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Emerging infectious disease and the challenges of social distancing in human and non-human animals

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The 'social distancing' that occurred in response to the COVID-19 pandemic in humans provides a powerful illustration of the intimate relationship between infectious disease and social behaviour in animals. Indeed, directly transmitted pathogens have long been considered a major cost of group living in humans and other social animals, as well as a driver of the evolution of group size and social behaviour. As the risk and frequency of emerging infectious diseases rise, the ability of social taxa to respond appropriately to changing infectious disease pressures could mean the difference between persistence and extinction. Here, we examine changes in the social behaviour of humans and wildlife in response to infectious diseases and compare these responses to theoretical expectations. We consider constraints on altering social behaviour in the face of emerging diseases, including the lack of behavioural plasticity, environmental limitations and conflicting pressures from the many benefits of group living. We also explore the ways that social animals can minimize the costs of disease-induced changes to sociality and the unique advantages that humans may have in maintaining the benefits of sociality despite social distancing.

1. Introduction

Recent decades have been characterized by an increase in the emergence of novel pathogens and the spread of existing ones, driven by factors such as human population growth, global commerce and travel, anthropogenic environmental change and interactions between humans, wildlife and domestic animals [1–3]. Because the reproductive rate of directly transmitted pathogens increases with the availability of hosts and their rate of contact [4,5], social animals (including humans) that live at high local densities of closely interacting conspecifics may be particular vulnerable to the threats posed by some of these emerging infectious diseases (EIDs). Reducing the degree of sociality (i.e. the tendency to congregate in groups with conspecifics) might therefore be an important strategy by which social animals can ameliorate the impacts of directly transmitted EIDs.

In social species, the extent to which individuals adjust their behaviour in response to EIDs (here defined as new or previously unrecognized infectious agents within a population) has been illustrated dramatically by the voluntary and mandated social distancing in humans during recent outbreaks of Ebola, H1N1 and COVID-19 [6–8]. Humans are only one of the many social animals that have recently been challenged by EIDs (e.g. [9–11]), creating an unprecedented opportunity to assess changes in the social behaviour of humans and wildlife in response to a breadth of novel pathogens (figure 1) and compare these responses to theoretical expectations (reviewed in [5,19,20]). Although we focus on responses to EIDs, we also draw on the better-established literature on

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potential responses to EID	mechanism	example
decreased sociality	A. Active avoidance of infected conspecifics by uninfected individuals; general declines in social attraction	A. Lobsters and PaV1 [10,12] 
	B. Reduced sociality/activity by infected individuals expressing sickness behaviour	B. Bats and WNS [13,14] 
	C. Self-removal of infected individuals from social groups	C. Bees and *Nosema* [15] 
increased modularity; xenophobia	D. Perception of foreign others as pathogen risks	D. Humans and COVID-19 [6] 
no change/limited change in sociality	E. Behavioural constraints	E. Tasmanian devils and DFTD [16] 
	F. Environmental constraints	F. Amphibians and Bd [17] 
increase in/ stabilization of sociality	G. Encounter-dilution effect	G. Roost size and WNV [18] 
	H. Affiliative interactions that promote recovery	H. Wolves and mange [11] 

Figure 1. Potential changes in the degree of host sociality in response to EIDs, along with putative mechanisms driving the change and examples. Examples are referred to by letter and explained further in the text. Citations for each example given in parentheses

behavioural responses to endemic pathogens to examine the potential for, and constraints on, adaptive social evolution in response to disease emergence.

Behavioural responses to disease akin to social distancing are almost certainly costly to all social animals, including humans, but the regular occurrence of these behaviours in nature (e.g. [9,12,21]) suggests that their benefits can (at least sometimes) outweigh their costs. In this review, we consider ways in which some social animals maximize benefits and minimize costs using risk-sensitive responses to pathogens. We also examine the extent to which technology might buffer modern humans from the negative consequences of pathogen-mediated reductions in sociality for our mental and physical health [22–24], or exacerbate the feelings of loneliness that can accompany social isolation [25–28].

