

Forum

Infected or informed? Social structure and the simultaneous transmission of information and infectious disease



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Social interactions present opportunities for both information and infection to spread through populations. Social learning is often proposed as a key benefit of sociality, while infectious disease spread are proposed as a major cost. Multiple empirical and theoretical studies have demonstrated the importance of social structure for the transmission of either information or harmful pathogens and parasites, but rarely in combination. We provide an overview of relevant empirical studies, discuss differences in the transmission processes of infection and information, and review how these processes have been modelled. Finally, we highlight ways in which animal social network structure and dynamics might mediate the tradeoff between the sharing of information and infection. We reveal how modular social network structures can promote the spread of information and mitigate against the spread of infection relative to other network structures. We discuss how the maintenance of long-term social bonds, clustering of social contacts in time, and adaptive plasticity in behavioural interactions, all play important roles in influencing the transmission of information and infection. We provide novel hypotheses and suggest new directions for research that quantifies the transmission of information and infection simultaneously across different network structures to help tease apart their influence on the evolution of social behaviour.

Keywords: dynamic network, epidemic, group-living, social evolution, social learning, social network

Synthesis

The elevated risk of infectious disease and benefits of information represent a clear tradeoff for animals engaging in social interactions with others, but this has rarely been considered in a systematic way. We review the latest developments in network modelling to evaluate how differences between information and parasite transmission, social structure and social dynamics can mediate this tradeoff. Our synthesis provides new predictions for this emerging area of ecological research and highlights how considering both information and infection together can transform our understanding of the evolutionary ecology of sociality in diverse systems.



Introduction

The diversity of social systems in animals is shaped by differences among populations in the costs and benefits of different types of social interaction (Krause et al. 2002). The sharing of information provides one key benefit that improves fitness of more sociable individuals (Danchin et al. 2004, Dall et al. 2005), while the risk of acquiring pathogens or parasites (collectively referred to as 'parasites' from here onwards) represents an important cost of sociality (Krause et al. 2002, Ezenwa et al. 2016b, Ezenwa and Worsley-Tonks 2018). While extensive work has been carried out examining the role of social interactions in information spread and infectious disease independently, the potential interactions and tradeoffs between them has only recently started to be considered (Romano et al. 2020). An important future challenge in evolutionary ecology will be to identify whether, and how, natural selection might favour social structures that can simultaneously optimise information-sharing and reduce the spread of infection in social species (Romano et al. 2020). The solution to this evolutionary problem will depend on the differences in transmission dynamics between information and infection.

Social network analyses and modelling are increasingly used to study animal social behaviour, and these approaches have greatly benefitted research into the spread of parasites (Godfrey 2013, VanderWaal and Ezenwa 2016) and information (Firth 2020) in wild animals. Interactions with more individuals result in increased opportunities for parasite transmission, while simultaneously making it possible for information to proliferate within a group or population. When an infection is present, the interplay between infection and information may lead to both long- and short-term changes in social structures, which can affect both individual fitness and entire populations (Pelletier et al. 2009, Shizuka and Johnson 2020). However, studying the tradeoff between efficient information transmission and rapid spread of parasites is challenging due to the difficulty of combining data that reveal infection status, and data that indicate information transmission. Consequently, while network studies have examined how social relationships impact the transmission of either infection or information separately, there has, until recently, been little consideration of the interplay between information and infection spread within animal social networks (Romano et al. 2020). As technology and techniques are increasingly becoming available that facilitate empirical research and data-driven modelling on the co-dynamics of information spread, parasite transmission and social network structure, it is important to synthesise existing knowledge across disciplinary boundaries to identify key research questions and challenges. Theoretical models, not just in the field of behavioural ecology, but also in network science and epidemiology more broadly, can also be integrated to provide a rich source from which to generate predictions about the tradeoff between infection and information, and how this tradeoff may shape the evolutionary ecology of animal social systems.

Here we synthesise knowledge on the role of social networks in transmission of information and parasites and develop hypotheses regarding how animal social systems may be adapted to reconcile the tradeoff between acquiring information and becoming infected by parasites. We briefly review studies examining the transmission of parasites and information in animal social networks. We then highlight potential differences between the transmission processes of information and infection that will mediate this tradeoff. Finally, we discuss how social relationships may be adapted to optimise both types of transmission, integrating insights from the network modelling literature and through empirical work in natural populations. Throughout we emphasise new avenues of study into the flow of parasites and information through animal social networks to promote a better understanding of how these two important ecological processes affect each other.

Parasite transmission in animal social networks

The transmission of parasites that cause infectious disease can happen directly via specific types of behavioural interaction or indirectly via the environment (e.g. an individual using a refuge that has been contaminated by an infectious individual) (White et al. 2017). Many infections are endemic, persisting stably within a host population for a long period of time (Viana et al. 2014). Others are emergent, acquired either from a long-term environmental reservoir or spilling over from alternative host species (Daszak et al. 2000). Networks of spatial associations and behavioural interactions are now known to be closely associated with epidemiology in wild animal populations (Weber et al. 2013, VanderWaal et al. 2014). Overall network structure is critical in determining how parasites spread through populations. For example, the presence of distinct social communities can limit the spread of infection in animal groups or populations (Griffin and Nunn 2012, Sah et al. 2017). Social network analysis can also help identify potential routes of transmission (Silk et al. 2017a, White et al. 2017), determine individual variation in transmission potential (VanderWaal and Ezenwa 2016) and predict or explain how infection spreads through populations (Craft 2015, Silk et al. 2017b). Network analyses have also revealed associations between individual phenotypes, infection and network position. For example, European badgers *Meles meles* that test positive for bovine tuberculosis tend to have fewer connections to their own social group and more social connections with neighbouring groups (Weber et al. 2013), and male-biased infection is associated with sex-differences in social network position (Silk et al. 2018c).

Fine-scale social networks can be used to identify if and how different types of social interaction generate transmission opportunities. The most important type of contact for transmission may vary among systems: in some species direct social contacts may be more important than shared space use (Blyton et al. 2014, VanderWaal et al. 2014). More recently,

the importance of cryptic contacts has been revealed in a mixed-species community of bats, with social networks based solely on the sharing of, or physical contact at, roosts not sufficient to capture fungal pathogen transmission dynamics (Hoyt et al. 2018). Together these studies reveal that using social networks in disease ecology might help to identify potential transmission routes, but might be uninformative and potentially misleading if the types of social interactions modelled are not those that facilitate parasite spread.

Infection may lead to temporal changes to network structure by changing patterns of social behaviour (Ezenwa et al. 2016a). Parasites often manipulate the host's social behaviour to facilitate further transmission (Berdoy et al. 2000, Loot et al. 2001, Randall et al. 2006), while the social behaviour of the infected host and/or the individuals that interact with it might change to prevent spread, resulting in co-dynamics between parasite spread and network structure (Silk et al. 2017a). In guppies *Poecilia reticulata* for example, infected individuals are avoided by uninfected fish, making sick individuals less well connected and causing the networks to become less clustered overall (Croft et al. 2011). At a network-level these behaviour–infection co-dynamics can have a protective effect. In ants, for example, social networks of infected colonies become more modular and assortative, resulting in them becoming less efficient in terms of information transmission capacity but more effective at limiting the spread of infection (Stroeymeyt et al. 2018). It is clear then that variation in connectivity among individuals, the resultant network structure and changes in network dynamics following infection, all have important implications for the emergence, spread and persistence of parasites in wildlife populations.

