The trade-off between information and pathogen transmission in animal societies

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Abstract

Social structure can regulate information and pathogen transmission via social contact or proximity, which ultimately affects individual fitness. In theory, the same network properties that favor social information transmission also favor the spread of socially-transmitted pathogens, creating a trade-off between them. The mechanisms underlying the development and stability of individual relationships considering this trade-off remain underexplored. Here, we outline the evolutionary mechanisms of social transmission and hypothesize that network topology can be optimized in a way that balances the costs and benefits of social relationships. In this context, emergent network properties might reflect a trade-off between information and pathogen transmission in animal societies. We then propose an implementation of Hinde's classical framework by incorporating the costs of socializing in a negative feedback loop in the emergence of social structure. We hope this manuscript encourages research into this underxplored social trade-off and the evolutionary processes underlying it.

Keywords:

social behaviour, individual decisions, network plasticity, evolution of sociality, group-living trade-offs

After all, it is an individual’s choice…

> “It is certain that either wise bearing or ignorant carriage is caught, as men take diseases, one of another: therefore, let men take heed of their company”. Shakespeare, Henry IV, part 2 (1600)

As observed by William Shakespeare, the rate of contact among individuals can lead to the transmission of information among conspecifics, for better or worse, just as it can for the agents of disease. It should therefore be upon each individual to decide with whom to interact. Like humans, many social animals make decisions that affect their social lives, such as whether or not to interact with a specific group mate. This set of decisions affects the number and quality of an individual’s social relationships, which in turn reflects the social structure into which those individuals are embedded [1]. Sociality has evolved repeatedly throughout the animal kingdom [2], and undoubtedly brings many benefits for individuals, such as defense against predators, increased foraging efficiency, and increased offspring survival [3]. But it also comes with certain costs, such as within-group competition where resources are limited in space and time [4], and infectious disease transmission due to frequent contact among conspecifics [5]. Consequently, individuals face trade-offs in maximizing the benefits and minimizing the costs of group-living. Differences in the pattern of social interactions emerge from individual strategies to deal with such inherent trade-offs in their social lives. This will ultimately impact the evolution of social systems.

Social transmission and animal societies

We can envisage social transmission as involving any entity (e.g. knowledge, behavior, disease-causing organisms) that can be transferred from one individual to another while in social contact or spatial proximity. Social transmission is an important component of animal society, with clear impacts on individual fitness (e.g. [6], [7]). Animals use social information (i.e. that acquired from conspecifics [8]) in a variety of contexts, such as in the identification of new foraging routes or threats from predators via alarm calls (Box 1). However, social contact among individuals, which is crucial to establish and reinforce social bonds, also leads to risk of contagion. Some pathogenic organisms, such as respiratory viruses, ectoparasites and sexually-transmitted diseases, are transmitted through socio-sexual contact and/or spatial proximity (Box 2). These costs and benefits of social transmission lead to an evolutionary trade-off: while social relationships favor the transmission of social information, they also favor the spread of socially-acquired pathogens.

Although the dynamics of information and pathogen transmission in animal societies are both well-studied [5], [9]–[11], they are typically treated independently. This might be partially due to the challenges inherent in investigating multiple forms of transmission within the same empirical framework, or to the research questions of each scientist being limited to a certain area. Nonetheless, a theoretical study of this nature does provide evidence that the spread of information and viruses happens as a function of the same properties of social structure [12].

Increasing information flow and contagion risk via social networks

In this section, we use a network-based framework to emphasize that structural properties of social interactions strongly influence social transmission. The conceptual framework of social network analysis is consolidated in Ethology, Behavioral and Evolutionary Ecology, and it is broadly accepted as a means of investigating patterns of social interactions in animal groups [13]. A synonym of social structure, social networks are pervasive in nature. Social networks encode nodes, which represent individuals, connected by ties (also called links or edges) that represent the interactions between pairs of individuals [14]. Network metrics are statistical measures used to characterize properties of the network, such as an individual's position within its network of contacts and the characterization of the network as a whole, or its topology. For exhaustive descriptions of the calculation and interpretation of these metrics, see [14], [15].