2. Inferring risk: cues of emerging infectious disease

In order to avoid pathogens, animals must first perceive them. The novelty of EIDs can pose a particular challenge to hosts in this regard because the specific cues associated with infection may be unfamiliar and not induce appropriate avoidance responses. Even endemic pathogens, with which hosts have had a longer evolutionary history, are often imperceptible [29]. Many animals must therefore infer and respond to infection risk from (imperfect) heuristic cues such as sickness behaviour and morphological abnormalities (e.g. [30,31]). The generality of the cues that uninfected animals use to alter their social behaviours in response to pathogen risk will determine the extent, speed and manner in which hosts respond to novel pathogens on ecological (within-generation) timescales.

Given the substantially greater fitness costs of false negatives (mistakenly categorizing an infected individual as healthy) as compared with false positives (mistakenly categorizing a healthy individual as infected), social organisms tend to overgeneralize disease-relevant cues. Fish and finches, for example, use general visual cues (e.g. lethargy) as an index of infection status [31,32], and chimpanzees (*Pan troglodytes*) ostracize group members who exhibit behavioural changes (e.g. after recovering from polio [33]). Similarly, humans avoid and stigmatize individuals with benign physical abnormalities such as obesity and facial asymmetry, despite the low diagnostic precision of these cues for infection risk [30,34]. Beliefs that one is especially vulnerable to disease also exacerbate the overperception bias of sickness cues, lowering the threshold at which humans identify others as potential health threats [35]. Across the animal kingdom, the emotion of disgust, an innate and learned response to these general cues of potential infection, is hypothesized to be one mediator of avoidance behaviour [29,36]. Overall, the use of fairly general cues of infection risk suggests that social distancing in response to EIDs could occur on rapid ecological timescales by some social animals. If these EIDs persist in a given population, hosts may then fine-tune their ability to recognize and effectively respond to a novel pathogen on evolutionary (across-generation) timescales, potentially leading to permanent reductions or alterations in sociality.

3. Emerging infectious diseases and reductions in sociality

An increased likelihood of parasite transmission has long been considered an 'automatic and universal' detriment to

living in groups [37], and parasite prevalence and intensity do increase with group size for a suite of social animals (e.g. [38,39]). Therefore, we might expect to see a general pattern of reduced sociality after the emergence of infectious pathogens, particularly for those that are directly transmitted and highly virulent. For example, an increased percentage of little brown myotis (*Myotis lucifugus*) was found roosting individually after the emergence of the devastating fungal pathogen *Geomyces destructans* [13], and uninfected Caribbean spiny lobsters (*Panulirus argus*) were more likely to den alone or abandon their group den [12,40] in the presence of a conspecific infected with *Panulirus argus* virus 1, a lethal pathogen first documented in 2000 ([10,12,41]; figure 1*a*).

Mechanistically, declines in sociality in response to EIDs can result from changes in the behaviour of infected and/or uninfected hosts. Infected hosts can reduce their sociality as a consequence of sickness behaviours (e.g. lethargy and apathy) ([14]; figure 1*b*) or active 'self-removal', a seemingly altruistic behaviour in which sick individuals leave their group to die in isolation [42]. For example, foraging honeybees (*Apis mellifera*) infected with the recently emerged pathogens *Varroa destructor* or *Nosema* sp. have a lower return rate to their hive, which could be a general response to infection that enhances colony survival ([15]; figure 1*c*). Such self-removal is hypothesized to be favoured in bees and other eusocial insects when the inclusive fitness benefits of protecting the colony from infection outweigh the survival cost to the individual [42]. Uninfected hosts can reduce their sociality by active avoidance of contaminated or infected conspecifics [12], or by generalized reductions in social attraction in response to elevated pathogen pressure ([10]; figure 1*a*). Although all of these mechanisms generally reduce pathogen spread and can be challenging to tease apart, the primary focus of this review is on reductions in sociality driven by the behaviour of uninfected individuals.