Information transmission in animal social networks

Information can be acquired by sampling the environment (personal information; Dall et al. 2005) or by observing or interacting with other individuals or their products (social information; Danchin et al. 2004, Dall et al. 2005). Individuals can spread social information inadvertently or can choose to deliberately transmit information via signals. A receiver must then decide whether to act on this information or not (Dall et al. 2005, Schmidt et al. 2010). The transfer of social information usually requires sensory contact between individuals and is therefore linked directly to spatial association and/or behavioural interactions. Consequently, as with parasite transmission, an individual's social network position causes variation in the probability and rate of receipt of information, and their contribution to the speed and quality of information transmission through a population (Lusseau 2003, Lusseau and Newman 2004, Modlmeier et al. 2014, Firth 2020). Depending on the duration information is useful for, an individual's network position will strongly influence how they can utilise this information. For example, information such as the discovery of a resource location (Blonder and

Dornhaus 2011, Aplin et al. 2012, Webster et al. 2013) may only be accurate for a short time if a resource is ephemeral or is rapidly depleted. A central network position or high level of connectivity to the individual who initially discovers such resources will be highly beneficial to potential recipients, as demonstrated in several studies of the influence of network position on food patch discovery in flocks of songbirds (Aplin et al. 2012, 2015, Jones et al. 2017, Tóth et al. 2017). Therefore, when information-gathering is beneficial, group members may be attracted to individuals who regularly provide information, changing their position in the social network. In ring tailed lemurs *Lemur catta*, for example, this led to informed individuals occupying more central network positions (Kulahci et al. 2018).

Social associations are also linked to the spread, through social learning, of behavioural innovations which can arise via trial and error learning (Allen et al. 2013, Aplin et al. 2014). Such innovations range from simply adopting a new foraging ground (Schakner et al. 2017) to tool use (Mann et al. 2012, Hobaiter et al. 2014, Coelho et al. 2015, St Clair et al. 2015) or novel foraging techniques (Kendal et al. 2010, Aplin et al. 2014, Boogert et al. 2014). Innovations of long-term value can be transmitted to subsequent generations (Cantor and Whitehead 2013, Aplin et al. 2014) and impact long-term social structure, provided individuals alter their social interactions to maximise their chances of acquiring information (Coelho et al. 2015, Kulahci et al. 2018). One possible outcome is that long-term, preferential associations with individuals who adopt the same behaviours (Mann et al. 2012) will homogenise behavioural repertoires in any given group and can establish 'animal cultures' (Krützen et al. 2005, Allen et al. 2013, Aplin et al. 2014). For example, bottlenose dolphins *Tursiops* spp. using marine sponges as tools during foraging have been shown to preferentially associate with other tool users (Krützen et al. 2005, Mann et al. 2012). This behavioural homogenisation may, depending on initial network structure, increase connectedness which can lead to the structure of networks becoming more random. Alternatively, if networks are already divided into distinct social communities, these groups might become increasingly isolated from each other (Morgan and Laland 2012, Cantor and Whitehead 2013).

Generally, the transmission of social information is considered to benefit the recipient individuals. However, there is potential for information transmitted to be outdated, poor, corrupted or misleading (Koops 2004, Ward et al. 2008, Schmidt et al. 2010, Preece and Beekman 2014, Klein et al. 2018). While such information might simply result in wasted time and energy (Giraldeau et al. 2002, Dall et al. 2005, Preece and Beekman 2014), more severe costs are possible depending on the value of accurate information (Koops 2004, Nocera et al. 2005, Rieucan and Giraldeau 2011). For example, inexperienced bobolinks *Dolichonyx oryzivorus* relying on social information to make breeding habitat choices were found to settle in and defend sub-optimal territories in response to misleading information (Nocera et al. 2005). The spread of misinformation through a network

could have impacts on fitness that resemble the spread of parasites (Laland and Williams 1998, Ward et al. 2008). When learning how to solve problems, individuals commonly show strong preference for the first solution to which they are exposed (e.g. birds: Aplin et al. 2014, fish: Laland and Williams 1998). In competitive situations, recipients of suboptimal information might lose out to better informed individuals or successful innovators. While the spread of misinformation has not yet been the subject of empirical study using network techniques, there is strong potential for it to be important in nature. Similar to parasites, misinformation may be more likely to spread through a population if an individual transmitting misinformation is highly central to the social network, as information from these individuals may be more likely to be utilised by others, and their central position provides more transmission opportunities (Giraldeau et al. 2002, Ward et al. 2008, Firth 2020).

Differences between information and parasite transmission

We have illustrated the importance of an individual's social connections both in their access to and sharing of information, and in their exposure to and onward transmission of parasites. This suggests that animal societies might suffer a direct tradeoff between the transmission of information and parasites. However, there are important general (though not universal) distinctions between the two transmission processes (Table 1).

Most importantly, information transmission will typically involve choice, sometimes for a transmitter, who can choose when to transmit information and to whom, and always for the receiver, who chooses whether to alter their behaviour based on the information. Choice by the receiver means that the social transmission of information does not necessarily depend on a simple probability of transmission associated with each interaction (Bakshy et al. 2009, Jackson and López-Pintado 2013). Individuals may require multiple exposures to a transmitter, or require a certain proportion of social connections to be transmitting before choosing to utilise a piece of information (Bakshy et al. 2009, Jackson and López-Pintado 2013). For example, chimpanzees were more likely to acquire a behaviour if it was demonstrated by three different individuals than when it was demonstrated three times by a single individual (Haun et al. 2012). Evidence for such social conformity, where naïve individuals disproportionately copy the behaviour demonstrated by the majority of conspecifics, has also been reported for mate-choice copying in fruit flies (Nöbel et al. 2018) and great tits solving puzzle boxes in the wild (Aplin et al. 2015). This information transmission process differs from parasite transmission where 1) the risk of acquiring infection rises monotonically with the duration and/or number of contacts with infected individuals, and 2) having multiple infected social connections presents more opportunities for contact with infected individuals, but does not alter the per-interaction probability of infection. Therefore, in species showing conformist social learning strategies, the acceptance of information depends on the relative magnitude of exposure to transmitters and non-transmitters

Table 1. Summary of the general key differences in mechanisms and consequences of information and parasite transmission.

