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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 underexplored social trade-off and the evolutionary processes underlying it.

Keywords:

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

28 **After all, it is an individual's choice...**

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

31

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

46

47 **Social transmission and animal societies**

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

57 of social transmission lead to an evolutionary trade-off: while social relationships favor the
58 transmission of social information, they also favor the spread of socially-acquired pathogens.

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

65

66 **Increasing information flow and contagion risk via social networks**

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

77

78 *An individual's position within its social network*

79 An individual's network position is usually determined by the relative number and strength of
80 its social relationships, hereafter called connections. Central individuals are those with large numbers
81 of direct (e.g. number of social partners) or indirect (e.g. number of distinct subgroups to which an
82 individual is related) connections. Thus, the position of an individual within its network mediates its
83 probability of acquiring or transmitting information and infectious agents. Central individuals are
84 expected to be key dispersers of information[16], [17], controlling its quality and access[18], but are
85 also expected to spread infectious agents to a broader number of individuals and to be more at risk

86 of pathogen exposure[19]–[21]. For example, hunter-gatherer women in the Philippines who are
87 more central in their proximity networks have higher reproductive success, but they also suffer from
88 greater disease burdens (e.g. gastro-intestinal disease and respiratory tract infections[22]). Such
89 findings emphasize the role of individual centrality in information and pathogen transmission. At the
90 same time, however, as important the position of each individual is, the overall structure of the group
91 (the social network itself) is crucial to transmission dynamics as well.

92

93 *Social network topology*

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

112

113

114

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

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

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

136 The topology of the network can be thus optimized in a way that balances the costs and
137 benefits of social relationships [28], [29]. The structure of the network mediates social transmission,
138 which in turn affects each individual's probability of acquiring information or pathogens and,
139 ultimately, individual fitness. Social structure is not expected to be selected for directly (see [30] for
140 arguments to the contrary), but since the network topology emerges from the collection of individual
141 behaviours/decisions, it may vary flexibly according to the different pressures individuals face [31].
142 The mechanism of an individual behaviour affecting the social structure in which they are embedded
143 was called "collective social niche construction" [31], in reference to the "niche construction"
144 perspective. Social networks are demonstrably dynamic [32], [33], and interaction costs such as
145 pathogen acquisition [28] as well as interaction benefits such as gaining access to food [29] each

146 cause variation in individual decisions about with whom and how frequently to interact, leading to
147 the emergent social structure observed and thereafter feeding back into social transmission.

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

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

161

162 **On the interface of social transmission and social structure**

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

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

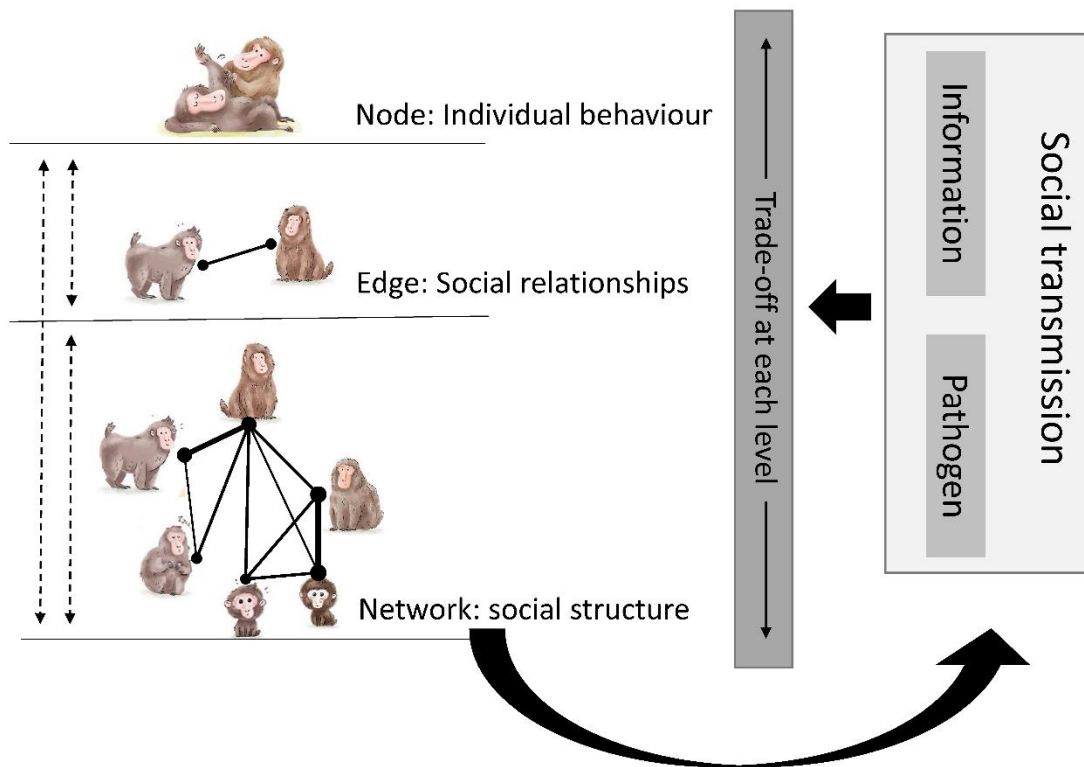
187 Indeed, evolved strategies apart from the physiological immune system also allow social
188 animals to combat the spread of infection, such as the conspecific avoidance behaviors just discussed
189 or other types of social immunity (Box 2). Although the mechanisms by which animals identify sick
190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