Regardless of the mechanism, disease-mediated reductions in sociality are likely to involve costs and trade-offs, including increased energetic output, increased susceptibility to predators or other opportunities lost [19]. Solitary roosting in little brown bats, for example, could increase the energetic costs of hibernation [43] and declines in social attraction of Caribbean spiny lobsters likely increase (non-human) predation risk, because conspecific chemosensory cues can reduce search time for appropriate shelters [10,41]. On evolutionary timescales, these costs must be outweighed by those of pathogen pressures to favour more permanent shifts away from sociality. Ultimately, however, if the selection pressure from EIDs is strong, sustained and outweighs conflicting selective pressures, and if the degree of sociality or avoidance of infected conspecifics is heritable, reductions in sociality could occur on evolutionary timescales. Although empirical data are scarce, one potential example has been documented in Caribbean spiny lobsters, among which attraction to conspecific chemical cues has declined over time and is lower in a region of higher PaV1 prevalence ([10]; figure 1*a*). This apparent reduction in sociality could be driven by the avoidance of conspecifics infected with PaV1 [10,12,41], although this interpretation must be made with caution, because reductions in social attraction might also be a response to human fishing pressure on larger lobster groups, and because the origin and exact timing of PaV1 emergence is unclear [10]. In general, given the costs associated with the loss of sociality, we might expect EIDs to favour temporary or dynamic shifts away from sociality in response to fluctuating disease pressures, or to favour specific changes in social structure (e.g. increased modularity) that minimize social costs by maintaining within-group interactions.

4. Modularity and xenophobia in response to infection risk

Some directly transmitted pathogens could favour greater differentiation within and among social groups, rather than a reduction in group size or degree of sociality per se, thereby limiting the movement of individuals (and their pathogens) within and among groups. For example, Stroeymeyt *et al.* [21] found that the social network of *Lasius niger* ants was more modular than predicted by chance, which slowed the spread of a hypothetical pathogen through the colony; moreover, modularity increased even further when ant colonies were exposed to an endemic fungal pathogen. Furthermore, parasites are posited to have played an important role in the evolution of group stability and resistance to immigrants among non-human primates [44], and a cross-species comparison of 19 non-human primate species indicated that modularity among social groups is associated with lower richness of directly transmitted parasites [45]. Likewise, in humans, recent modelling of the spread of COVID-19 across social networks suggests that increased modularity based on geographical location and similarity would dramatically reduce spread ([6]; figure 1*d*). On the other hand, female gorillas (*Gorilla gorilla gorilla*) are more likely to emigrate between groups when infectious skin lesions are present on troopmates [46]. Thus, behavioural avoidance in response to some EIDs may increase the degree of connection among social groups, at least at the temporal resolution of dispersal decisions, and thus may decrease modularity.

In humans, pathogens may increase modularity by increasing ingroup–outgroup distinctions. In the presence of cues suggesting high pathogen stress, humans adopt a pathogen-avoidance psychology that is hypervigilant and particularly error-prone, during which even benign physical and behavioural deviations from expected phenotypes may be treated as potential cues of infection [47,48]. The resulting increased aversion to and avoidance of 'foreign others' and a corresponding preference for familiar ingroup individuals [34,49,50] can manifest as a general antipathy towards outgroup members. Moreover, historical pathogen prevalence at the country level is positively associated with collectivism (characterized, in part, by stronger ingroup–outgroup distinctions), greater ingroup loyalty, preference for conformity and obedience in others, and stricter adherence to and policing of social norms, as well as negatively associated with extraversion, openness to experience and normative physical contact (e.g. handshake greetings and romantic kissing [51–54]). These patterns highlight functional behavioural plasticity in response to the presence of infectious disease. For example, in a social species like humans, being extraverted can afford numerous benefits (e.g. mating opportunities and social allies), but can come at the cost of increased infection risk [55]. Whether such costs outweigh the benefits depends, in part, on the likelihood of incurring the costs; thus, the higher the pathogen prevalence, the more strongly disease-specific costs depress the functional benefits of extraversion [54]. An increasing risk of EIDs might therefore favour the

balance towards a more risk-averse, more xenophobic and less social phenotype.

