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# Stemming the Flow: Information, Infection, and Social Evolution

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# Trends in Ecology and Evolution

## Stemming the flow: social evolution an information-infection trade-off

--Manuscript Draft--

<b>Manuscript Number:</b>	
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<b>Abstract:</b>	In the midst of Covid-19, we are witnessing just how critical disseminating reliable information and social distancing are in limiting pathogen transmission. This article highlights how evolution has dealt with similar information versus pathogen spread trade-offs in animal societies. We encourage an integrated theory about how we envision social networks to emerge.

Strasbourg, the 01<sup>st</sup> of April 2020Cover letter

Dear editor

We are submitting the manuscript: "*Stemming the flow: information versus infection in social evolution*" to be considered for publication in *Trends in Ecology and Evolution – Science & Society*.

The current pandemic caused by SARS-CoV-2 has raised a number of issues related to social strategies to avoid infection. Humans are trying to significantly downsize their physical contact networks to slow transmission, and this raises countless concerns given our reliance on an increasingly globalized world. We also speed up our information transmission through social media to find better solutions in the face of outbreak situations. Like humans, other group-living animals make decisions constantly that affect their social lives. Though other species cannot revolutionize their mechanisms of information exchange, as we do through digital means, they nonetheless use diverse communication modalities to spread information. According to socio-ecological pressures, individuals modify their contact rates and this has a scaling-up effect seen in the structure of the networks in which they are embedded. Individual decisions thus affect the contact network, which in turn affects the probability of an individual acquiring a pathogen. This is what humans are trying to optimize when fighting pandemics.

In this article, we explore recent advances in the field of social transmission in animal societies and propose an integrated theoretical framework through which to investigate an under-researched evolutionary trade-off facing all social animals: how to maximize information gains while minimizing pathogen acquisition. Such a framework can help us understand the evolution of social structure under competing selection pressures and may provide insight into the design and/or implementation of health interventions. We believe this topic is suitable for the section Science & Society because it addresses a highly important subject in the midst of today's Covid19 Pandemic. The thematic of study is of interest to a broader audience, including behavioural ecologists, network scientists, epidemiologists, general community etc.

The manuscript has been written to appeal to a broader audience of non-specialists by avoiding jargons (whenever possible). All authors are aware that the manuscript has been submitted for publication and have agreed on its content.

We thank you for considering our manuscript for publication in *Trends in Ecology and Evolution – Science & Society*, and we look forward to hearing from you soon.

Sincerely yours,

Valéria Romano, Andrew J.J. MacIntosh, Cédric Sueur

1                    **Stemming the flow: Information, Infection, and Social Evolution**

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13

14   **Keywords**

15   Outbreaks; Individual decisions; Social Behavior; Network plasticity; Evolutionary trade-off

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20 **Abstract**

21 In the midst of Covid-19, we are witnessing just how critical disseminating reliable information  
22 and social distancing are in limiting pathogen transmission. This article highlights how  
23 evolution has dealt with similar information versus pathogen spread trade-offs in animal  
24 societies. We encourage an integrated theory about how we envision social networks to  
25 emerge.

26

27 **Introduction**

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

31

32 As William Shakespeare observed, the contacts that individuals make lead to the passage of  
33 information among them, for better or worse, just as it does for the agents of disease. The  
34 current SARS-CoV-2 pandemic has brought into focus numerous social mechanisms to  
35 mitigate transmission. Social customs like handshaking have become anathema, while digital  
36 communications are now preferred over in-person meetings. Ultimately, humans must  
37 significantly downsize their physical contact networks to slow transmission, and this raises  
38 countless concerns given our reliance on an increasingly globalized world.

39 Like humans, other group-living animals make decisions constantly that affect their  
40 social lives, such as whether or not to interact with a particular group mate. Though other  
41 species cannot revolutionize their mechanisms of information exchange, as we do through

42 digital means, they nonetheless use diverse communication modalities to spread information.  
43 According to socio-ecological pressures, individuals modify their contact rates and this has a  
44 scaling-up effect seen in the structure of the networks in which they are embedded. Individual  
45 decisions thus affect the contact network, which in turn affects the probability of an individual  
46 acquiring a pathogen. This is what humans are trying to optimize when fighting pandemics.  
47 The field of biomimetics has produced invaluable solutions to myriad systemic and  
48 engineering challenges [1], but is there scope to use animal behavior research in search of  
49 solutions to promote global health?