206 decrease in pathogen transmission. Such research shows that, indeed, individual strategies cause
207 changes in network topology, and that network plasticity affects the dynamics of pathogen
208 transmission [41].

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

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

230



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

237

238 **Concluding remarks and future perspectives**

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

245 We draw attention to the exploration of this social trade-off by showing how network
 246 properties might interact to maximize information flow and minimize pathogen transmission. It may
 247 be the combination of properties rather than any specific property, such as being central in the group,
 248 that leads to optimization of social trade-offs. Network properties at both the individual- and global-
 249 levels may then fluctuate over time according to the accumulation of individual decisions. The

250 resulting network topology feeds back on the transmission dynamics, influencing individual fitness.
251 This opinion article represents a step towards a more comprehensive framework for examining the
252 connection costs and benefits inherent in animal societies. We hope it encourages researchers to
253 venture deeper into the evolutionary significance of this under-investigated social trade-off.

254

255 **Box 1. Social information transmission**

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

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

271 One example of information transmission comes from a wintering sub-population of great tits
272 (*Parus major*) inhabiting the Wytham woods, England [45]. Researchers aiming to investigate the
273 establishment of foraging techniques in the wild birds introduced a puzzle box with two opening
274 options: slide right or left [45]. By examining the number of individuals within the flock that acquired
275 the behavior, the research team showed that from only two trained birds in each sub-population, the
276 information spread quickly through the social network, reaching an average of 75% of individuals in
277 approximately 20 days. Interestingly, the sub-populations were biased toward the foraging technique
278 originally introduced, demonstrating that informational conformity, in which individuals matched

279 their behavior to the most common variant when first learning, is present in these wild birds [45]. In
280 this study case, individuals chose social information over personal information.

281 **Box 2. Infectious agent transmission**

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

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

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



307

308 **Figure 1.** Empirical studies demonstrating the link between social connectivity and pathogen
309 transmission. On the left side, free-living mice meet at a feeding spot demonstrating the periods in
310 which social transmission occurred outside the box nets. On the right side, a female grooms an adult
311 male as an example of the multiple bouts that occurred during the period of study. Reproduced, with
312 permission, from Barbara Koenig and Paul Amblard-Rambert, respectively.

313

314

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

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

318 1. Combination of empirical and theoretical approaches

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

329 2. Taking advantage of state-of-the-art technology

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

343

344 **Outstanding questions**

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

- 360
- How do sudden temporal shifts in a network, e.g. through the death or dispersal of key
- 361 individuals, influence the cost-benefit ratio in a social transmission trade-off?
- Which factors drive variation in individual attributes associated with the probabilities of
- 362 possessing information or being vulnerable to pathogen infection?
- 363

364 **Highlights**

- 365
- Mounting evidence shows that being social favours the transmission of information, yet it also
- 366 mediates exposure to socially transmitted pathogens. How individuals deal with this group-
- 367 living trade-off remains largely unknown.

368

 - By connecting empirical and theoretical studies that investigate the influence of network

369 properties on information and pathogen transmission independently, we draw attention to

370 the mechanisms underlying behavioural flexibility and network plasticity.

371

 - We argue that while access to crucial information is expected to drive individuals to cluster

372 around knowledgeable individuals, avoidance of potential social sources of infectious disease

373 should operate to reduce connectivity in a network.

374

 - We propose a theoretical framework that incorporates the benefits and costs of socializing as

375 interactive factors mediating social structure. This framework generates useful predictions

376 for the analysis of animal societies.