Although heightened disease threat can promote differentiation among social groups, it may also increase within-group cohesion for both human and non-human animals. Care of infected individuals is particularly well documented within colonies of eusocial insects, for which infection risk may be especially high because of high local density, high relatedness among group members and a pathogen-rich environment [56]. Similarly, mandrills (*Mandrillus sphinx*) will groom close maternal kin infected with oro-faecally transmitted protozoa, whereas they avoid grooming other infected conspecifics [57]; maintaining these social interactions with close kin may be more important than infection avoidance in this system. In humans, signs of illness can promote caregiving and helping behaviour with social allies [58] and strengthen family ties [59]. Human caring and helping behaviours offer numerous potential benefits, including enhanced prestige and downstream reciprocity [60].

5. Constraints on social behaviour, emerging infectious diseases and extinction risk

In some systems, hosts might not be able to alter social behaviour rapidly or sustainably in response to a novel pathogen pressure, potentially elevating their extinction risk. On ecological timescales, animals may not possess the sensory or behavioural ability to respond appropriately to cues of conspecific EID infection. On evolutionary timescales, even if there is sufficient heritability in sociality, the key benefits of sociality may constrain the ability of some taxa to respond. For example, living in social groups appears to increase Ebola-Zaire virus risk in western lowland gorillas: the death rates of solitary male gorillas were 77% following the emergence of the virus in the Congo, whereas death rates among group-living gorillas were estimated at 97% [61]. However, an evolutionary shift towards increasing solitariness is unlikely to be sustainable in western lowland gorillas, as living in groups serves essential functions for predator avoidance and protection against infanticide among females with juveniles [62].

Disease-mediated reductions in specific social interactions can pose a particular challenge when their loss impacts fecundity, even among relatively solitary animals. For example, Tasmanian devils (*Sarcophilus harrisii*) are threatened with extinction by devil facial tumour disease (DFTD), which causes conspicuous lesions that eventually lead to death [63,64]. Aggressive conspecific interactions (e.g. when a dominant devil bites the tumour of a subordinate) are the primary transmission route for the tumour cells that cause DFTD [64]. Although less aggressive devils could therefore have lower exposure, selection pressure for a less aggressive phenotype could be opposed by sexual selection: aggressive, socially dominant individuals have relatively high reproductive output, along with an elevated likelihood of infection ([16]; figure 1*e*). Nevertheless, Hubert *et al*. found recent evidence for intense selection on genes associated with cancer progression in devils, and a subset of these genes have human orthologues associated with deficits in communication (e.g. intellectual disabilities and autism spectrum disorder, [65]). These data suggest that devils might be under selection pressure from transmissible cancer to alter their social interactions, despite potential fecundity costs. It is unclear if potential evolution of social behaviour will be sufficient to protect devils from extinction, however, because the prevalence of the disease remains high even at low host population densities, because it impacts both survival and recruitment, and because disease-driven reductions in devil populations may have increased their vulnerability to extinction by stochastic processes [66].

Environmental factors might also constrain the ability of organisms to alter their social interactions in response to pathogen pressure [67]. In many amphibian species, for example, dependence on water for egg-laying and a tendency to lay communal egg masses that produce highly social tadpoles could increase transmission risk of Ranavirus and the fungal pathogen *Batrachochytrium dendrobatidis* [68,69]. Even though these EIDs are considered important cofactors in amphibian declines and extinctions [70], the lack of behavioural and environmental flexibility could constrain adaptive reductions in aggregation ([17]; figure 1*f*). Similarly, reliance of waterfowl on a limited set of increasingly polluted water bodies, in which they congregate at high densities along migratory pathways, has been linked to the increasing occurrence of die-offs driven by avian cholera [71]. By contrast, species with a broad environmental tolerance combined with relatively flexible behavioural strategies might be better poised to weather novel disease pressures by altering their social behaviours, although the extent to which this is true remains an important question for future work.