	Infection	Information
Transmitter decisions	Individuals inadvertently infect others (though parasites might change host behaviour to facilitate infection).	Individuals can inadvertently inform others (e.g. through cues/eavesdropping) or choose to deliberately inform others (e.g. signals).
Receiver decisions	Recipients of parasites cannot choose whether they become infected or not.	Individuals decide whether to alter their behaviour based on the information received.
Number of transmitters	The probability of infection depends directly on the absolute magnitude of exposure. The number of simultaneously infected associates does not affect per-contact likelihood of infection.	The probability of accepting information can depend on the relative magnitude of exposure to transmitters and non-transmitters. The proportion and phenotypic traits of associates transmitting information can influence whether an individual uses information received (i.e. social learning strategies).
Social relationships	Prior social relationships have no effect on the per-contact likelihood of infection.	Prior social relationships can influence whether an individual adopts information received.
Transmission vectors	Parasites spread mainly through direct physical contact or close proximity, or via shared use of environmental reservoirs.	Information spread does not tend to require physical contact and can potentially occur via long-range sensory interactions.
Heterospecific transmission	Parasites can spread between species, though this may require adaptation by the parasite.	Information can spread between species. Receiver may require adaptation or learning to utilise information from heterospecifics.
Selection	Selection acts on both the host and the parasites they transmit.	Selection acts on the information transmitter and receiver, but only indirectly on the information being transmitted.
Behavioural changes	Infected individuals are often avoided by group members, and become less well-connected in the social network. Infections might manipulate host behaviour to increase probabilities of onward transmission.	Informed individuals can be desirable to associate with, and become better connected in the social network.

of information in a frequency-dependent manner, and similar non-linear changes in the likelihood of transmission can also occur for other social learning strategies.

Another key difference between information and infection is the effect that prior social associations can have on the likelihood of transmission. The current and previous social relationships of an individual can directly impact the probability of using information acquired through a particular social interaction. This phenomenon was first coined 'directed social learning' (Coussi-Korbel and Fragaszy 1995) and later described as one of many potential 'social learning strategies' (Laland 2004). Some of the clearest evidence of such a 'Whom to learn from' social learning strategy comes from the importance of familiarity for the rate of social learning in many species (Swaney et al. 2001, Kavaliers et al. 2005). Information from a familiar individual may result in an immediate change in behaviour, whereas an animal may require more exposures to a piece of information if the source is unfamiliar. Transmitter familiarity is one of several relationship traits that might influence the decision to use a piece of information, with traits such as relatedness or social rank also potentially important (Valsecchi et al. 1996, Radford 2004, Kavaliers et al. 2005, Boogert et al. 2018, Evans et al. 2018). Relationship traits can also interact with the ambiguity of transmitted information (Ward et al. 2008) and the phenotype of the transmitter, such as their experience (McComb et al. 2001) or obvious fitness cues (Toth and Griggio 2011), to shape the likelihood of information being used. Similarly, it is possible for prior social relationships with other group members to have a profound effect on the health of individuals in social species (Sapolsky 2005), and the social buffering hypothesis (Ezenwa et al. 2016b) proposes that positive social relationships can increase resistance to, and tolerance of, infection in group-living species (Walker and Hughes 2009, Scharf et al. 2012, Almberg et al. 2015, Balasubramaniam et al. 2016, Ezenwa and Worsley-Tonks 2018). However, unlike the spread of information, this is a general effect and specific prior relationships with infected individuals do not influence the transmission process in the same way that prior relationships with informed individuals do.

Another important consideration is how information and infection are transmitted. Social information can be transmitted in multiple ways (Danchin et al. 2004, Blanchet et al. 2010), which may require prolonged or close interactions (e.g. the waggle dance in bees; Von Frisch 1967, Ward et al. 2008), may be possible with much looser associations (e.g. auditory cues; Hollen and Radford 2009), or may be transmitted indirectly via environmental signals or cues (e.g. scent marking; Gosling and Roberts 2001). Conversely, parasites are likely to be transmitted through a different set of interactions, such as prolonged close contact that facilitates aerosol transmission (Delahay et al. 2001); shared use of environmental reservoirs of parasites (Godfrey et al. 2009); aggressive interactions or mating (Hamilton et al. 2019). The extent of the overlap in the types of social interaction that expose individuals to either information or infection will be important

in determining the costs and benefits of being central in different types of social network.

Both parasites and information can be transmitted between as well as within species. The spillover of parasites will typically depend on ecological opportunity provided by the frequency of direct and/or indirect (epidemiologically relevant) contacts between members of the different species (Woolhouse et al. 2001, Plowright et al. 2017, Faust et al. 2018), the phylogenetic similarity of potential hosts (Longdon et al. 2011, Kreuder Johnson et al. 2015) and the evolvability of the parasite; parasites with higher mutation rates (e.g. some viruses) can infect a larger range of different host species (Woolhouse et al. 2001, Kreuder Johnson et al. 2015). As with parasite transmission, information transmission is also more likely to occur between closely related species (Coolen et al. 2003, Seppänen et al. 2007, Goodale and Kotagama 2008, Goodale et al. 2010, Dawson and Chittka 2012, Farine et al. 2015a), often an outcome of them having similar information requirements due to sharing ecological challenges (though see: Anne and Rasa 1983, Whiting and Greeff 1999, Lilly et al. 2019, for transfer between less related species). An animal's ability to utilise information from heterospecifics will also depend on the type of information. For example, seeing a heterospecific fleeing from a predator and using this as information about a potential threat is relatively simple, requiring no advanced learning processes or adaptation. However, using a heterospecific alarm call to assess threat may require prior experience with the calling species, so as to learn the association between the alarm call and threat (Templeton and Greene 2007, Ferrari and Chivers 2008, Magrath et al. 2015). As a result, the type and quality of information passed between species can be highly variable across contexts and species, and rates of social learning can differ between conspecific and heterospecific relationships (Goodale and Kotagama 2008, Farine et al. 2015a).

A final important distinction between information and parasite transmission is that the former is the subject of selection only on the host population, while the latter depends on selection on both the host and the parasite being transmitted. For example, individuals that acquire novel social information may develop new social associations and become more central within a social network (Kulahci et al. 2018), which may benefit both themselves and other group members, especially in highly related groups. This is in direct contrast to transmission of infection, where group members would be expected to avoid contact with infected individuals (Croft et al. 2011, Stephenson et al. 2018), which can lead uninfected individuals to become more central as a result of parasite spread (Shaw and Schwartz 2008). A key component of this difference between infection and information is that there is often antagonistic selection on sickness behaviours between hosts and their parasites, whereby hosts will be selected to behave to avoid infecting (related) group members (Croft et al. 2011, Lopes et al. 2016), while parasites will be

selected to cause host behaviours that maximise transmission (e.g. furious behaviour in rabid canines; Randall et al. 2006).