An individual's position within its social network

An individual's network position is usually determined by the relative number and strength of its social relationships, hereafter called connections. Central individuals are those with large numbers of direct (e.g. number of social partners) or indirect (e.g. number of distinct subgroups to which an individual is related) connections. Thus, the position of an individual within its network mediates its probability of acquiring or transmitting information and infectious agents. Central individuals are expected to be key dispersers of information[16], [17], controlling its quality and access[18], but are also expected to spread infectious agents to a broader number of individuals and to be more at risk of pathogen exposure[19]–[21]. For example, hunter-gatherer women in the Philippines who are more central in their proximity networks have higher reproductive success, but they also suffer from greater disease burdens (e.g. gastro-intestinal disease and respiratory tract infections[22]). Such findings emphasize the role of individual centrality in information and pathogen transmission. At the same time, however, as important the position of each individual is, the overall structure of the group (the social network itself) is crucial to transmission dynamics as well.

Social network topology

Emergent properties of the network at a global-level include assessments of properties such as network density (i.e. the total number of observed links as a function of the maximum number of possible links in the network) or modularity (i.e. the extent to which a network is sub-divided into modules). Several comparative studies demonstrate that the topology of the network distinctly affects transmission processes [23]–[25]. Increasing network density, for instance, results in faster social transmission: the more connected the network, the lower the number of connections that are necessary for information or pathogens to be transmitted from the spreader to the most peripheral individual(s) in the group [25]. However, the relationship between a network property and social transmission might not always be straightforward, since other properties may induce contrasting effects in the process. For example, researchers have examined the association between group size and social network metrics in 43 vertebrate and invertebrate species and showed that modularity, which is expected to increase in larger groups, acted as a buffer, reducing disease spread between subgroups [24]. Recent studies provide supporting evidence for this phenomenon, but also highlight that only after reaching some threshold does modularity slow down transmission processes [23]. Modularity may thus have a dual role in network efficiency and transmission dynamics [26]. There is great diversity in social structure throughout the animal kingdom, all mediated by countless environmental and social factors [1], and it is within these myriad social structures that the dynamics of social transmission are encoded.

Do social network properties reflect a trade-off between information and pathogen transmission?

A huge array of empirical studies demonstrate that network properties can be used as a powerful estimation of transmission processes in animal societies [10], with each property potentially working as a buffer and/or facilitator of social transmission (see previous section). If individuals optimize their relationships to deal with costs and benefits of social relationships, network properties reflect snapshots of these relationships and they may potentially reflect the trade-off between information and pathogen transmission. For example, a recent work suggests that we might expect to find real-world networks in which values of modularity may vary accross some limited range if social interactions are occurring to balance the costs and benefits of sociality [26].

To some extent, network structure could be optimized to favor information flow and decrease contagion risk. For example, a theoretical model of roost selection, aiming to investigate the mechanisms underlying fission-fusion behaviour in bats, highlighted that individual decisions were driven toward maximizing information accuracy and minimizing infectious disease risk [27]. The model showed that all members of the colony stayed in the roost when information about the roost's quality was accurate and there was no risk of contagion. However, since colonization increases the abundance of parasites in the environment, fissioning into smaller groups was effective in reducing parasite spread. These results demonstrate how individuals might deal with the trade-off between information and pathogen spread; while bats mitigate the risk of contagion by fissioning into small groups (thus increasing network modularity), they lose opportunities to gather information about roost quality. Fission-fusion behaviour was thus suggested to allow bats to balance such conflicting needs by altering roosting group size [27].

The topology of the network can be thus optimized in a way that balances the costs and benefits of social relationships [28], [29]. The structure of the network mediates social transmission, which in turn affects each individual's probability of acquiring information or pathogens and, ultimately, individual fitness. Social structure is not expected to be selected for directly (see [30] for arguments to the contrary), but since the network topology emerges from the collection of individual behaviours/decisions, it may vary flexibly according to the different pressures individuals face [31]. The mechanism of an individual behaviour affecting the social structure in which they are embeded was called “collective social niche construction” [31], in reference to the “niche construction” perspective. Social networks are demonstrably dynamic [32], [33], and interaction costs such as pathogen acquisition [28] as well as interaction benefits such as gaining access to food [29] each cause variation in individual decisions about with whom and how frequently to interact, leading to the emergent social structure observed and thereafter feeding back into social transmission.