6. Emerging infectious diseases that do not lead to reduced sociality

Not all EIDs are expected to select against living in groups. For example, the encounter-dilution effect (a decline in a per capita vector biting rate with increasing group size) predicts that risk of infection by vector-borne pathogens will be lower in groups [72]. Evidence for this effect has been documented in flocks of American robins (*Turdus migratorius*) during the transmission season for West Nile virus, an emergent mosquito-borne flavivirus ([18]; figure 1*g*): the estimated per capita bite rate by infected mosquitoes was lower for robins within roosts, and the seroconversion rate was lower for sentinel house sparrows (*Passer domesticus*) within roosts relative to non-roost sites, indicating that West Nile virus risk was lower for birds in groups. In general, pathogens that do not have a higher transmission rate within social groups will not drive selection against sociality.

Even for pathogens that are directly transmitted, characteristics such as their virulence and length of infectious period could influence the extent to which they ultimately select against sociality. For low-virulence pathogens (e.g. the common cold in humans; sarcoptic mange in wolves), the benefits of group living could balance or outweigh the costs of increased transmission risk [11]. Across taxa, perceived social isolation and low social integration can promote stress, disease and mortality [73,74] and accelerate disease progression [75], whereas affiliative interactions have the potential to promote recovery [76], all of which can balance some of the infection risks of living in a group. Furthermore, group living can directly compensate for some of the costs of infection when groups have more effective predator vigilance, benefitting infected prey species [77] and more efficient foraging,

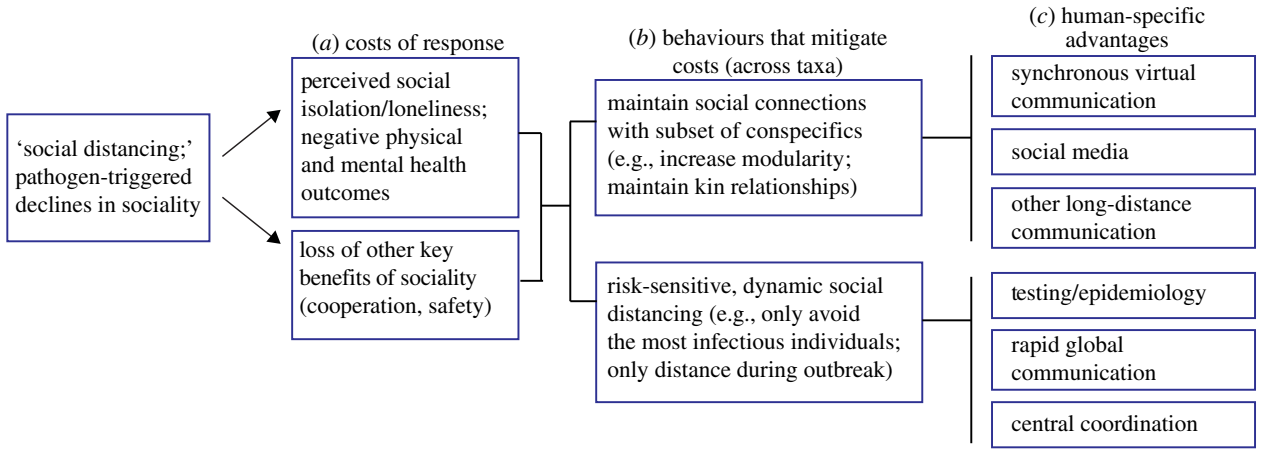

Figure 2. Social distancing in response to disease (*a*) can result in severe costs for social animals. (*b*) Behavioural adaptations such as risk-sensitive social distancing and the maintenance of some social connections could mitigate these costs. (*c*) Humans have numerous potential advantages for implementing risk-sensitive social distancing and mitigating the costs of social isolation. (Online version in colour.)