The outcome of these differences between the transmission of infection and information is that while infection can be considered a simple contagion process, the spread of information is increasingly considered a complex contagion (Macy 1991, Centola 2010) affected by many of the social learning rules described above. Consequently, the spread of parasites has normally been modelled as a simple contagion using cascade models (Moore and Newman 2000), in which the probability of infection increases with increasing absolute exposure to infected individuals. In contrast, the transmission of information could be either a simple or complex contagion depending on the social learning rules used by individuals. As a result, the spread of information has been modelled using a

variety of dose–response models, including simple cascades, threshold models (Kempe et al. 2003), and hybrid cascade–threshold models (de Kerchove et al. 2009) models (Fig. 1). The precise nature of the threshold, and whether it is a true threshold (deterministic), a stochastic transmission process with a threshold or a continuous dose–response curve, will depend on the social learning rules used. The measure of exposure used in these models might be relative exposure (conformist social learning in response to the prevalence of information among social contacts), absolute exposure (social learning in response to a minimum number of neighbours behaving in a particular way) or based on temporal rules (e.g. learning in response to a threshold number of interactions with informed individuals in a given time period). Variation in the status of informed individuals or their relationships to

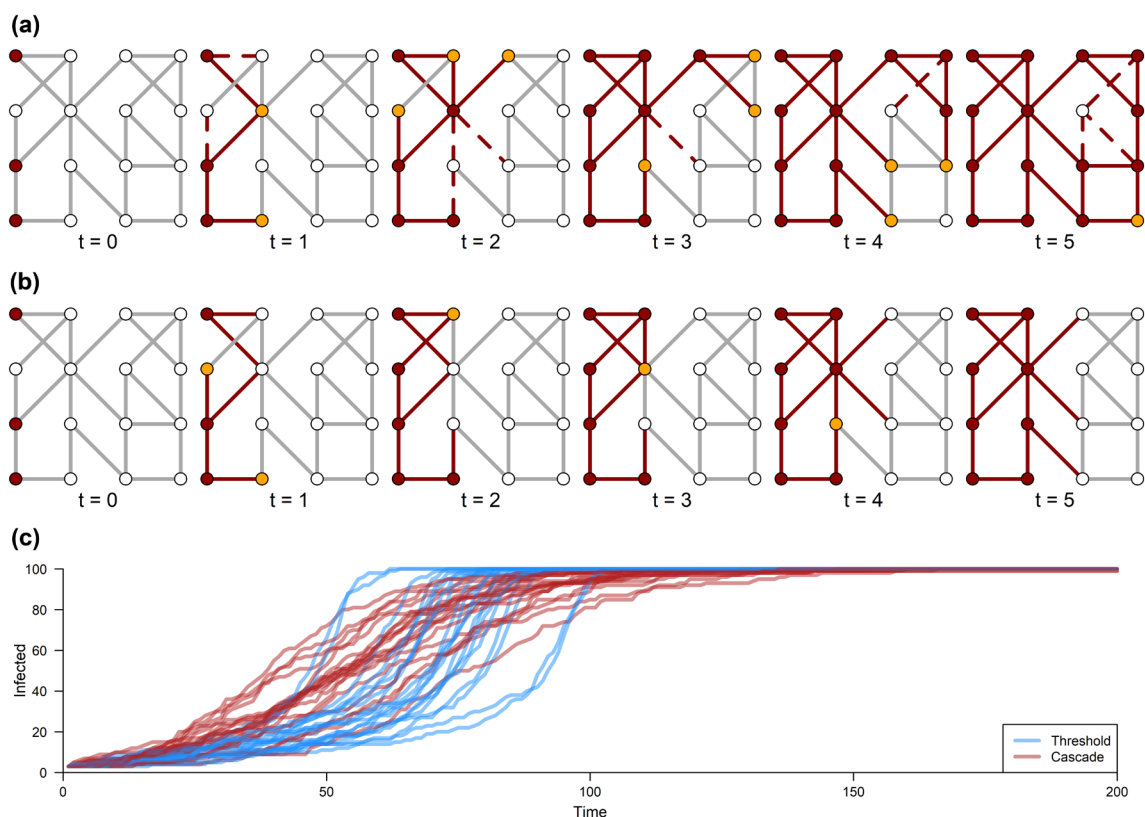


Figure 1. Illustration of cascade and threshold transmission models. (a) Example of a cascade model of simple contagion acting on an unweighted network (all individuals have an association strength of either 1 or 0) of 16 individuals over four time steps. Grey lines represent social associations, red nodes represent infected/informed individuals while yellow nodes represent individuals who will become infected/informed in the next time step. In this cascade model an infected/informed individual infects/informs each uninfected neighbour with a probability of 0.5 per time step. Solid red lines indicate an infected/informed node successfully infecting/informing a neighbour, while a dashed line represents a failure. If successful, the neighbour will become infected/informed in the next time step. (b) A conformist transmission model (here a true threshold model, but a stochastic implementation would produce similar results) acting on the same network as (a). Individuals become infected/informed when 50% of their neighbours are infected/informed. In this simulation, spread stalls at timestep 4 as there are not enough infected/informed individuals to result in transmission. (c) Comparison between simple and conformist contagion models in a random network of 100 individuals, showing the percentage of the population infected over 200 arbitrary time-steps. For the simple contagion model there is a probability of 0.8% chance per time-step that infection is transmitted through an edge between an infected and susceptible individual. In the conformist model a sigmoid curve is fitted to the likelihood of an individual exploiting information with a baseline (asocial) individual learning rate of 0.2% per time-step, a maximum probability of learning of 30% per time-step and the threshold (pivot point of the sigmoid function) occurring at 50% of connected individuals providing information. Full R code for the model is provided in the Supplementary material Appendix 1.

the focal individual could be key mechanisms which push the transmission process even further away from simple contagion.

Using models to capture the differences between information and parasite transmission

The similarities and differences between information and parasite transmission can be captured using dynamic computational modelling tools (Fig. 1), such as compartmental models. Compartmental models consider the transition of individuals between states, with individuals in each state assumed to have the same characteristics (Stattner and Vidot 2011). For example, a susceptible–infected–recovered (SIR) model (used commonly in epidemiology) contains three states: susceptible (or naïve) individuals; infected with a parasite (or exposed to and exploiting the information); and recovered individuals who are now immune to that infection (or who no longer use the information to inform their behaviour, Supplementary material Appendix 1 Table A1). When applied to transmission through networks, compartmental models are typically applied as stochastic individual-based models, in which the transition of each individual between compartments is modelled separately and depends on the properties of their network connections. Such models are usually impossible to solve analytically (Craft 2015). These models avoid the assumption that populations mix freely, so that any individual will be able to infect any other individual in a population. General compartmental models applied to networks can be used to study parasite transmission (Volz 2008, Tunc and Shaw 2014), information flow (Wang and Wood 2011, Gurley and Johnson 2016), or both simultaneously (Wu et al. 2012, Juher et al. 2015). See Supplementary material Appendix 1 Table A1 for many examples of simple compartmental models that can be applied to both information and parasite transmission, and those more suitable for detailed models of particular transmission types.

Cascade, threshold and hybrid compartmental models can all be adapted to capture system-specific nuances regarding the importance of transmitter identity, social history and behaviours that change in response to exposure (Fig. 1). Cascade models are typically implemented as stochastic models, with each additional unit of social interaction associated with a linear increase in the risk of infection (Fig. 1a). True threshold models are deterministic with individuals moving between states following fixed rules that are determined by the states of their neighbours, and can be used to model strictly conformist social learning, for example. Hybrid models can be used to mix properties of either model, for example by introducing stochasticity to the threshold model or incorporating continuous dose–response curves. For example, the latter might be applicable to studying imperfect conformist social learning where changes in state are governed by the states of neighbouring individuals according to a sigmoidal function rather than a strict threshold (Fig. 1c).

