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Group living and pathogen infection revisited

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Group living enhances the costs of pathogen infection by increasing the exposure of social individuals to infectious organisms. This hypothesis is well-supported, particularly for pathogens transmitted by close contact. However, recent and compelling research suggests that it is time to revisit this idea. Here, we focus on new findings which suggest that group living can: (i) enhance host resistance to pathogen infection, and (ii) reduce the fitness impacts of infection. This research raises the exciting possibility that there may be common anti-parasite benefits of group living, in addition to well-known pathogen costs.

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Introduction

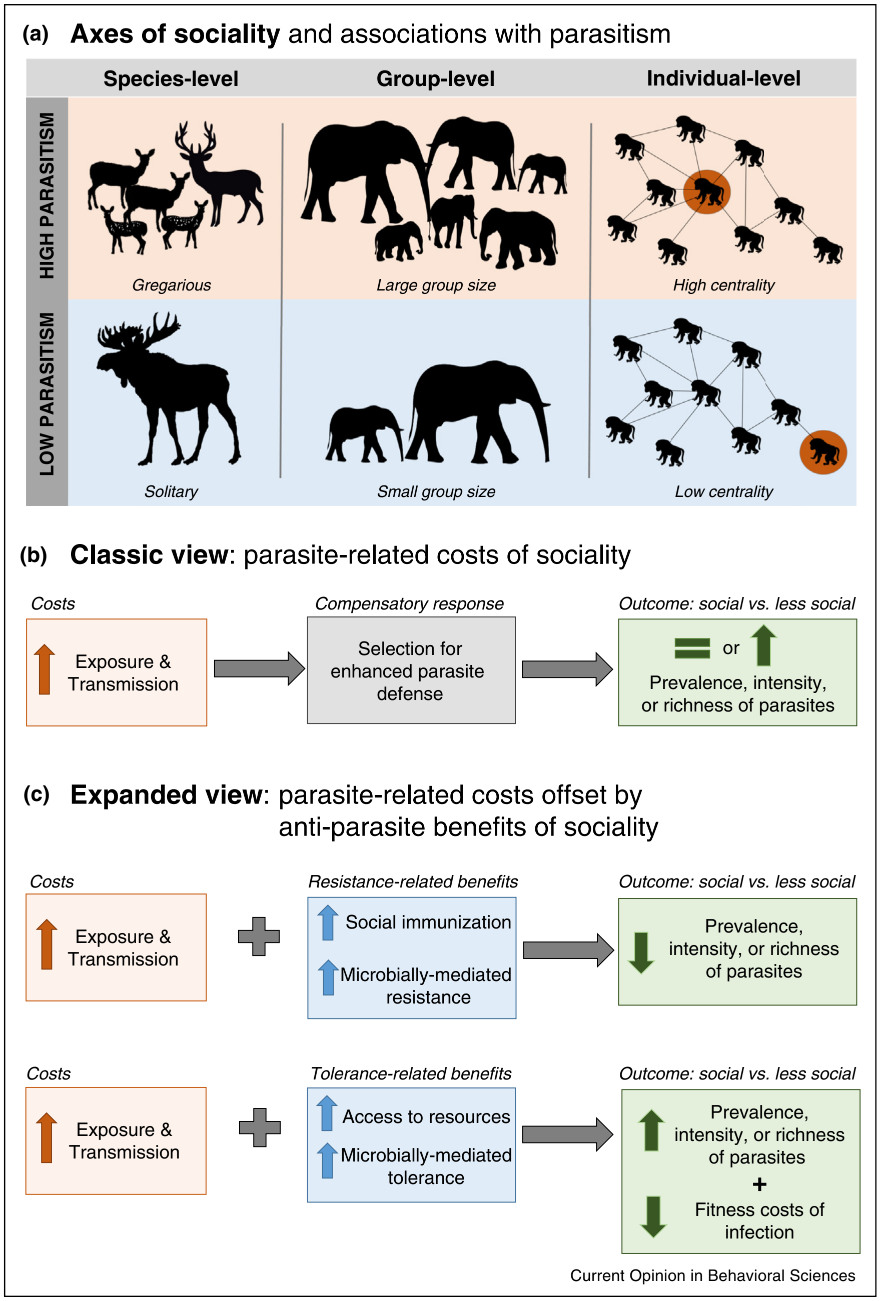
Animals form groups for a number of reasons, ranging from improved access to resources and mates to reduced predation [1]. However, group living also comes with diverse costs, making sociality one of the most intriguing aspects of animal behavior. One of these costs in particular — the cost of increased pathogen transmission — has generated considerable attention among researchers interested in the links between animal behavior and infectious diseases [2–5]. A considerable body of evidence now confirms that certain pathogens (defined here as any infectious organism that causes disease) pose a threat to individuals living in groups [6–8]. Less frequently discussed, however, is the notion that some aspects of group living may confer 'anti-parasite' benefits that directly reduce the pathogen costs of being social. Recently, several intriguing studies suggest that certain features of sociality may reduce, rather than enhance, pathogen costs. Such benefits, when they occur, could make group living advantageous rather than costly in terms of pathogen infection. At the very least, these benefits could modify expected relationships between group living and the costs of infection, a nuance that is integral to how we think about the costs and benefits of group living as they relate to infectious disease.