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385 **References**

- 386 [1] R. A. Hinde, 'Interactions, relationships and social structure', *Man*, vol. 11, no. 1, pp. 1–17,
387 1976.
- 388 [2] J. Maynard Smith, *The major transitions in evolution*. Oxford University Press, 1995.
- 389 [3] E. O. Wilson, *Sociobiology : the new synthesis*. Harvard: Harvard University Press, 1975.
- 390 [4] R. W. Wrangham, 'An Ecological Model of Female-Bonded Primate Groups', *Behaviour*, vol.
391 75. pp. 262–300, 1980.
- 392 [5] L. A. White, J. D. Forester, and M. E. Craft, 'Using contact networks to explore mechanisms of
393 parasite transmission in wildlife', *Biol. Rev.*, vol. 92, no. 1, pp. 389–409, Feb. 2017.
- 394 [6] N. Weber *et al.*, 'Badger social networks correlate with tuberculosis infection.', *Curr. Biol.*,
395 vol. 23, no. 20, pp. R915-6, Oct. 2013.
- 396 [7] M. East, 'ALARM CALLING AND PARENTAL INVESTMENT IN THE ROBIN ERITHACUS
397 RUBECULA', *Ibis (Lond. 1859)*., vol. 123, no. 2, pp. 223–230, 2008.
- 398 [8] S. R. X. Dall, L.-A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens, 'Information
399 and its use by animals in evolutionary ecology.', *Trends Ecol. Evol.*, vol. 20, no. 4, pp. 187–93,
400 Apr. 2005.
- 401 [9] A. Whiten, C. A. Caldwell, and A. Mesoudi, 'Cultural diffusion in humans and other animals',
402 *Curr. Opin. Psychol.*, vol. 8, pp. 15–21, Apr. 2016.
- 403 [10] J. Duboscq, V. Romano, A. MacIntosh, and C. Sueur, 'Social information transmission in
404 animals: lessons from studies of diffusion', *Front. Psychol.*, vol. 7, p. 1147, 2016.
- 405 [11] P. M. Kappeler, S. Cremer, and C. L. Nunn, 'Sociality and health: impacts of sociality on
406 disease susceptibility and transmission in animal and human societies', *Philos. Trans. R. Soc.
407 B Biol. Sci.*, vol. 370, no. 1669, pp. 20140116–20140116, 2015.
- 408 [12] L. Weng, F. Menczer, and Y.-Y. Ahn, 'Virality Prediction and Community Structure in Social
409 Networks', *Sci. Rep.*, vol. 3, no. 1, p. 2522, Dec. 2013.
- 410 [13] H. Whitehead, *Analyzing Animal Societies: Quantitative Methods For Vertebrate Social
411 Analysis*. The University of Chicago Press, 2008.

- 412 [14] J. Scott, *Social Network Analysis*. SAGE Publications Ltd, 2017.
- 413 [15] D. R. Farine and H. Whitehead, 'Constructing, conducting and interpreting animal social
414 network analysis', *J. Anim. Ecol.*, vol. 84, no. 5, pp. 1144–1163, 2015.
- 415 [16] N. Claidière, E. J. E. Messer, W. Hoppitt, and A. Whiten, 'Diffusion dynamics of socially
416 learned foraging techniques in squirrel monkeys', *Curr. Biol.*, vol. 23, no. 13, pp. 1251–1255,
417 Jul. 2013.
- 418 [17] L. M. Aplin, D. R. Farine, J. Morand-Ferron, and B. C. Sheldon, 'Social networks predict patch
419 discovery in a wild population of songbirds', *Proc. R. Soc. B Biol. Sci.*, vol. 279, no. 1745, pp.
420 4199–4205, Oct. 2012.
- 421 [18] C. Vital and E. P. Martins, 'Using Graph Theory Metrics to Infer Information Flow Through
422 Animal Social Groups: A Computer Simulation Analysis', *Ethology*, vol. 115, no. 4, 2009.
- 423 [19] V. Romano, J. Duboscq, C. Sarabian, E. Thomas, C. Sueur, and A. J. MacIntosh, 'Modeling
424 infection transmission in primate networks to predict centrality-based risk', *Am. J. Primatol.*,
425 vol. 78, no. 7, 2016.
- 426 [20] S. S. Godfrey, C. M. Bull, R. James, and K. Murray, 'Network structure and parasite
427 transmission in a group living lizard, the gidgee skink, *Egernia stokesii*', *Behav. Ecol.*
428 *Sociobiol.*, vol. 63, no. 7, pp. 1045–1056, 2009.
- 429 [21] A. J. J. MacIntosh *et al.*, 'Monkeys in the middle: parasite transmission through the social
430 network of a wild primate.', *PLoS One*, vol. 7, no. 12, p. e51144, Jan. 2012.
- 431 [22] A. E. Page *et al.*, 'Hunter-Gatherer Social Networks and Reproductive Success', *Sci. Rep.*, vol.
432 7, no. 1, p. 1153, Dec. 2017.
- 433 [23] P. Sah, S. T. Leu, P. C. Cross, P. J. Hudson, and S. Bansal, 'Unraveling the disease
434 consequences and mechanisms of modular structure in animal social networks', *Proc. Natl.*
435 *Acad. Sci.*, vol. 114, no. 16, pp. 4165–4170, 2017.
- 436 [24] C. L. Nunn, C. M. McCabe, J. L. Verdolin, F. Jorda, J. H. Fewell, and C. L. Nunn, 'Infectious
437 disease and group size: more than just a numbers game', *Philos. Trans. R. Soc. B Biol. Sci.*, vol.
438 370, p. 20140111, 2015.
- 439 [25] C. Pasquaretta *et al.*, 'Social networks in primates: smart and tolerant species have more