Social structure and the infection–information tradeoff

In the following sections, we highlight ways in which animal social networks might reflect the outcome of selection acting on individuals to maximise their acquisition of beneficial information and minimise their risk of being infected by parasites. Specifically, we focus on the role of structural heterogeneity in social networks, temporal heterogeneity in interactions and responsive changes in social interactions. We integrate the extent of our current knowledge of animal social systems with insights from compartmental network models (Supplementary material Appendix 1 Table A1) applied to theoretical and data-driven network structures in other disciplines.

Structural heterogeneity and transmission in animals

The structure of contact networks is integral to transmission dynamics for cascade models (Moore and Newman 2000, Newman 2002) and threshold models (Alkemade and Castaldi 2005, Hodas and Lerman 2014). We focus on three aspects of social network structure that have received considerable research interest and have clear applications to the study of animal societies: 1) variation in connectivity among individuals causing networks to possess heterogeneous degree distributions (the extreme case being networks with scale-free properties), 2) small-world structure, which is best envisaged as individuals (or ‘nodes’) being connected mostly with (spatial) neighbours, but possessing occasional contacts with much more distant nodes, resulting in transmission pathways through the network that are typically short compared to random or modular networks, and 3) modular structure that is characterised by densely connected regions (called communities) with rather few connections between these communities. We depict these different aspects of network structure in Fig. 2. Animal social structure is highly variable and can display one or multiple of varying connectedness, small-world properties or modular properties introduced here (Wey et al. 2008).

Heterogeneous degree distributions

Many animal social networks have highly heterogeneous degree distributions, with certain highly connected individuals acting as ‘hubs’. Taking these differences in connectivity into account is important to understand transmission dynamics. For parasite spread, models show that more heterogeneous degree distributions increase the speed of epidemic spread and result in a higher prevalence of epidemic peaks due to the presence of highly connected superspreader individuals (Barthélemy et al. 2004, Lloyd-Smith et al. 2005), but reduce the frequency of epidemics (Lloyd-Smith et al. 2005). In more extreme situations where networks are truly scale-free, epidemics can spread almost instantaneously through populations (Barthélemy et al. 2004), making them especially vulnerable to parasite spread. For information transmission, the role of degree heterogeneity is more complex. In

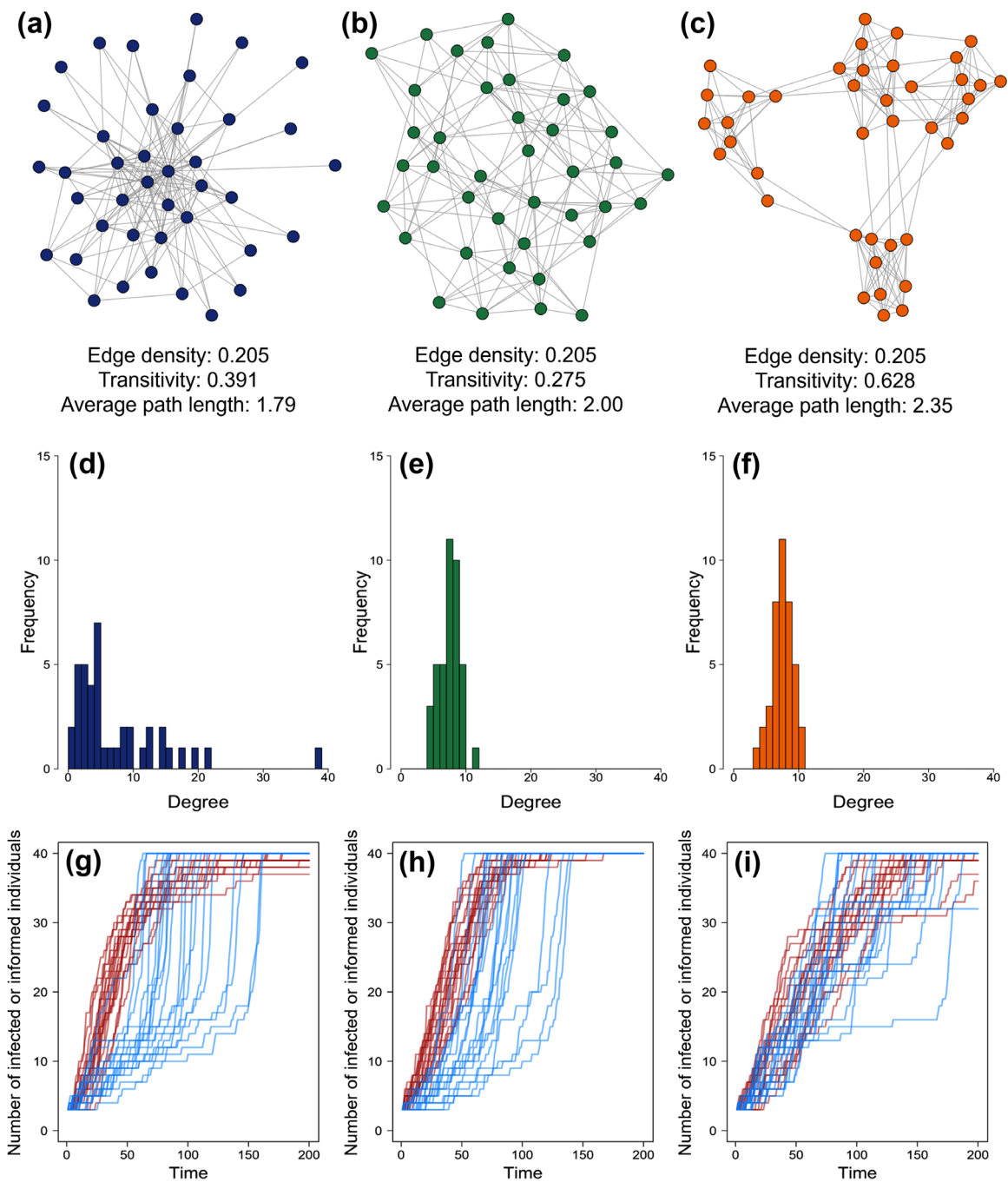


Figure 2. Demonstration of three key types of network structure with important implications for transmission. The network structure (a–c), degree distribution (d–f) and transmission dynamics (g–i) of a simple contagion model for infection (red) and conformist contagion model for information (blue) are illustrated. All networks plotted here have the same edge densities (proportion of potential edges that are connected). Scale-free (or approximately scale-free) networks (a, d, g) have highly heterogeneous degree distributions (i.e. high variation in connectivity) with some high-degree (very well connected) individuals acting as ‘hubs’, causing average path lengths to be short and resulting in very rapid spread of parasites but slower spread of information. In small-world networks (b, e, h) most connections are to neighbours, but occasional long-range contacts act as ‘bridges’, maintaining short average path lengths and enabling more rapid diffusion than random networks, and permitting faster spread via the cascade than the threshold model. In modular networks (c, f, i) most connections are to individuals in the same social community or module, resulting in high transitivity (or clustering of connections to ‘friends of friends’) and high average path lengths. Modular networks can have mixed effects on transmission speed that can depend on whether transmission follows a simple or conformist contagion dynamics. In this example, infection and information are able to spread at similar speeds through the modular network (i) but infection spreads more rapidly through scale-free (g) and small-world (h) network structures. Code for generating and plotting the networks and running the stochastic models is provided in the Supplementary material Appendix 1.