In this opinion article, we do not intend to suggest that there is one single network structure whereby individuals optimize the costs and benefits of social relationships. This indeed depends on the collection of socioecological pressures and environmental conditions present in each case. Instead, we propose that the degree to which individuals interact socially varies dynamically, plausibly to optimize information flow and minimize connection costs, neither of which will be static across time nor stable across environments. Network topology is dynamic, as changes in node states affect edges, and changes in edges affect node states (for a comprehensive review see [33], [34]). Flexible interactions allow individuals to deal with conflicts and both social and environmental changes, which may ultimately result in significant increases in individual fitness [27].

Among the several trade-offs individuals must face in social groups, we focused specifically on the trade-off between information and pathogen transmission caused by the same social contact or proximity among individuals. From this perspective, individuals that better adjust their behaviors to meet the challenges inherent in social relationships might be able to increase their own fitness.

On the interface of social transmission and social structure

Hinde's (1976) seminal paper introduced a conceptual framework for relationships at the individual level and their multidirectional influence on the emergence of social structure and variation therein [1]. Although his framework did not consider any causal direction, he highlitghed that the quality and patterning of relationships could be strongly affected by social structure, and that social structure could be affected by other factors, such as kinship, physiological variables, among others [1], [13]. More recently, a scheme proposed by Cantor & Whitehead (2013) extended Hinde's framework by incorporating information transmission at the final level of the diagrammatic representation (Figure 1). The authors highlighted bidirectional effects between social structure and information flow: group structure influences the way information spreads, while the flow of information can in turn affect social structure [35]. For example, similarities in behavior, as expressed in the vocal repertoires of cetaceans, cause clustering of individuals [36]. Within clusters, associates are also more likely to share information [36]–[38].

While the relationship between network structure and information flow has been firmly demonstrated in animal social networks [35], we emphasize that multiple lines of evidence also demonstrate an influence of social structure on pathogen transmission [11]. Pathogen acquisition affects social structure directly through mortality rates, as well as indirectly depending on the degree to which individuals avoid social interactions involving infected individuals (i.e. avoidance behavior; Box 2). For example, Caribbean spiny lobsters (*Panulirus argus*) avoid individuals that are infected with PaV1, a lethal virus [39]. Mandrills (*Mandrillus sphinx*) were shown to recognize parasitized individuals and avoid grooming the anogenital areas of group mates shedding infective stages [28]. Therefore, pathogens that are or can be transmitted through social channels may negatively affect social cohesion, directly or indirectly, by reducing social connectivity, while social structure continues to set the conditions under which individuals are exposed to potentially deleterious infectious agents, creating a bidirectional feedback effect (Figure 1).

Indeed, evolved strategies apart from the physiological immune system also allow social animals to combat the spread of infection, such as the conspecific avoidance behaviors just discussed or other types of social immunity (Box 2). Although the mechanisms by which animals identify sick individuals are still unclear for most vertebrates, demonstrations of social avoidance in mammalian species are increasing (e.g. olfactory recognition of sick individuals [28]). Yet, it is important to bear in mind that reduced social interaction with diseased individuals can also occur as a byproduct of lethargy caused by the pathogen itself, and the decrease of social interactions may represent the inability of sick individuals to maintain proximity to healthier group members. There is also the possibility that infected individuals actively self-isolate for reasons other than lethargy. Nonetheless, active forms of social immunity are better understood in social insects, where cooperation between group members constrains disease spread throughout the colony via several mechanisms, such as not cannibalizing infected corpses and guarding nest entrances to prevent infected individuals from entering [40]. A recent experimental study demonstrated that pathogen exposure induced behavioural changes in the black garden ant (*Lasius niger*), which resulted in the reinforcement of transmission-inhibitory characteristics (i.e. increased modularity and clustering, decreased transmission efficiency) in the contact network [41]. Not only did foragers exposed to the fungus *M. brunneum* (natural to the ants' habitat) isolate themselves from the colony, but healthy foragers also decreased their contact time with the rest of the colony [41]. The overall network structure and the relative network positions of individuals that resulted from these behavioral changes led to a decrease in pathogen transmission. Such research shows that, indeed, individual strategies cause changes in network topology, and that network plasticity affects the dynamics of pathogen transmission [41].