50           In this article, we explore recent advances in the field of social transmission in animal  
51 societies and propose an integrated theoretical framework through which to investigate an  
52 under-researched evolutionary trade-off facing all social animals: how to maximize  
53 information gains while minimizing pathogen acquisition. Such a framework can help us  
54 understand the evolution of social structure under competing selection pressures and may  
55 provide insight into the design and/or implementation of health interventions.

56

### 57 **The trade-off between information and pathogen transmission**

58 Diversified patterns of social interaction are reflected in population-level outputs such as  
59 information and pathogen transmission. For example, the number and strength of social  
60 interactions affect how fast information and/or a pathogen is transmitted through a  
61 population. This leads to an evolutionary trade-off: while social relationships facilitate the  
62 transmission of information (e.g. behavior, knowledge), they also favor the spread of socially-  
63 acquired pathogens (e.g. respiratory viruses, ectoparasites) [2]. Fine-scale details of these

64 social interactions, i.e. as revealed by social network analysis (SNA), can help us understand  
65 how individuals deal with the challenges of group-living.

66 Network metrics are statistical measures used to characterize properties of the  
67 network, such as an individual's position within its network of contacts and the  
68 characterization of the network as a whole, or its topology. Through SNA, researchers have  
69 discovered that network properties fluctuate in time with the accumulation of individual  
70 decisions. Depending on circumstance, informed individuals might find themselves in a more  
71 central position within a network [3], while individuals avoiding contact with others showing  
72 signs of sickness might instead contribute to a more subdivided, and thus less connected,  
73 network [4]. Such behavioral and network plasticity ultimately determines the structure of  
74 information and pathogen exchange, and is thus a critical component of the resilience of  
75 populations to socio-environmental challenges. With this in mind, in Box 1 we propose an  
76 integrated framework for understanding emergent social structure given the competing  
77 demands of information acquisition and pathogen avoidance, while offering some examples  
78 of pathogen control among social animals in Box 2 and in the next section.

79

## 80 **Mechanisms of social avoidance**

81 The relationship between sociality and infectious disease is, on the surface, straightforward:  
82 animals living in closer proximity and with higher contact rates should experience higher rates  
83 of pathogen transmission. However, species have evolved myriad defenses to prevent and/or  
84 respond to pathogen invasions. These anti-parasite strategies have been collectively termed  
85 the '*ART of pathogen handling*': avoidance, resistance, tolerance [5]. To complement  
86 immunological defenses, behaviors such as hygiene, self-medication and social avoidance

87 have evolved, the latter of which, as humans are currently experiencing through worldwide  
88 lockdowns, may be among the most important mechanisms of 'social immunity' [6] and other  
89 forms of behavioral immunity preventing pathogen transmission [7].

90 Mechanisms of avoidance, however, may vary. Individuals may actively self-isolate, or  
91 due to their own lethargy may engage in fewer social interactions as part of a generalized  
92 sickness response. Uninfected individuals may also actively avoid infected conspecifics,  
93 especially those showing signs of sickness. Isolation of the infected may even be imposed or  
94 enforced by others. But whatever the case may be, restricted social interaction impacts social  
95 structure in ways that down-regulate social transmission and reduce a pathogen's basic  
96 reproduction number ( $R_0$ ) to below replacement ( $R_0 < 1$ ), after which point the outbreak  
97 becomes unsustainable.

98 Examples of social avoidance in animals are widespread, in taxa as divergent as  
99 arthropods and mammals (Box 2). One poignant example seen in the black garden ant (*Lasius*  
100 *niger*) demonstrates that pathogen exposure induces behavioral changes that reinforce  
101 transmission-inhibitory characteristics in the contact network: i.e. increased modularity,  
102 clustering and assortativity, and decreased transmission efficiency [4]. Not only did foragers  
103 exposed to a fungus natural to the ants' habitat isolate themselves from the colony, healthy  
104 foragers also decreased their contact time with the rest of the colony [4]. If this sounds  
105 familiar, it is because it is: humans around the world are currently using the same approach  
106 to COVID-19.