some contexts, individuals occupying globally central roles in a network are more likely to acquire information (Aplin et al. 2012, Jones et al. 2017). However, when considering information transmission as a complex contagion (as might be appropriate when individuals have conformity biases and accept information based on relative exposure), it is possible that individuals with many social connections might require stronger signals to distinguish a piece of information from the general ‘noise’ received from their many associates (Hodas and Lerman 2012, 2014). Conversely, lower-degree individuals may be more likely to utilise information sooner, as having a smaller number of ties means that fewer transmitting associates are required to achieve conformist transmission (González-Avella et al. 2011). Differences in the nature of transmission between information (when considered to spread through complex contagion) and infection may generate differences in the ‘most susceptible’ network position between the two types of transmission that will reduce the intensity of any tradeoff between the acquisition of information and parasites.

Networks with highly heterogeneous degree distributions will allow the rapid spread of infection and (often) information through populations. However, we hypothesise that information will spread more slowly than infection through these types of network when conformist social learning strategies are used. Individuals with a larger number of connections will require a larger proportion number of their associates to transmit the information in order to achieve the same relative magnitude of exposure, compared to less centrally positioned individuals. Hubs may therefore be slower to respond to information than less well-connected individuals. This will drive differences in which network positions are most likely to acquire information and those which are most likely to become infected. Being highly connected may be disproportionately risky in terms of the risk of infection per unit of social information acquired (and used), while being embedded within a network region (i.e. sharing contacts with your associates) will minimise the risk of becoming infected per unit of social information gathered.

Small-world networks

Small-world networks can arise as a result of the majority of social associations or interactions occurring mainly with close neighbours within groups, but with infrequent longer-range connections acting as ‘bridges’ between regions of the network. It is easy to see how small-world properties might arise in animal networks through behaviours such as territoriality with occasional extra-territorial forays. For example, in African lions *Panthera leo* contacts between prides are normally driven by space use, with prides from neighbouring territories coming into contact much more frequently. However, occasional contacts between prides that are normally spatially well-separated do occur, resulting in a network with small-world properties (Craft et al. 2009). In small-world networks the epidemic threshold (i.e. the transmission probability at which epidemics become possible) decreases considerably

as the likelihood of long-range connections in the network increases (Moore and Newman 2000). For example, in a territorial, monogamous animal this would equate to epidemics of a sexually-transmitted infection becoming more likely as extra-pair copulations occurred over greater distances rather than happening only among neighbouring territories.

As with models of parasite transmission, theoretical models predict that information flow will be faster in small-world networks than random networks (Alkemade and Castaldi 2005, Delre et al. 2007, Nekovee et al. 2007, de Kerchove et al. 2009) and the importance of multiple social contacts in enabling transmission will be increased (de Kerchove et al. 2009). The findings of de Kerchove et al. (2009) suggest that to spread information effectively, an individual with long-range connections must have somewhat stable associations to ‘seed’ individuals within the region of the network it is connected to, as a single interaction may be insufficient to enable transmission. If relative exposure to new information is important (i.e. it is necessary for a threshold proportion of contacts to be informed before an individual accepts information) then we can speculate that these ‘seed’ individuals are more likely to be low-degree individuals who adopt information more rapidly due to their small number of other connections. The exception to this will occur if highly central individuals in the naïve group have a low information-use threshold (i.e. they require few demonstrators to transmit the information before adopting it themselves), which may be the case if individuals that acquire useful information tend to become more central in networks or if the bridging individuals are extremely influential due to their social status (or another trait).

Small-world networks are characterised by the importance of occasional long-range social connections involving small number of individuals. We suggest that the importance of these ‘bridge’ individuals is easier to predict for parasite transmission, while for threshold models of information transmission their role will depend to a greater extent on the social learning rules of the individuals they are connected to, and therefore be more variable. We also predict that social dynamics will play a greater role in these small-world networks as the death of these ‘bridge’ individuals or changes to their interactions will reduce the rate of global transmission of infection and information.

Modular network structure

Social networks with distinct social community structure are widespread in animals, especially in species living in stable social groups (Weinrich 1991, Drewe et al. 2009, Weber et al. 2013). Both community structure and transitivity (the tendency to be connected to ‘friends of friends’) reduce the size of parasite outbreaks but can lower the epidemic threshold. This makes it easier for less transmissible infections to spread, as the presence of many connections among the same set of individuals increases the probability of local spread, but these local connections reduce the probability of large-scale epidemics (Newman 2003, Salathé and

Jones 2010, Sah et al. 2017). The effect of modular structure is greater when interactions between individuals in different social communities are more infrequent so that sub-divisions between them are stronger (Salathé and Jones 2010, Sah et al. 2017). A meta-analysis of animal social networks has shown that the impact of modularity on the spread of parasites is limited except when there are very few connections between communities (Sah et al. 2017). The impact of modularity will also depend on the transmissibility of the parasite. For example, Rozins et al. (2018) demonstrated that the effect of the modular structure of empirically-derived European badger contact networks was greatest for simulated parasites with intermediate transmissibility (i.e. infectious enough to cause an outbreak but not so infectious that it can spread easily between social groups).

In contrast, models suggest that modularity may not interfere with information diffusion in the same way. In some scenarios a modular network structure may actually increase global diffusion by enhancing within-community spreading. For example, Nematzadeh et al. (2014) used a threshold model to show that conformist social learning strategies could lead to information being transmitted most quickly in networks of intermediate modularity. The networks of species living in stable groups would therefore be expected to have reduced epidemic spreading, and potentially enhanced (or unchanged) information diffusion, as an outcome of being highly modular (Fig. 2). In this way, structural heterogeneity in animal social networks may mediate the tradeoff between the transmission of information and infection, especially for group-living or fission–fusion social systems with more modular social networks.

We therefore suggest that a modular network structure may be critical in mediating the tradeoff between minimising the spread of parasites and maximising the spread of information. Community structure can promote the spread of social information when individuals follow conformist social learning strategies, while trapping infection within particular regions of the network. We predict that the dual selection pressures imposed by the access to information and the risk of acquiring parasites will lead to natural selection generating modular network structures. The modularity of these structures will depend on the relative benefits information and costs of infection to individuals, and the social learning strategies that they use.