In this opinion article, we propose to extend the framework of social transmission and incorporate the costs of socializing in networks by including the spread of socially-transmitted pathogens (Figure 1). Instead of considering transmission as the final factor in the loop or assume that information flow is the only relevant factor, we suggest simultaneous examination of information and pathogen transmission as explicit and opposing entities (see suggestions for future studies in Box 3 and Outstanding Questions). Each feeds back into individual behavior and thereby influences social structure. Indeed, while access to crucial information is expected to drive individuals to cluster around knowledgeable individuals [36], affinity for enemy-free space, i.e. avoidance of potential social sources of infectious disease [41], should operate to reduce connectivity in a network. This presents a classical fitness trade-off for individuals that aim to exploit social relationships for their own benefit on the one hand while avoiding potential costs on the other. While the concept of information transmission is well-integrated in the classical framework proposed by Hinde (1976) [35], whether and how pathogen pressures interact with social structure in ecological and evolutionary terms, e.g. via their dependence on social contact or proximity for transmission, has received far less attention in this regard.

Behavioral ecologists have long been aware of the complex relationships formed among individuals, but few have attempted to evaluate the resulting social structure quantitatively, accounting for the interplay between these complex relationships. In addition to an extensive evaluation of both social structure and transmission dynamics underlying animal networks independently, we encourage researchers to investigate the trade-off between information and pathogen transmission in the social interaction-social structure scheme.

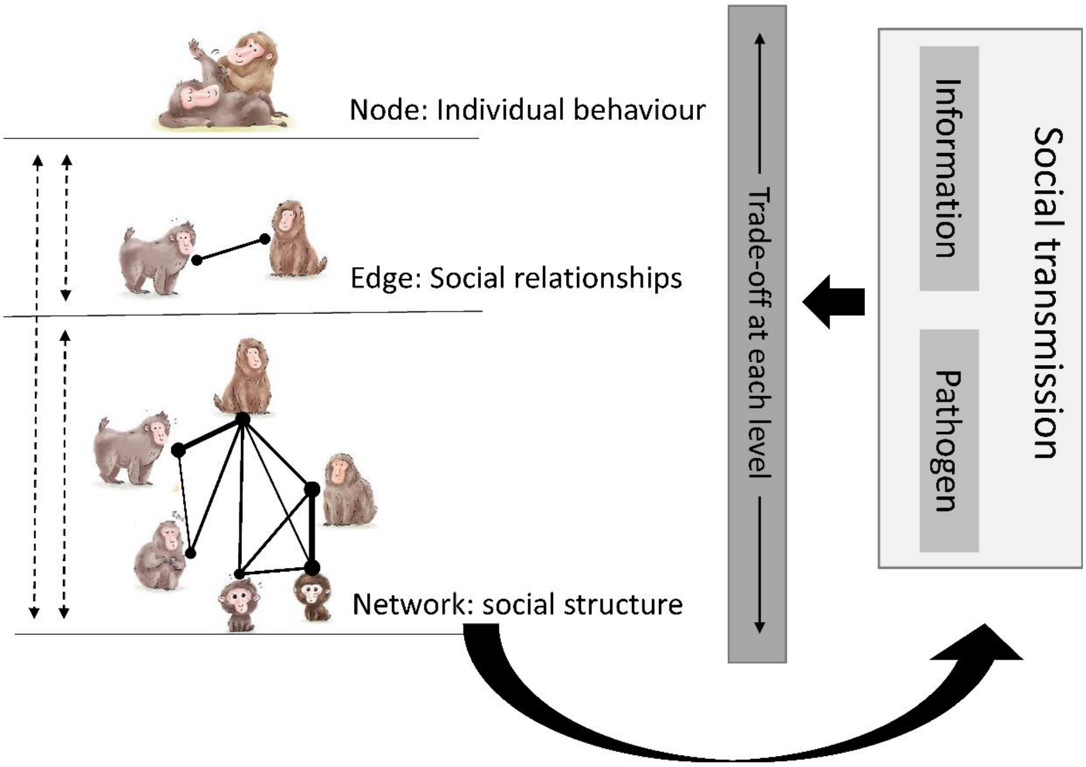

Figure 1. Schematic representation of the feedback loop between individual social structure and social transmission. Individual behavior leads to different patterns of social interactions, which in turn influence and are influenced by social structure and social transmission. We propose an implementation of Hinde's (1976) and Cantor and Whitehead's (2016) framework by integrating a simultaneous examination of information and pathogen flow as explicit and opposing entities, with emergent network properties reflecting the trade-off between each transmission process.