benefitting infected predators [11]. In a grey wolf (*Canis lupus*) population, for example, the negative effects of sarcoptic mange 7 years after its emergence were ameliorated in larger packs, such that the mortality risk of an infected wolf surrounded by five pack-mates was equal to that of an uninfected wolf ([11]; figure 1*h*). Similarly, theoretical models parametrized with data from human societies suggest that only high-virulence pathogens will select for an increase in social avoidance, whereas pathogens of low or moderate virulence, particularly when widespread, will not select for increases in avoidance [76]. Finally, pathogens with relatively long infectious periods, such as those that typically produce chronic infections (e.g. [11]), may not favour social distancing because the costs of distancing would need to be tolerated for unsustainable lengths of time.

7. Minimizing costs of distancing: risk-sensitive responses to infection

The costliness of distancing behaviours for all social animals should favour the evolution of risk-sensitive responses. For example, guppies with the weakest physiological defences against a parasitic worm are the ones most likely to avoid potentially parasitized conspecifics [78], particularly those that pose the greatest risk for transmission [79]. While these fine-tuned, risk-sensitive responses are most likely to evolve in response to long-term selection from endemic parasites, social species also show risk-sensitive responses to the general sickness cues that might be associated with EIDs. For example, house finches (*Haemorhous mexicanus*) with the lowest levels of two immune markers are most likely to avoid conspecifics expressing generalized sickness behaviours [31]. In humans, disease-avoidance responses vary with actual or perceived vulnerability to disease: people with a greater dispositional tendency to worry about disease, as well as those whose immunological defences are suppressed (e.g. pregnant women in their first trimester), exhibit greater ethnocentrism and xenophobic attitudes [49,80]. Individuals who exhibit chronically heightened disease concern or disgust sensitivity also have a greater tendency to classify unfamiliar individuals as threatening [81]. Furthermore, experimentally increasing pathogen salience among humans in the laboratory elevates avoidant motor movements in response to photos of strangers [55]. Overall, risk-sensitive responses of social animals to general infection cues would enable individuals to capitalize on the benefits of social interactions whenever possible while minimizing their specific infectious disease risk.

8. Can virtual communication mitigate costs of social distancing for humans?

The costs of social distancing in humans are as profound as those of other animals ([74]; figure 2*a*). Both objective social isolation (the actual loss of social ties) and perceived social isolation (the feeling of a lack of engagement with others; loneliness) in humans can, through various mechanisms, cause substantial increases in morbidity and mortality rates [82,83], similar to those associated with obesity [84]. Indeed, some research suggests that the size and quality of our friendship networks has a greater effect on our susceptibility to disease and death than any variable save quitting smoking [85]. However, friendships are highly sensitive to interaction frequency, with reduced contact leading to rapid decay in perceived quality [86].

Despite our similarities with other social taxa, humans have several advantages in implementing risk-sensitive social distancing and minimizing its costs (figure 2*c*). These include the ability to communicate disease risk globally, enabling social distancing to be implemented prior to the emergence of disease [87] and the use of diagnostic tests, contact tracing approaches and epidemiological models to assess and respond to risk in a targeted manner [88,89]. Moreover, it is possible that virtual communication and social media could ameliorate some of the costs of perceived social isolation. Some hope may come from the observations that one may be objectively socially isolated and not feel lonely: objective and perceived isolation are related but not the same [25]. Indeed, the effects of perceived social isolation on health are comparable to, and appear better supported than, those of objective social isolation [73,82,90]. Potentially, then, if technology can alleviate our perceived social isolation, it may allow us to maintain the physical and mental health benefits of sociality while avoiding the associated disease transmission risk.