Different types of associations–multilayer relationships

As outlined in the previous section, different types of interaction will not all be equivalent for the transmission of infection or information. Considering how transmission dynamics vary for different types of interactions is therefore critical in understanding how animal societies might be adapted for efficient information transmission and minimal parasite spread. Multilayer networks allow multiple interaction types to be incorporated within a single conceptual

framework (Kivelä et al. 2014). A layer can denote different types of behavioural interaction between the same (or similar) set(s) of individuals, such as one layer for affiliative interactions and another for agonistic interactions (Silk et al. 2018b, Finn et al. 2019). Layers can also consist of interactions between different types of individuals, such as different sexes (Silk et al. 2018c) or species (Silk et al. 2018a), with edges between layers representing interactions between those types of individuals.

Theoretical models using multilayer networks have been valuable in understanding the spread of a single parasite species or piece of information through multiple types of interaction, and the consequences of multiple spreading processes occurring across the same set of individuals (for example, multiple information types: Liu et al. 2018, multiple parasites: Azimi-Tafreshi 2016 or infection and information together: Funk et al. 2009, Funk and Jansen 2010, Marceau et al. 2011, Granell et al. 2013, 2014, Zhao et al. 2014, Guo et al. 2016). Applying these approaches to animal behaviour research (Silk et al. 2018b, Finn et al. 2019) requires data on multiple types of social connections simultaneously (Franz et al. 2015, Gazda et al. 2015), and quantification of the importance of these different social connections for transmission (Aplin et al. 2015).

Taking a multilayer approach also enables the integration of the indirect effect of positive and negative social relationships on transmission processes. Theoretical models on multilayer networks consider the effects of these different types of social relationships by modelling them as a type of transmission through the network, alongside infection and/or information. For example, one type of model considers the flow of social support that improves recovery rate from infection (which could, for example, represent the strength of affiliative relationships) on a second layer and has been used to show that social support can suppress parasite outbreaks, but that the effect is dependent on network structure and the correlation between the layers (Chen et al. 2018a, b). Using models such as these enables the impact of social buffering to be integrated into network models, to determine how it may shape the tradeoff between encountering useful information and risking infection. At its simplest, if well-connected individuals are healthy and capable of resisting infection, then they do not face a tradeoff at all.

Multiple spreading processes can also interact to promote or interfere with each other. For example, Liu et al. (2018), when modelling the synergistic spread of multiple pieces of information transmitted simultaneously, showed that individuals having adopted one piece of information were subsequently more likely to adopt the other piece of information, one enhancing the other. A similar scenario in animal societies may be choosing to follow a particular individual's migratory route leading to an increased likelihood of socially learning a more efficient version of that route (Berdahl et al. 2018). Alternatively, different types of information might compete, with one piece of information overriding/displacing the other (Kostka et al. 2008, Trpevski et al. 2010).

structure), demonstrating that regulation of spread is typically dominated by one or the other (Delvenne et al. 2015). This suggests that the importance of heterogeneous contact dynamics for transmission in animal societies may vary systematically with other aspects of the social system, such as the stability of social groups.

We recommend research that focuses on the implications of temporal clustering of interactions and/or contacts for the spread of information and parasites, providing valuable insights into how individuals balance the costs and benefits of their social interactions. We predict that ‘bursty’ contact dynamics could enhance the transmission of some types of information (depending on the social learning strategies of individuals), while having no effect or even reducing the risk of parasite transmission – a good example may be lek mating systems. It would be possible to test these predictions in established experimental systems and then scale the findings to a population or network level using stochastic models. We also expect that accounting for the effects of heterogeneous contact dynamics will be most important for species living in highly fluid societies rather than more stable social groups.

Responsive network dynamics and transmission in animals

Animal social networks can change in response to the spread of infection (Croft et al. 2011, Stroeymeyt et al. 2018) and information (Kulahci et al. 2018) with a key difference between infection and information being that changes to network structure during the spread of infection may be determined by the phenotype of both the hosts and their parasites (Franz et al. 2018), while any changes to network structure in response to the acquisition of information are solely an outcome of selection on the ‘host’, or ‘hosts’ in the case of heterospecific transmission (Table 1). Theoretical models can provide some useful predictions as to how this affects transmission dynamics. Models where network connections can be altered in response to infection or information are referred to as adaptive network models (Bansal et al. 2010, Funk et al. 2015). The most common assumptions in infectious disease modelling are that individuals display infection–avoidance behaviour by either losing or reducing the strength of connections with infected individuals (Van Segbroeck et al. 2010) or by replacing them with connections to other non-infected individuals (Shaw and Schwartz 2008). In the case of parasite spread, computational models indicate that adaptive networks typically have higher epidemic thresholds, delaying outbreaks and reducing peak prevalences (Gross et al. 2006, Shaw and Schwartz 2008, Van Segbroeck et al. 2010). These behavioural responses to infection also frequently impact aspects of the network structure, for example by increasing variation in the connectivity of susceptible individuals and causing infected individuals to be much more poorly connected (Shaw and Schwartz 2008) or by increasing community structure with community membership assorted by infection state (Yang et al. 2012). While these changes reduce the impact of the current epidemic, they may make endemic disease more likely (Gross et al. 2006, Shaw and Schwartz 2008) or even result in long-term epidemic re-emergence

(Zhou et al. 2012), which may have important implications for longer-term eco-evolutionary dynamics in animal populations. It is also possible for infection avoidance behaviour to exacerbate epidemics if individuals switch their connections from infected to susceptible individuals subsequent to being infected, although this remains relatively poorly explored (but see Zhang et al. 2012b).

Many adaptive network models have previously assumed perfect knowledge about the infection status of other individuals, and this is unlikely to be the case in many natural host–parasite systems. Identifying when information is available about the infection status of individuals relative to when the infection is most transmissible (Stephenson et al. 2018) will be crucial to understanding how ‘adaptive’ changes to network structure can mediate the tradeoff between information and parasite transmission. It may also be important to consider changes to the behaviour of infected individuals; sickness behaviour. Sickness behaviours in particular could be influenced by selection on hosts or parasites. At times, sickness behaviour could be favoured by both host and parasite (e.g. dispersal away from a highly related group; Iritani and Iwasa 2014), but at other times optimal outcomes may be directly opposed (e.g. reduction in number of contacts; Lopes et al. 2016) and generate antagonistic co-evolution between the host and parasite.