Concluding remarks and future perspectives

In this opinion article, we emphasized the importance of investigating mechanisms of social transmission with the potential to understand the complexity underlying individual relationships and, consequently, the great diversity in social structure observed across animal societies. Theoretical and empirical studies provide consistent evidence that social structure influences information and pathogen transmission by mediating social contact or spatial proximity. Yet, the trade-off between social information transmission and contagion risk remains under-explored.

We draw attention to the exploration of this social trade-off by showing how network properties might interact to maximize information flow and minimize pathogen transmission. It may be the combination of properties rather than any specific property, such as being central in the group, that leads to optimization of social trade-offs. Network properties at both the individual- and global-levels may then fluctuate over time according to the accumulation of individual decisions. The resulting network topology feeds back on the transmission dynamics, influencing individual fitness. This opinion article represents a step towards a more comprehensive framework for examining the connection costs and benefits inherent in animal societies. We hope it encourages researchers to venture deeper into the evolutionary significance of this under-investigated social trade-off.

Box 1. Social information transmission

In animal societies, information is broadly understood as knowledge possessed by a potential resource-holder, which may benefit other individuals if transmitted ([42], but see [8] for uncertainty on information reliability). There is a range of possible information sources, including the environment – leading to "personal information" - or conspecifics – leading to "socially acquired information", if transmitted [8]. Socially acquired information consists of behavior, innovations or knowledge transferred from one individual to another [8].

Information can be produced advertently (a signal) or inadvertently (a social cue or public information). A signal is produced by an individual for the purpose of communication [8], with a classic example being predator alarm calls [43]. Inadvertent social cues, on the other hand, might also provide information about the presence or absence of a feature, such as the spatial location of a food patch [44]. In this situation, however, the emitter has no control over the kind of information being transmitted, but natural selection might favor the abilities of other individuals to perceive such cues. Using social information is known to provide faster or better responses to environmental changes than solely using personal information. Information is thus an important currency of exchange among individuals in a society [8].

One example of information transmission comes from a wintering sub-population of great tits (*Parus major*) inhabiting the Wytham woods, England [45]. Researchers aiming to investigate the establishment of foraging techniques in the wild birds introduced a puzzle box with two opening options: slide right or left [45]. By examining the number of individuals within the flock that acquired the behavior, the research team showed that from only two trained birds in each sub-population, the information spread quickly through the social network, reaching an average of 75% of individuals in approximately 20 days. Interestingly, the sub-populations were biased toward the foraging technique originally introduced, demonstrating that informational conformity, in which individuals matched their behavior to the most common variant when first learning, is present in these wild birds [45]. In this study case, individuals chose social information over personal information.

Box 2. Infectious agent transmission

Parasites are pervasive in the lives of animals, and although in some cases infection can appear benign, without visible symptoms or obvious impacts on individual fitness, infectious organisms can nonetheless contribute significantly to mortality and morbidity [46]. For example, many microparasites, such as bacteria and viruses, are highly virulent and can cause significant population declines (e.g. Anthrax in Central and West Africa, [47]). On the other hand, macroparasites such as helminths and arthropods are more likely to exhibit chronic effects on host survival and reproduction by decreasing the potential number and quality of offspring [48].

The relationship between group-living and infectious disease seems to be generally straightforward: animals living in closer proximity and with higher contact rates should experience higher rates of pathogen transmission (e.g. primates, [49]). However, individuals have also developed defenses to prevent or respond to pathogen invasions. These anti-parasite strategies include immunological defenses to combat infection [50] as well as behavioral counterstrategies, such as hygiene [51], self-medication [52] and social avoidance [28].

Changes in the rate of contact with conspecifics may be one of the important mechanisms preventing pathogen transmission. Whether infected individuals actively avoid social interactions or become lethargic and therefore engage in fewer social interactions in general as part of the sickness response [53], or whether uninfected individuals actively avoid infected conspecifics (especially if they show signs of sickness), reduced social interactions might impact social structure in ways that can down-regulate social transmission and thereby constrain the infection to a few individuals. For example, house mice (*Mus musculus domesticus*) challenged with lipopolysaccharide (LPS), which mimics bacterial infection, reduced their own rates of social contact by avoiding encounters with other group members [54]. In contrast, mandrills (*Mandrillus sphinx*) avoided grooming at the peri-anal area of infected individuals [28]. The result in both cases, despite the different mechanisms at play, is that uninfected or healthy individuals were less likely to interact with infected conspecifics, which should theoretically slow down the spread of infection through the population.