- 440 efficient networks', *Sci. Rep.*, vol. 4, p. 7600, 2014.
- 441 [26] V. Romano, M. Shen, J. Pansanel, A. J. J. MacIntosh, and C. Sueur, 'Social transmission in
442 networks: global efficiency peaks with intermediate levels of modularity', *Behav. Ecol.
443 Sociobiol.*, vol. 72, no. 9, p. 154, 2018.
- 444 [27] K. Kashima, H. Ohtsuki, and A. Satake, 'Fission-fusion bat behavior as a strategy for balancing
445 the conflicting needs of maximizing information accuracy and minimizing infection risk', *J.
446 Theor. Biol.*, vol. 318, pp. 101–109, 2013.
- 447 [28] C. Poirotte *et al.*, 'Mandrills use olfaction to socially avoid parasitized conspecifics', *Sci. Adv.*,
448 vol. 3, no. 4, 2017.
- 449 [29] C. Fruteau, B. Voelkl, E. van Damme, and R. Noë, 'Supply and demand determine the market
450 value of food providers in wild vervet monkeys.', *Proc. Natl. Acad. Sci. U. S. A.*, vol. 106, no.
451 29, pp. 12007–12012, 2009.
- 452 [30] M. A. Nowak, 'Five rules for the evolution of cooperation.', *Sci.*, vol. 314, no. 5805, pp. 1560–
453 1563, 2006.
- 454 [31] C. Sueur, V. Romano, S. Sosa, and I. Puga-Gonzalez, 'Mechanisms of network evolution: a
455 focus on socioecological factors, intermediary mechanisms, and selection pressures',
456 *Primates*, vol. 60, no. 3, pp. 167–181, 2019.
- 457 [32] M. G. Zimmermann, V. M. Eguiluz, and M. S. Miguel, 'Coevolution of dynamical states and
458 interactions in dynamic networks', *Phys. Rev. E.*, vol. 69, p. 065102, 2004.
- 459 [33] C. Castellano, S. Fortunato, and V. Loreto, 'Statistical physics of social dynamics', *Rev. Mod.
460 Physics.*, vol. 81, no. 2, pp. 591–646, 2009.
- 461 [34] T. Gross and B. Blasius, 'Adaptive coevolutionary networks: a review', *J. R. Soc. Interface*, vol.
462 5, no. 20, pp. 259–271, Mar. 2008.
- 463 [35] M. Cantor and H. Whitehead, 'The interplay between social networks and culture :
464 theoretically and among whales and dolphins', *Philos. Trans. R. Soc. B Biol. Sci.*, vol. 368, p.
465 2012340, 2013.
- 466 [36] M. Cantor, L. G. Shoemaker, R. B. Cabral, C. O. Flores, M. Varga, and H. Whitehead,
467 'Multilevel animal societies can emerge from cultural transmission', *Nat. Commun.*, vol. 6, p.

