *Trichosurus vulpecula* [34]. Yet, SNA revealed that targeting specific classes of highly connected Tasmanian devils *Sacrophilus harrisii* would only have limited potential to control disease spread in the population [29].

By quantifying the social connectivity of a population, we can determine the likelihood that infected individuals encounter, and hence potentially infect, currently disease-free individuals. This could be important in wildlife disease management, as well as in managing captive disease outbreaks, because it could allow key spreaders to be selectively targeted. Indeed network-informed vaccination programs permit more efficient pathogen control and a smaller total number of vaccines required, as shown by the simulation of pathogen transmission based on association networks informed by wild chimpanzee *Pan troglodytes* behavioral data [35]. However, while those that are highly connected are generally thought to be the most likely spreaders of disease [29,36], more central individuals might also be less susceptible to infection due to the effects of social buffering [37]. This highlights the importance of social bonds in heavily managed populations. Finally, it is possible that infected hosts change their behavior as a result of infection and consequently their network position, increasing or decreasing the chance that a disease or parasite will quickly spread through the population [38]. When aiming for effective disease management, this feedback between the causes and consequences of social network position must be understood.

Relationship-Based Management in Animal Groups

Breeding programs play an essential role in endangered and threatened species management by preventing species extinction and by providing individuals for reintroduction programs (Box 3). However, breeding success can be limited where captivity imposes restrictions on the adjustments individuals can make to decrease social tension [39,40]. In addition, translocations of individuals between captive populations, frequently carried out to maintain population genetic diversity, might reduce reproductive success via impacts on social stability [10]. SNA can be used as a tool to monitor social stability during such changes in group compositions [26,41]. Given that unstable groups are prone to excess aggression that can result in 'cage wars' [42], applying SNA in this context could contribute to improving the reproductive success and welfare of key breeding groups [40]. The application of SNA to optimize captive breeding is a field far in its infancy and in two key areas this approach could be especially valuable.

First, longitudinal welfare studies are needed to quantify the effects of changes in management strategies or enclosure design on group dynamics and individual welfare and breeding success. By quantifying changes in the social network structure, changes to the welfare status of group members can be inferred [40], or the formation of new social groups to specifically reduce aggression levels [41] could be more effectively informed. For example, Atlantic salmon *Salmo salar* were found more likely to suffer fin biting during times of food restriction (such as during transport). Interaction networks were revealed to be denser during these times and showed decreased transitivity (linear order), with initiators showing high out-degree and receivers high in-degree centrality [43]. Removing the individuals that are central to such aggression networks could be a practical solution, but with the risk of others just taking their place. Using SNA to also understand the social mechanisms underlying excessive aggression, and social coping strategies, could help to generate practical warning signals and management actions that will be generalizable to other species.

Box 3. Relationship-Sensitive Reintroductions and Translocations

Effective Group Size and Composition

Animal reintroduction programs are vulnerable to Allee effects and the behavioral mechanisms modulating these effects are elusive. SNA, both prerelease and postrelease, could determine if certain social relationships/structures underlie successful cooperation [19]. Such an SNA approach to Allee effect problems might be particularly profitable for programs involving obligately cooperative species, such as African wild dogs *Lycaon pictus*. By contrast, territorial species' social networks are often characterized by preferential avoidance; here SNA could disentangle which attributes drive aggressive interactions and thus be used to reduce deleterious aggressive interactions following release [28,56].

Pre-existing social structures can facilitate social stability after release. A SNA approach can identify existing subgroups (Box 2). Admittedly, in several species subgroups can be easily identified without SNA. Black-tailed prairie dogs *Cynomys ludovicianus* translocated with the family structure kept intact were more likely to survive and reproduce than those released without relatives [57]. Yet, even in groups in which the social structure appears relatively obvious, certain individuals might end up playing a somewhat cryptic, but essential, social role in group stability [23,26], for example, via social policing or facilitating hormonal suppression. Recently, Dunston *et al.* [58] calculated individual centrality and degree values in an *ex situ* introduction program for African lions *Panthera leo*, to identify the social keystone females, but SNA was also applied to examine if the social structure of the captive prides was sufficiently comparable to a wild pride. If such protocols enhance reintroduction success, they could be adopted widely.

Dispersal

Dispersal of individuals or groups can be a problem in reintroduction programs and in several species dispersal is influenced by social context. Female, but not male, yellow-bellied marmots that were more strongly socially integrated were less likely to disperse [59]. Similarly, a SNA approach was used during a reintroduction of river otters *Lontra canadensis*. Social networks were quantified both in captivity and following release, showing that both social distance in captivity and age predicted postrelease geographic distance between individuals [60]. SNA can help to predict under which structural social conditions (decreased social cohesion [19]) individuals might disperse, and also which social mechanisms might drive entire groups to move [18].

Second, SNA can contribute to disentangling the factors driving variance in reproductive success, since reproductive variance might be correlated with group-level measures. Heterogeneity of association strength (social conflict) was negatively correlated with *per capita* fitness of wild female degus *Octodon degus* [44]. By obtaining such metrics in captive populations, we can target interventions aimed at improving overall breeding rates once the effects of network position on fitness have been understood. For example, the status and hence breeding potential of certain individuals might be improved by providing high-quality food in locations in which these individuals are present [45].