107 The ant example highlights that social animals are capable of modulating their  
108 behavior in ways that increase the benefits and avoid the costs of social interactions  
109 dynamically, and this should lead to detectable changes in network structure, which in itself



110 up- or down-regulates social transmission (Figure 1). But how are individuals expected to  
111 behave when, despite the risks of infection, there remains the need to acquire social  
112 information? While empirical studies in animals are lagging, a recent theoretical model of  
113 roost selection in bats has demonstrated that fission-fusion behavior, whereby individuals  
114 fluctuate in their degree of sociality through time, resulting in more or less modular networks,  
115 is a strategy that can result from a collection of individual decisions aimed at maximizing  
116 information accuracy and minimizing infectious disease risk [8]. Collectively, network  
117 properties like modularity and density can be used as powerful estimators of transmission  
118 processes, with each property potentially working as a buffer and/or facilitator of social  
119 transmission.

120

121 (Figure 1)

122

### 123 **The evolutionary mechanisms of social transmission**

124 Social networks have self-organizing components in their local interactions and  
125 individual behavior, which remain flexible and responsive to the divergent pressures each  
126 individual face. Humans know this and try to use this information to manage network flows  
127 in myriad contexts. The mechanism by which individual behavior influences the social  
128 network into which they are embedded is known as *“collective social niche construction”*.  
129 Social networks are demonstrably dynamic, and interaction costs and benefits cause variation  
130 in individual decisions about with whom and how frequently to interact. The emergent social  
131 structure observed then feeds back into the dynamics of social transmission. From this

132 perspective, individuals that better adjust their behaviors to meet the challenges both  
133 external to and inherent in social relationships might be able to increase their own fitness (i.e.  
134 survival and reproductive success). These individual traits would then be favored by natural  
135 selection, and the social networks they form will have gained resilience through evolutionary  
136 time.

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### 138 **Prognosis**

139 Illuminating the role of individuals, as they navigate their social worlds and contribute to the  
140 various flows within their respective social networks, highlights that effective epidemic  
141 control strategies depend on the collective sum of their behavior. We have shown that  
142 solutions do exist in social animals, and that, like in humans, other species can adapt their  
143 contact rates, their communication modalities and their network structure to limit pathogen  
144 spread. Our modern understanding of pathogen spread and its mitigation has a history of less  
145 than two centuries, whereas evolution has used hundreds of millions of years to hone  
146 solutions to this critical challenge in nature. More attention on this topic is needed, on a  
147 greater diversity of species and on the underlying mechanisms of network plasticity and  
148 resilience. In this context, we call for more research into the information-pathogen trade-off  
149 in network evolution among social animals. Such research may reveal novel solutions to  
150 infectious disease outbreaks with relevance even to human social systems. We propose that  
151 consideration not only of how infectious diseases emerge in animal populations but also how  
152 they are regulated and even mitigated through processes like those described in this essay is  
153 well within the purview of the One Health paradigm, and may thus contribute to the fostering  
154 of global health and well-being.

155 **Beyond our social world**

156 Perhaps one of the least controversial lessons we have learned during the COVID-19  
157 pandemic, yet one that has garnered far less media attention since the world shifted into  
158 lockdown of human interaction, is that, for better and for worse, our own social networks are  
159 situated within a broader ecological context of interaction with nature. As the onrushing of  
160 human consumption invades deeper and deeper into the wild places of the world, we are  
161 increasingly exposed to all manner of novel infectious organisms that circulate undetected in  
162 wildlife. It is common knowledge that most emerging infectious diseases in human  
163 populations are zoonotic, i.e. of animal origin, with as much as 70% of those originating in  
164 wildlife [9]. Social distancing and digital communication can slow the spread of SARS-CoV-2,  
165 but more responsible interaction with the natural world [10] might have mitigated its  
166 emergence altogether.

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176 **Box 1. At the interface of social transmission and social structure**

177 Hinde's framework of animal society [11] posits that the quality and patterning of  
178 relationships is molded by social structure, while social structure itself is driven by socio-  
179 ecological factors. Cantor & Whitehead [12] extended Hinde's framework by incorporating  
180 information transmission at the final level of the model shown in Figure B1, highlighting  
181 bidirectional effects. For example, variation in the vocal repertoires of cetaceans causes  
182 clustering of individuals with similar patterns [13]. Within clusters, individuals are also more  
183 likely to share information.

