*In Focus*

# The dynamics of transmission and the dynamics of networks

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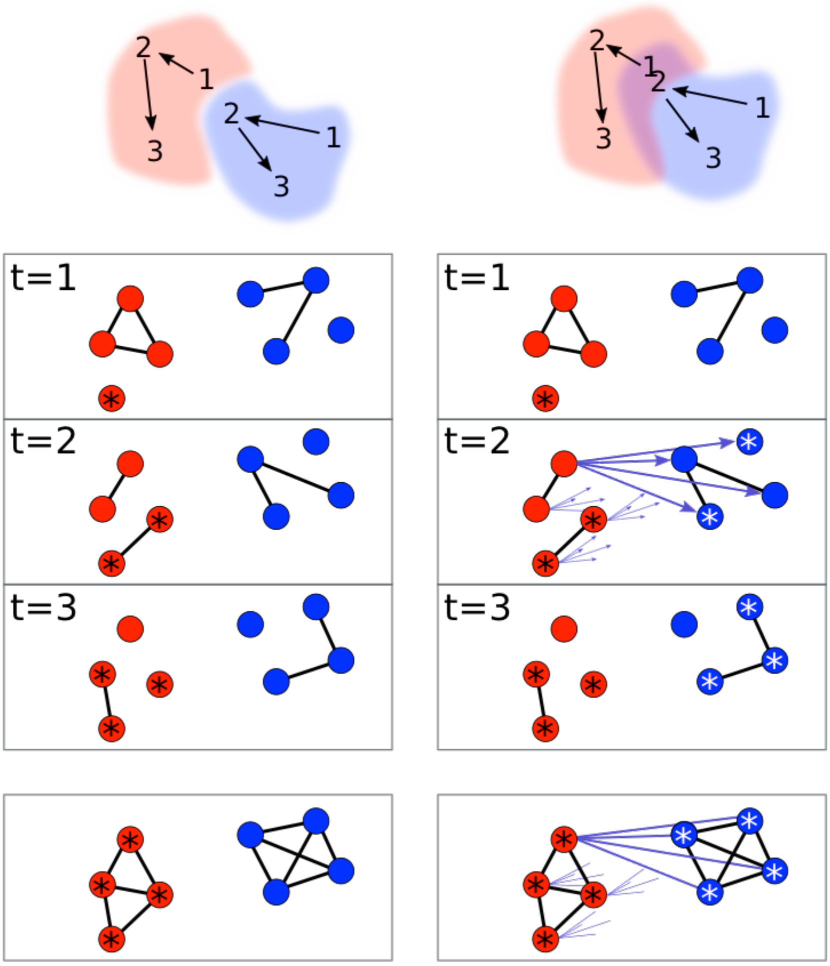

A toy example depicted here highlighting the results of a study in this issue of Journal of Animal Ecology that investigates the impact of network dynamics on potential disease outbreaks. Infections (stars) that spread by contact only (left) reduce the predicted outbreak size compared to situations where individuals can become infected by moving through areas that previously contained infected individuals (right). This is potentially important in species where individuals, or in this case groups, have overlapping ranges (as depicted on the top-right). Incorporating network dynamics that maintain information about the ordering of contacts (central blocks; including the ordering of spatial overlap as noted by the arrows that highlight the blue group arriving after the red group in top-right of the figure) are important for capturing how a disease might not have the opportunity to spread to all individuals. By contrast, a static or 'average' network (lower blocks) does not capture any of these dynamics. Interestingly, although static networks generally predict larger outbreak sizes, the authors find that in cases when transmission probability is low this prediction can switch as a result of changes in the estimated intensity of contacts among individuals.

## Short Abstract

Social network structure can fundamentally shape transmission dynamics. However, networks can capture different modes of interactions and can vary in structure at different temporal scales. Taking such factors into account can change predictions about outbreak size and population susceptibility, and should be carefully considered in studies of animal social networks.

## Abstract

The spread of disease or information through networks can be affected by several factors. Whether and how these factors are accounted for can fundamentally change the predicted impact of a spreading epidemic. Springer, Kappeler and Nunn (2017) investigate the role of different modes of transmission and network dynamics on the predicted size of a disease outbreak across several groups of Verreaux's sifakas, a group-living species of lemur. While some factors, such as seasonality, led to consistent differences in the structure of social networks, using dynamic versus static representations of networks generated differences in the predicted outbreak size of an emergent disease. These findings highlight some of the challenges associated with studying disease dynamics in animal populations, and the importance of continuing efforts to develop the network tools needed to study disease spread.

## Main text

Sociality provides both opportunities and costs for animals. While individuals might receive a range of benefits from aggregating into larger groups, they also increase their risk of coming into contact, or close spatial proximity, with a sick individual (Krause & Ruxton 2002). However, the risk and benefits accrued from having more social contacts will depend on the patterns of connections formed among the individuals, i.e. the social network in which the individuals are embedded. There has been increasing interest in understanding the role that social network structure can play in shaping transmission dynamics for both disease and information. While this question can appear relatively straightforward, the challenges associated with generating useful insights have been somewhat surprising.

To date, studies of transmission on social networks have primarily focused on two primary questions: (i) whether an individuals' connectivity in their social network influences its likelihood of acquiring information or catching a disease; and (ii) how the overall social network structure of the population influences the size of the outbreak or number of individuals that acquire the information. There is a growing body of evidence that an individual's centrality in the network (i.e. individuals with more or stronger connections, or with more movement between groups) is linked to both information acquisition (Aplin *et al.* 2012; Allen *et al.* 2013) and parasite load or diversity (MacIntosh *et al.* 2012; VanderWaal *et al.* 2013b; Weber *et al.* 2013; Rimbach *et al.* 2015). Thus, network connections clearly play an important role in population transmission processes. However, it remains much less clear how the overall structure of the network can modulate the reach and speed of transmission across networks.