The effects of social media on perceived social isolation has received much attention, but evidence is mixed. On one hand, social media can promote the formation of networks among people with rare interests or conditions, increasing feelings of social connectedness [23,24]. However, among a large cohort of young adults, social media usage is correlated with *increased* perceived social isolation [25], perhaps because social media often presents the 'highlight reel' of people's lives, making observers feel less happy and more socially isolated by comparison [26–28]. The use of Facebook, in particular, has been linked to low mood and depression in many populations [27,28,91]. We note, however, that inferring causality from these data is challenging: for example, a predisposition to 'fear of missing out' (FoMO) and social comparison [92], and potentially objective social isolation [25], predict an individual's likelihood of engaging with social media.

Although asynchronous interactions via social media may not buffer us against the potential health impacts of enforced social isolation, synchronous virtual communication (e.g. Zoom, Skype or FaceTime) might. For example, rare data from confined populations of humans using technology as their only source of contact with their networks indicate that synchronous virtual communication can mitigate some of the negative effects of confinement [22]. Furthermore, people rate the quality of interactions with their close friends via Skype as similar to in-person interactions; both considerably outperform phone, text, email and social networking. This may be because synchronous interactions permit 'copresence' and repartee, as well as providing visual cues that make interaction more effective [82,93]. The benefits of synchronous virtual communication also apply to professional settings. For example, computer-mediated discussions promote more equal participation from minorities and women than in-person discussions [94], and virtual communication also facilitates (non-threatening) interactions with diverse individuals and groups [95]. While there are undeniable benefits to synchronous video communication, it has long been established that the extended use of computer displays can cause visual fatigue [96]; likewise, virtual meetings may cause greater fatigue than in-person meetings. Technological issues can also affect how we perceive others: a delay of 1.2 s makes people seem less attentive and conscientious [97]. Overall, however, the effective use of synchronous virtual communication platforms could maintain or even enhance some of the benefits of sociality for humans, giving us a unique advantage over other animals during periods of social distancing.

9. Conclusion

EIDs have been credited as major contributors to recent population declines across a range of social taxa, from bats, bees and tortoises to amphibians, primates and marsupials [13,61,63,70,98,99]. In general, EIDs are more likely to arise in populations that are experiencing other forms of stress and may therefore exacerbate the challenges faced by those already in decline or near extinction [70,99]. As this review has shown, however, behavioural responses of social animals to EIDs may offer some reprieve, depending on the transmission mode and virulence of the pathogen. Characteristics of the host (e.g. the importance of sociality or specific social interactions [16,61]) or the environment (e.g. habitat limitations [17]) will constrain the ways in which social animals respond to novel pathogens and mediate the effects of EIDs on their behaviour and populations, although the potential links between social flexibility and disease-driven extinction risk have not been fully evaluated.

In humans, disease-mediated pressure on social behaviour is likely to increase as factors such as overpopulation, poverty, intensive agriculture and global commerce accelerate the rate of infectious disease emergence [3]. Directly transmitted EIDs, in particular, are likely to have powerful impacts on human social behaviour, potentially increasing within-group cohesion and altruism [59], while increasing the avoidance of social interactions and entities that pose potential infection risk [55,81]. Although increased insularity in response to novel disease pressures might have been adaptive in the past, Schaller *et al*. [100] argue that xenophobic responses (e.g. blaming foreigners for EIDs) are unlikely to be adaptive in modern human societies: such responses stymy efforts to find effective solutions to outbreaks and potentially prevent breakthroughs in prevention and treatment, while exacerbating socioeconomic and racial inequality [6]. Moreover, the social isolation and exclusion in humans that will arise as a consequence of social distancing could bring with it a suite of behavioural, emotional and physical costs [82,85], and perceived social isolation and loneliness could be exacerbated by social media [25,26,28]. By contrast, however, virtual communication that involves synchronous interactions could buffer humans, to some extent, from the negative health effects of perceived isolation [22], providing interactions crucial for maintaining social relationships in our highly social species.

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