184 What remains missing from Hinde's framework, however, is a role for deleterious  
185 forms of social transmission like those that lead to infectious disease. Socially-transmissible  
186 pathogens may negatively affect social cohesion, either directly or indirectly, by reducing  
187 social connectivity. Concurrently, the overarching social structure sets the conditions under  
188 which individuals are exposed to such pathogens, creating bidirectional feedback (Figure B1).  
189 Here, we extend Hinde's framework to incorporate connection costs like the spread of  
190 pathogens (Figure B1). Instead of considering transmission as an endpoint, or assume that  
191 information flow is all that matters, we suggest simultaneous examination of information and  
192 pathogen transmission as explicit and opposing entities driving social structure and behavior.  
193 The result is a classical fitness trade-off in which the need to exploit social relationships while  
194 minimizing the associated costs drives the evolution of social behavior.

195 (Figure B1)

196

197

198 **Box 2. Examples of social avoidance behaviors across the animal kingdom**

199 Evolved strategies other than the physiological immune system allow social animals to  
200 combat the spread of infection, such as conspecific avoidance. Examples of social avoidance  
201 and self-isolation abound in nature (Figure BII). Caribbean spiny lobsters (*Panulirus argus*)  
202 avoid dens housing individuals infected with a lethal virus [14]. Immune-challenged mice (*Mus*  
203 *musculus domesticus*) reduced their own rates of social contact by avoiding encounters with  
204 group members [15]. Trinidadian guppies (*Poecilia reticulata*) avoid conspecifics infected with  
205 an ectoparasite in the late stages of infection [16]. Mandrills (*Mandrillus sphinx*) recognize  
206 parasitized conspecifics and avoid grooming contaminated body regions [17]. Critically,  
207 mandrills appear not to avoid interactions with infected maternal kin [18]. This last discovery  
208 should resonate with those taking risks to make quarantine with family. Social insects go so  
209 far as to engage in collective defense against parasites through so-called ‘social immunity’,  
210 where they cooperate in different ways to combat colony infection [6]. These examples  
211 emphasize how social behavior can influence the dynamics of pathogen transmission via an  
212 added layer of defense.

213 (Figure BII)

214

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262 **Figures legend**

263 **Figure 1.** Evidence for network plasticity and its effects on pathogen transmission rates. We  
264 present the behavioral mechanisms underlying human (a), ant (b), and non-human primate  
265 (c) social contact. When a pathogen is introduced in a system and detected, infected and non-  
266 infected individuals usually change their contact rates. This leads to changes in network  
267 structure, such as increasing the number of subgroups, which affects the efficiency of  
268 pathogen transmission (d). Conceptually, the feedback is similar across the three systems  
269 depicted. The communication system can also change, as exemplified by both ants and  
270 humans, from a targeted and local contact-based modality to a global or more broadly-  
271 disseminated modality (e.g. public information such as online communications or pheromone  
272 trails/clouds). The networks in (b) and graph in (d) were reprinted from Stroeymeyt et al. 2018  
273 ‘Social network plasticity decreases disease transmission in a eusocial insect’, *Science* 941–  
274 945. Copyright (2018), with permission from the American Association for the Advancement  
275 of Science. Images from macro and microorganisms created with BioRender.com.

276

277 **Figure BI.** Schematic representation of the feedback loop between social structure and social  
278 transmission, both beneficial and detrimental. Individual behavior leads to different patterns  
279 of social interaction, which in turn influence and are influenced by cultural and pathogen  
280 transmission pressures. We propose a framework that integrates the two, simultaneously  
281 examining information and pathogen flow as explicit and opposing entities, with emergent  
282 network properties reflecting a trade-off between them. Macaque images, credit: Delphine  
283 Vaufrey.

284



285 **Figure BII.** Empirical studies demonstrating that social avoidance is an important strategy for  
286 controlling pathogen spread: (a) Trinidadian guppies (*Poecilia reticulata*) (credit: Darren  
287 Croft), (b) mandrills (*Mandrillus sphinx*) (credit: Paul Amblard-Rambert), (c) Caribbean spiny  
288 lobsters (*Panulirus argus*) (credit: Donald Behringer) and (d) house mice (*Mus musculus*  
289 *domesticus*) (credit: Barbara Koenig).

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