The results from equivalent models of information transmission are more diverse. One model suggests that individuals may be more likely to cluster with those who are more inclined to use information they are deliberately transmitting (Jackson and López-Pintado 2013), while another model suggests individuals will break ties with those who do not use the information they deliberately transmit (Zhang et al. 2012a). In some species of animal, individuals may preferentially associate with those who will accept foraging information from them, so as to maximise the likelihood of gaining benefits from recruiting others to feed (Wright et al. 2003). Similarly, a male displaying within a lek will attempt to maximise the number of individuals who receive their signals, while also choosing to give up and stop transmitting to those who are unlikely to mate with them (Patricelli et al. 2009). In a similar manner to signalling individuals manipulating their physical environment (e.g. birds singing from prominent perches), individuals may also dynamically alter their social interactions so as to maximise their chances of transmitting information to less informed node (Liu and Zhang 2014) if it is beneficial for them to do so (e.g. in highly related groups). In contrast to the avoidance behaviour expected in response to the spread of parasites, ‘adaptive’ behaviours that favour the acquisition of useful information while minimising exposure to misinformation would be expected (Kulahci and Quinn 2019), depending on previous interactions between the individuals involved. An individual who produces useful information may be more likely to have others use that information in the future, while an individual that frequently provides inaccurate information may be ignored (refractory behaviour). An important caveat to this idea is that an individual who has previously produced useful information may

subsequently be more likely to cause misinformation to be transmitted (Modlmeier et al. 2014), especially if the value of information changes over time (e.g. by becoming outdated). This can be exploited by individuals aiming to transmit misinformation to manipulate the receivers' behaviour to their advantage, as is the case in fork-tailed drongos *Dicrurus adsimilis* who mimic other species' alarm calls to steal food from meerkats (Flower et al. 2014). Whether drongos flexibly change their social associations with heterospecifics once they have been identified as cheats by the local meerkat group remains to be determined.

Considering behavioural dynamics alongside transmission dynamics is important to our understanding of how individuals may resolve the conflict between the acquisition and transmission of information and infection. Obvious signs of infection or regular transmission of misinformation can result in individuals becoming less well connected in a network while transmission of useful information can lead to the opposite pattern. We predict that behavioural plasticity that causes patterns of social interactions to be modified in the presence of infection or innovations will therefore be a key mechanism by which this balance between the costs and benefits of being highly socially connected is mediated and expect that these behavioural dynamics are much more widespread than previously described. Behavioural dynamics are also likely to be closely interlinked with network structure, and we predict that behavioural responses to parasitism and information will co-vary with social structure (especially group dynamics and modularity) between populations.

Future research priorities

Our review highlights several key priorities for future research. First, it is essential that we continue to build on our understanding of how infection and information are transmitted through natural populations. In particular, discovering how widespread the use of complex social learning strategies is in animals will be critical in revealing whether particular social network structures, and particular social network positions within them, favour the transfer or acquisition of information over and above that of parasites. Revealing the use of complex contagions or directed social learning strategies will require experimental approaches in study systems for which high-quality social network data are also available (e.g. in primates: Carter et al. 2016, or passerine birds: Farine et al. 2015a). However, it would also be valuable to extend our understanding of social learning strategies away from these model systems to better quantify the generality of different forms of information spread. This could exploit experiments that test for learning being directed by traits such as social dominance (Benskin et al. 2002, Kendal et al. 2015, Jones and Monfils 2016) or by conformity (Aplin et al. 2015, Danchin et al. 2018). In addition, we have emphasised how the transmission of information can also depend on different types of association or interaction than those influencing

parasite transmission. A renewed effort to consider the consequences of the multilayer structure of animal social networks will be crucial to understanding differences in the opportunities for transmission of information and parasites within animal groups. Comparisons of the structure of interactions relevant for social learning, and those that provide opportunities for parasite transmission, are likely to be particularly informative.

We have also highlighted the importance of temporal heterogeneity in transmission-relevant contacts and the role of behavioural plasticity in response to parasite prevalence in mediating the tradeoff between acquiring information and avoiding infection. Further research into social network dynamics will therefore also be critical in understanding how these two ecological processes shape the evolution of social network structure. Network dynamics that result from infection avoidance behaviour provide a context where both information and parasites are spreading, and the outcomes are inter-dependent. Therefore, work that builds on existing research addressing how social network structure responds to changes in parasite prevalence will be valuable (Stroeymeyt et al. 2018), especially if it provides a mechanistic understanding of how individuals learn to change their behaviour (rapid spread of behavioural changes via conformist social learning, for example). Social insect colonies would be ideal for such experimental studies. These species lend themselves to high-throughput construction of replicated social networks, and studies quantifying the role of these networks in the transmission of information and parasites have already been conducted using such systems (Blonder and Dornhaus 2011, Bos et al. 2012, Stroeymeyt et al. 2018). The final piece of this puzzle will be understanding changes in the behaviour of infected individuals (Lopes et al. 2016) in a variety of different social systems and contexts, especially when social networks are kin-structured, given that the evolution of sickness behaviour is predicted to depend on population structure (Iritani and Iwasa 2014).

These experimental approaches will be most powerful when paired with novel mathematical models that examine the evolutionary ecology of individual social behaviour. Such models could demonstrate how social network positions are associated with different fitness outcomes when the costs and benefits provided by parasitism and social learning are varied. The theoretical transmission models described in this review, although extremely detailed, focus on the transmission processes themselves rather than placing them in a broader ecological and evolutionary context. Thus, combining these techniques for simulating transmission with evolutionary modelling will represent a key priority. In addition, tailoring theoretical network models to more accurately reflect typical contact behaviours of animals using recently established data repositories (Sah et al. 2019) will help to provide more detailed predictions for different social systems. Combining theoretical and empirical work to develop data-based evolutionary models will be important to fully understand the implications of these differences in the transmission

of infection and information for the evolution of animal social systems.

Conclusions

Social network structure is fundamental to both the transmission of information and parasites through populations. Both represent important selection pressures on how individuals structure their social interactions. Individuals face a tradeoff to maximise the acquisition of reliable information while minimising the risk of becoming infected with parasites. However, our understanding of this tradeoff is complicated by how these processes depend on social network structure in different ways. The risk of acquiring infection typically increases monotonically with the frequency and duration of interaction with infectious individuals. In contrast, information acquisition is more complex, with the likelihood of accepting information often depending on exposure to that information in a non-linear fashion. For example, empirical evidence from some animal social networks suggests that acquisition of information might often be a threshold trait. A receiver's threshold of exposure could be determined by the proportion of associates demonstrating the behaviour, or could be determined more broadly by the identity, influence or traits of transmitters (e.g. social learning directed by dominance, familiarity, relatedness). Information transmission is also complicated by the sharing of both good and bad (or out-dated) information, and by 'refractory' behaviours among recipients that result in the acquisition of information not affecting the behaviour of all individuals in the same way.

Crucially, these differences in the nature of transmission and the types of interactions that result in transmission can mediate the apparent tradeoff between acquiring information and infection in social systems. Furthermore, plasticity of social behaviour can generate changes to social structures that can protect against the spread of parasites or promote the spread of information. In this way, behavioural plasticity is likely critical in regulating infection risk and information benefits obtained by social animals. Information transmission is often integral to behavioural responses to avoid infection, making quantifying differences in how information and infection are transmitted and their different routes of transmission even more important. Consequently, our understanding of the interplay between information and infection in shaping animal social systems requires a better grasp of how transmission is affected by the structural, temporal and multi-layered heterogeneities that are inherent to animal social networks.

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Supplementary material (available online as Appendix oik-07148 at <www.oikosjournal.org/appendix/oik-07148>).
Appendix 1.