In this paper, we integrate recent findings from a diverse literature to explore the idea that common anti-parasite benefits of group living may offset pathogen-related costs. We begin by describing a framework for classifying ways in which the anti-parasite benefits of group living might accrue; this framework links sociality to two main strategies hosts use to defend themselves against pathogens: resistance and tolerance. Next, we review recent studies that provide support for enhanced pathogen resistance or tolerance connected with social living. We end by discussing the potential implications of anti-parasite benefits of group living for understanding social evolution and pathogen transmission, and by highlighting important areas for future research.

Anti-parasite benefits of group living

The pathogen-related costs of group living accumulate for one fundamental reason — contact rates between individuals are higher in social situations which facilitates pathogen transmission [3]. As a consequence, levels of pathogen infection (e.g. prevalence, intensity, richness) are generally expected to be higher for: (i) social versus solitary species [9]; (ii) individuals living in larger compared to smaller groups [10]; and (iii) individuals within groups who engage in the most relevant or frequent contacts [11,12] (Figure 1a). In practice, there are at least three reasons why these predictions are sometimes only weakly supported [7]. First, higher sociality might select for strategies that reduce infection risks in social animals [13] (Figure 1b). Second, the effects of group living on pathogens might depend on other aspects of host behavior, physiology, life-history, or ecology [14,15]. For example, factors such as host sex, social rank, personality and kinship can all influence the degree to which group living affects infection risk [e.g. 16–18]. A third possibility is that group living animals may be more resistant to infection as a direct consequence of sociality itself (Figure 1c). Resistance refers to an animal's ability to avoid or prevent infection or to reduce the number or growth of parasites once infected. Resistance can involve immunological or behavioral mechanisms, and is one of the major ways in which hosts defend themselves against

Figure 1



(a) Animals vary on the axis from more to less social at multiple scales: (i) gregarious versus solitary species; (ii) larger versus smaller groups; and (iii) more versus less socially-connected individuals. **(b)** Sociality across these scales has traditionally been predicted to increase the transmission of pathogens, although compensatory selection for parasite defenses might fully or partially reduce these costs leading to no change or only moderate increases in pathogen burdens in social compared to less social animals. **(c)** However, recent work supports the idea that resistance-related benefits of sociality could lead to social animals harboring fewer pathogens than less social animals if these benefits fully offset socially-mediated increases in transmission. Moreover, even when social animals do have higher pathogen burdens tolerance-related benefits of sociality could reduce the fitness costs of these infections.

pathogens [19]. There are several plausible pathways by which group living could enhance individual resistance, such as by enhancing resource acquisition, facilitating direct removal of parasites (e.g. via allogrooming), or promoting cultural transmission of parasite defense behaviors ([4], see Box 1). As a result, social animals may be no more parasitized than their non-social counterparts. In other words, the pathogen resistance benefits of group living could fully or partially offset the transmission costs.

Box 1 Features of group living that may enhance pathogen resistance or tolerance.

Examples of pathways that might link group living to pathogen resistance or tolerance using primates, a vertebrate group in which sociality is well-studied.

Allogrooming. Grooming plays an important role in maintaining affiliative relationships within primate groups. However, it also serves the important function of removing external parasites (e.g. ticks, fleas, lice). In baboons, individuals who are groomed more by others have fewer ticks, suggesting that increased access to allogrooming available in social groups may enhance resistance by reducing both tick infestations and exposure to tick-borne diseases [58].

Self-medication. Accumulating evidence suggests that animals use chemicals to prevent parasite infection or to combat parasites once infected. For example, red colobus monkeys increase ingestion of plant species and plant parts with known anti-helminthic activity during periods in which they are infected with whipworms [59]. Since foraging choices can be culturally transmitted in primates [60], social living and larger group sizes might help promote the transmission of knowledge about medicinal plants providing a resistance benefit to group living.

Thermoregulation. Improved thermoregulation has been proposed as a benefit of group living in several species. As one example, vervet monkeys, with more social partners maintain more stable body temperatures in cold conditions because huddling reduces individual energy expenditure [61]. Animal thermoregulatory behavior often varies with pathogen infection status, in part because individuals might adjust their body temperature to better cope with infection (e.g. fever [21,62]). If group living improves an individual's capacity to regulate or adjust body temperature this may provide pathogen tolerance benefits.