Figure I. Empirical studies demonstrating the link between social connectivity and pathogen transmission. On the left side, free-living mice meet at a feeding spot demonstrating the periods in which social transmission occurred outside the box nets. On the right side, a female grooms an adult male as an example of the multiple bouts that occurred during the period of study. Reproduced, with permission, from Barbara Koenig and Paul Amblard-Rambert, respectively.

Box 3. Moving forward: perspectives for studying the social transmission trade-off

With regard to future research, we can think of two steps that will help to assess and clarify individual decisions and behaviour when facing the social-transmission trade-off.

1. <u>Combination of empirical and theoretical approaches</u>

   Untangling the mechanisms of social transmission requires the combination of information and pathogen transmission experiments. Such an approach is undoubtedly challenging, but here we address how the combination of theoretical and empirical approaches can contribute to filling this gap in our knowledge. Controlled environments, such as those found in the laboratory, mathematical models and computer simulations, provide the adequate conditions under which to assess how certain variables might influence individual decisions. Suggestions for experiments might include: i) the experimental infection of knowledgeable individuals while simultaneously varying the levels and values of information these individuals possess; or ii) the induction of ‘sickness states’ in individuals central to their respective networks. As in any other field, experiments should be carefully designed with respect to ethical guidelines.

2. <u>Taking advantage of state-of-the-art technology</u>

The study of animal behaviour now advances in parallel to the remarkable leaps in animal-tracking technology that has occurred over the last decades [55]. Automated techniques offer the collection of seemingly unlimited amounts of behavioural data with high resolution (e.g. small intervals of data collection). This has enhanced the robustness with which we can reconstruct social networks from data collected under both controlled and natural conditions. Examples include the use of firewire cameras to track individual fruit flies and their rates of contact [56], the use of the global positioning system (GPS) to collect proximity data from wild baboons [57], the use of proximity loggers (radio) to monitor proximity and encounters in crows [58], among several others [55]. These technologies provide data on fine aspects of social structure and thereby facilitates our investigation of the drivers behind its emergence and maintenance. Taking advantage of these emerging technnologies to highlight individual decisions under an information-pathogen transmission trade-off holds great promise for advancing our understanding of the evolutionary processes underpinning social behaviour.

Outstanding questions

- How do animals perceive others as sick? Are there mechanisms that are common among closely-related species? For example, sight and olfaction in primates?
- What are the behavioural responses towards infected individuals? To what degree does the state of infection lead to conspecific avoidance?
- How risk-sensitive should individuals be when confronted with opportunities to receive social information? Does the value of information have consequences for the development of social connections? For example, if a piece of information is difficult to perceive personally, should individuals become more risk-prone, i.e. take greater social risks, to become better informed?
- Through its impact on social connections, what are the outcomes of the global network structure? To what extent could certain network topologies simultaneously favor the spread of information and constrain pathogen transmission?
- How frequently do individual decisions take into consideration both information possession and pathogen avoidance? And to what extent might a social transmission trade-off drive the resultant social structure that emerges?
- What consequences might a social transmission trade-off have for fitness traits?

- How do sudden temporal shifts in a network, e.g. through the death or dispersal of key individuals, influence the cost-benefit ratio in a social transmission trade-off?
- Which factors drive variation in individual attributes associated with the probabilities of possessing information or being vulnerable to pathogen infection?

Highlights

- Mounting evidence shows that being social favours the transmission of information, yet it also mediates exposure to socially transmitted pathogens. How individuals deal with this group-living trade-off remains largely unknown.
- By connecting empirical and theoretical studies that investigate the influence of network properties on information and pathogen transmission independently, we draw attention to the mechanisms underlying behavioural flexibility and network plasticity.
- We argue that while access to crucial information is expected to drive individuals to cluster around knowledgeable individuals, avoidance of potential social sources of infectious disease should operate to reduce connectivity in a network.
- We propose a theoretical framework that incorporates the benefits and costs of socializing as interactive factors mediating social structure. This framework generates useful predictions for the analysis of animal societies.

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