A study by Springer, Kappeler and Nunn (2017) in the current issue addresses two fundamental issues that underlie the challenge involved with linking network structure to overall outbreak size or population susceptibility. The first issue is whether to the temporal changes in connections, i.e. the dynamics of the social network, need to be considered. The second is what modes of transmission could realistically take place, and therefore what data should be used to characterise the edges (or relationships) between each individual in the network. The study in and of itself also highlights a third issue, particularly with studying disease transmission on networks, which is the difficulty in conducting field experiments and therefore the over-reliance on using simulations.

A primary motivation for taking a network perspective to study population processes is the fact that animals generally do not mix or interact randomly with others. However, this 'non-randomness' could equally have a temporal component—that is, individuals do not necessarily interact consistently with their associates. This has implications for transmission dynamics, for example properties of the network (density, degree distribution, etc.) can change over time (Blonder *et al.* 2012), and thus also speed up or slow down transmission. Additionally, it is often argued that some relationships captured in the static network may be present prior to an outbreak, but absent by the time transmission would be possible. A static network would thus over-estimate the potential reach of the outbreak. Overall, Springer, Kappeler and Nunn (2017) found largely overlapping estimates when comparing simulated spreads on dynamic and static representation of the same observation data: networks constructed from a population containing multiple groups of Verreaux's sifakas (*Propithecus verreauxi*). However, there was a general trend for larger outbreak sizes in static representations of the network, in line with expectations. Further, by exploring the parameter space, Springer, Kappeler and Nunn (2017) found evidence that estimated outbreak size was sometimes predicted to be larger in the dynamic network, particularly where transmission probability and recovery probabilities are both low. These results are likely to be linked to the fact that strong links (high interaction rates) present in the dynamic network are often averaged down in static networks. These results add a useful dimension to previous studies, such as (Volz & Meyers 2009) who found that mixing rates can influence the relative predictions of outbreak size across dynamic versus static networks. However, the jury is still out on the relative merits of both approaches.

A major concern with most studies that use social network analysis is with identifying appropriate definitions for edges—or the links that define the relationships among individuals. In studies of transmission through networks, this definition should capture realistic pathways along which information or disease can spread. Springer, Kappeler and Nunn (2017) explore the potential for spread via overlap in space use. Although the studied population of sifakas contains multiple groups, these have partially overlapping ranges. They found that including this information (i.e. allowing disease to spread via the environment, not just via body contact) significantly increased the estimated outbreak size. While this is perhaps not surprising, it warrants careful consideration in studies of social processes, including those focused with information spread. The expression of a behaviour by an individual could leave traces in the environment that provide information for others. For example, while New Caledonian crows (*Corvus moneduloides*) seem to learn to fashion tools by observing others, the availability of discarded tools also appears to play an important role in juvenile development of this foraging technique (Holzhaider, Hunt & Gray 2010). The relative importance in shared space use is likely to differ across taxa. For example, feeder use was found to be important in spreading disease amongst house finches (*Haemorhous mexicanus*) (Adelman *et al.* 2015) but common use of waterholes was not suggested as a mechanism underpinning pathogen similarity in giraffes (*Giraffa camelopardalis*) (VanderWaal *et al.* 2013b). Considering and quantifying additional modes of transmission is clearly important.

Finally, while studies simulating transmission dynamics through social networks can reveal a range of insights, they also suffer from some significant limitations. Notably, when individuals change state from uninfected to infected (or uninformed to informed), this can also result in a change in behaviour. Thus, the spreading process can itself be responsible for a changing dynamic on the social network, and thus greatly limiting the insights that can be gained from studies based on simulating spread in observed or simulated networks. The reason why I have highlighted cases of information transfer throughout this *In Focus* piece is because studies of information spread have a distinct advantage—they can relatively easily be replicated across contexts or, even more powerfully, combined with experimental treatments, thus overcoming some of the limitations of studying disease spread. Recent studies of information transmission provide some of the best evidence on how networks can shape spread through populations. For example, Aplin *et al.* (2015) demonstrated that distinct solutions to a puzzle-box spread through replicated social networks of great tits (*Parus major*), Farine *et al.* (2015) quantified variation in transmission rates among different types of individuals in mixed-species social networks, and Firth, Sheldon and Farine (2016) experimentally manipulated social network structure to reveal its effect on transmission pathways. Further, several on-going studies are investigating potential effects of population structure on transmission processes by studying information transmission in different types of populations (e.g. comparing urban and rural populations, Jones 2016).

Ultimately, many questions about how network structure impacts transmission dynamics remain. Models generally suggest that clustering among individuals in populations should slow down epidemics, as is supported by a study investigating the spread of a parasite through two populations of Belding's ground squirrels (*Spermophilus beldingi*) (VanderWaal *et al.* 2013a). Further, the mechanisms that shape network structure, and thus ultimately affect opportunities for spread, also warrant careful study. In an influential study, Brockmann and Helbing (2013) demonstrated that the intensity air traffic, rather than distance between cities, predicted the spread of two recent global epidemics. Thus, social network analysis is clearly an important and powerful tool in animal ecology (Farine & Whitehead 2015), and continued investment is needed to expand our understanding of the mechanisms that shape the structure of populations and the role of such structures in shaping transmission processes.

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