- 468 8091, 2015.
- 469 [37] M. Rosvall and K. Sneppen, 'Reinforced communication and social navigation generate
470 groups in model networks', *Phys. Rev. E*, vol. 79, no. 2, p. 026111, 2009.
- 471 [38] G. Iñiguez, J. Kertész, K. K. Kaski, and R. A. Barrio, 'Opinion and community formation in
472 coevolving networks', *Phys. Rev. E*, vol. 80, no. 6, p. 066119, 2009.
- 473 [39] D. C. Behringer, M. J. Butler, and J. D. Shields, 'Avoidance of disease by social lobsters',
474 *Nature*, vol. 441, p. 421, 2006.
- 475 [40] S. Cremer, S. A. O. Armitage, and P. Schmid-Hempel, 'Social Immunity', *Curr. Biol.*, vol. 17, no.
476 16, pp. 693–702, 2007.
- 477 [41] N. Stroeymeyt, A. V Grasse, A. Crespi, D. P. Mersch, S. Cremer, and L. Keller, 'Social network
478 plasticity decreases disease transmission in a eusocial insect', *Science (80-.)*, vol. 945, no.
479 November, pp. 941–945, 2018.
- 480 [42] D. W. Stephens, 'Variance and the Value of Information', *The American Naturalist*, vol. 134.
481 pp. 128–140.
- 482 [43] B. Iqic, C. P. Ratnayake, A. N. Radford, and R. D. Magrath, 'Eavesdropping magpies respond to
483 the number of heterospecifics giving alarm calls but not the number of species calling', *Anim.
484 Behav.*, vol. 148, pp. 133–143, 2019.
- 485 [44] B. G. Galef and L.-A. Giraldeau, 'Social influences on foraging in vertebrates: causal
486 mechanisms and adaptive functions', *Anim. Behav.*, vol. 61, no. 1, pp. 3–15, Jan. 2001.
- 487 [45] L. M. Aplin, D. R. Farine, J. Morand-Ferron, A. Cockburn, A. Thornton, and B. C. Sheldon,
488 'Experimentally induced innovations lead to persistent culture via conformity in wild birds',
489 *Nature*, vol. 518, no. 7540, pp. 538–541, Feb. 2015.
- 490 [46] P. W. Price, *Evolutionary biology of parasites*. Princeton: Princeton University Press, 1980.
- 491 [47] C. Hoffmann *et al.*, 'Persistent anthrax as a major driver of wildlife mortality in a tropical
492 rainforest', *Nature*, vol. 548, no. 7665, pp. 82–86, Aug. 2017.
- 493 [48] R. M. May and R. M. Anderson, 'Regulation and Stability of Host-Parasite Population
494 Interactions: II. Destabilizing Processes', *J. Anim. Ecol.*, vol. 47, no. 1, pp. 249–267, Feb. 1978.

- 495 [49] C. L. Nunn and S. M. Altizer, *Infectious diseases in primates: behavior, ecology and evolution*.
496 Oxford University Press, 2006.
- 497 [50] K. Wilson, R. Knell, M. Boots, and J. Koch-Osborne, 'Group living and investment in immune
498 defence: an interspecific analysis', *J. Anim. Ecol.*, vol. 72, no. 1, pp. 133–143, 2003.
- 499 [51] C. Sarabian and A. J. J. MacIntosh, 'Hygienic tendencies correlate with low geohelminth
500 infection in free-ranging macaques', *Biol. Lett.*, vol. 11, no. 11, p. 20150757, 2015.
- 501 [52] M. A. Huffman, 'Current evidence for self-medication in primates: A multidisciplinary
502 perspective', *Am. J. Phys. Anthropol.*, vol. 104, no. S25, pp. 171–200, 1997.
- 503 [53] B. L. Hart, 'Biological basis of the behavior of sick animals.', *Neurosci. Biobehav. Rev.*, vol. 12,
504 no. 2, pp. 123–37, 1988.
- 505 [54] P. C. Lopes, P. Block, and B. König, 'Infection-induced behavioural changes reduce
506 connectivity and the potential for disease spread in wild mice contact networks', *Sci. Rep.*,
507 vol. 6, no. August, pp. 1–10, 2016.
- 508 [55] J. Krause, S. Krause, R. Arlinghaus, I. Psorakis, S. Roberts, and C. Rutz, 'Reality mining of
509 animal social systems', *Trends in Ecology and Evolution*, vol. 28, no. 9. pp. 541–551, Sep-
510 2013.
- 511 [56] M. Battesti *et al.*, 'Ecology of information: Social transmission dynamics within groups of non-
512 social insects', *Proc. R. Soc. B Biol. Sci.*, vol. 282, no. 1801, Feb. 2015.
- 513 [57] A. Strandburg-Peshkin, D. R. Farine, I. D. Couzin, and M. C. Crofoot, 'Shared decision-making
514 drives collective movement in wild baboons', *Science (80-.)*, vol. 348, no. 6241, pp. 1358–
515 1361, Jun. 2015.
- 516 [58] C. Rutz *et al.*, 'Automated mapping of social networks in wild birds', *Current Biology*, vol. 22,
517 no. 17. 11-Sep-2012.

518