Relationship-Based Behavioral Modifications in the Wild

For many species, social information is transmitted not just between two single individuals, but can be propelled through a group's entire social network. Social transmission can act as a force multiplier, rapidly spreading foraging innovations in a way that is similar to disease transmission. Where these foraging innovations create conflicts with humans, knowledge of network structure can be essential for effective control. California sea lion *Zalophus californianus* populations have recovered from years of overexploitation but their expanding population has begun to create conflicts with the fishing industry and, in at least one instance, with fishery conservation. At the Bonneville Dam on the Columbia River in Washington State, USA, sea lions have discovered that 13 species of endangered salmonids migrate upriver and become concentrated at the dam's tailrace. Here sea lions have learned to gorge on these endangered species, creating a fisheries management problem. Recent work has shown that social relationships forged at the opening of the Columbia River influence both sea lion discovery of and return to the Bonneville dam [46]. Network-based diffusion analyses showed that contact with successful foragers at haul-out sites at the mouth of the river (235 km away from the dam) recruited other successful foragers and that by removing those individuals when they initially discover the dam, the rate of spread of this novel foraging innovation could be effectively stopped or drastically reduced. SNA could thus have assisted in protecting the endangered salmonids, while refraining from more unpopular management actions such as a massive culling of the sea lion population. It is likely that the success of interventions to block transmission of unwanted behaviors in many cases can be improved with specific knowledge of network structure.

A management aim could also be to promote the transmission of certain behaviors or skills. Problems with maladaptive behaviors after release of group-living animals in the wild are common and in these cases being able to teach many animals as quickly as possible to avoid or prefer certain stimuli or to acquire a specific skill will be key [47]. Social learning, in which one individual increases the probability of learning for another, is a key facilitator of acquisition of learned behaviors across many taxa and is, in many cases, more effective than asocial learning. Social learning even takes place in solitary species [48]. Social networks can play an important role in such learning processes and have indeed been shown to predict the spread of seeded novel behaviors in the wild [49,50]. SNA could thus optimize the profitable use of social learning in conservation and management.

SNA is however not always required to enhance social learning. While species are still in captivity the social conditions needed to facilitate spread of skills can also become clear via manipulating these social conditions. Identifying the ideal number of tutors via straightforward manipulation of social group composition was sufficient to promote effective social learning in the hatchery-raised Saimaa Arctic charr *Salvelinus alpinus* [51]. By contrast, when species are (already) in the wild, social conditions can usually no longer be manipulated and then being able to know and use the social structure in place might be critical. When the appropriate social network is quantified (e.g., the foraging network when the aim is to spread a foraging skill), focusing training on the potential ‘super spreaders’ (Figure 1E) will likely facilitate quick propagation of a desired skill in populations of wild group-living animals.

Concluding Remarks

In a field in which funds and time are limited, any newly suggested approach should have a distinct added value. We have therefore specified which kinds of conservation and management challenges we think SNA could particularly impact (Figure 1; see Outstanding Questions). We acknowledge that these suggestions should be viewed as hypotheses ripe for testing. In some cases, we expect large benefits from applying knowledge of social relationships to management problems but in other cases the effect might be relatively small or not cost effective. In addition, we contend that our understanding of the adaptive value of relationships can be advanced through combining SNA with insights into wildlife conservation and management. Thus, collaborations between social network scientists and conservationists – who are reintroducing populations of threatened species – can generate insights into population viability and how to control problem behaviors. This could also lead to important insights into the ontogeny, function, and plasticity of animal social structures [52].

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Outstanding Questions

To understand which specific indirect relationships are most important in maintaining viable populations as well as controlling the spread of problem behaviors, we need more studies on more species that are focused on different behaviors (affiliative, grooming, play, agonistic, etc.).

Hormonal suppression of certain individuals in the population by individuals with distinct social roles could be a key mechanism in the maintance of social stability. We need studies investigating how social network structures modulate hormone levels in vulnerable populations and in populations with problem behaviors.

To better understand network plasticity, we need studies that document the network recovery times from non-fatal anthropogenic disturbances. At the same time, we need more studies that use dynamic social network analyses to test the adaptive significance of social network plasticity in response to environmental changes.

We need a better understanding of how selective culling influences social structure, and whether there are specific network traits that can serve as indicators of population viability and resilience. Congruently, we need to understand whether selective culling effectively removes super-spreaders of problematic behavioral innovations as well as disease.

Epidemiologists target specific individuals with vaccines and treatments to effectively and efficiently limit disease spread. Are these techniques effective in populations of free-living animals and what specific network traits should be targeted (e.g., individuals with high ‘betweenness’ centrality)?

Ecologists have recognized the importance of interactions between species. It is therefore likely that specific knowledge of relationships between species (i.e., multispecies networks) can be relevant for conservation and management. For instance, many species respond to alarm calls from other species – do direct (dyadic) or indirect relationships enhance survival? Similarly, diseases might be transmitted between species and understanding the importance of each species in

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these transfer events could be enhanced with SNA tools. Finally, the control of invasive species or the knowledge on impact of invasive species might be enhanced by a SNA perspective on the interactions between native and invasive species.

Ecotourism is increasing in its global popularity. What are the measurable effects of this type of anthropogenic disturbance on, for example, communication and foraging networks, especially in marine environments? How can these effects be minimized? Are certain species' networks more resistant to these effects than others and which network properties can predict such resilience?

Analyses of animal social networks have started to be used to inform wildlife conservation and management. We view these interventions as empirical experiments that should be applied in an adaptive management framework. If successful, comparative effectiveness evaluation is essential to determine whether the benefits of an SNA approach outweigh potential costs.

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