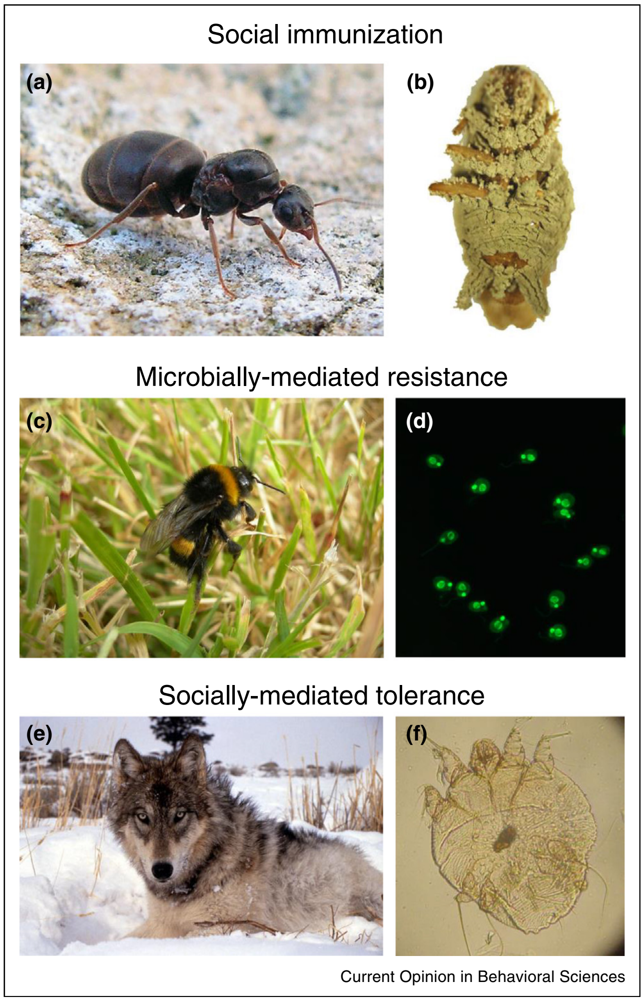
In many situations, though, the positive relationships between parasite infection and group living are in accordance with the traditional expectation, and social animals do have more parasites [7,8]. However, the fact that social individuals have more parasites may not necessarily translate into greater fitness impacts of these parasites. This is because hosts have at least one other strategy available to them for pathogen defense: tolerance. Whereas resistance acts by minimizing the level of infection, tolerance acts by reducing the damage inflicted by pathogens rather than their numbers [20,21]. If group living animals are more tolerant to infection, then sociality might confer an advantage where social animals mitigate pathogen-induced damage, and its fitness consequences, more effectively (Figure 1c). In this case, pathogen tolerance benefits of group living could directly offset the costs of higher parasitism in groups. Although the mechanisms of tolerance are only beginning to be studied in animals, a diverse range of immunological and physiological processes are likely involved [22–24]. Notably, a number of these processes might be affected by sociality in direct or indirect ways (see Box 1). Given increasing evidence of pathogens having profound impacts on the ecology, evolution and behavior of their hosts [25–27], in high risk environments where infection is inevitable, it is worthwhile to consider whether pathogen resistance and tolerance-related benefits of group living might be sufficiently advantageous to favor the evolution of sociality.

Resistance benefits of group living

Resistance is often viewed as a property of an individual, related to genotype or level of investment in immunological and behavioral traits associated with pathogen defense. However, the concept of 'social immunity' expands this view, referring to collective defenses some organisms use to protect themselves and conspecifics against parasites [28]. One of the outstanding questions about social immunity is whether these defenses evolved in response to the pathogen pressures of group living, or whether they instead facilitated the evolution of group living by moderating pathogen costs. A recent study evaluated whether social immunity is a by-product or driver of sociality in insects by compiling evidence on defense mechanisms reported across different insect social systems [29•]. The work showed that nearly half of the types of collective defenses seen in eusocial insects also occur in social and solitary insects, providing preliminary evidence that social immunity may have been a prerequisite for the evolution of complex social systems in insects [29•]. In terms of the resistance benefits of sociality, one form of social immunity that is particularly relevant is social immunization, where close contact between pathogen-exposed and naïve group members enhances resistance among naïve individuals [30]. A compelling example of social immunization comes from experiments with the ant, *Lasius neglectus*, and the common fungal pathogen, *Metarhizium anisopliae*, which showed that social contact between pathogen-exposed and unexposed nest mates caused low-level infections in unexposed individuals, ultimately leading to upregulation of anti-fungal defenses and an enhanced ability to inhibit fungal growth [31] (Figure 2). This mechanism of low dose 'protective' exposure to pathogens through social contact could potentially apply in a number of situations.

Facilitating inoculation with low doses of pathogen is not the only way that group living might enhance pathogen resistance. Many non-pathogenic microbes that make up the host microbiome are also transmitted by close contact among group members. Mounting evidence suggests that the diversity and composition of a host's microbiota can affect resistance to pathogens. In the mammalian gut, for example, commensal microbes can contribute to pathogen resistance by outcompeting pathogens for resources, producing by-products that directly inhibit pathogens, and by stimulating host immunity [13,32]. Therefore, if social contact promotes the exchange of commensal microbes and the maintenance of a more diverse microbiome, it is plausible that microbially-mediated pathogen resistance might be an underappreciated benefit of living in groups [33,34]. A study on bumblebees provides strong support for this hypothesis, demonstrating first that close social contacts among nest mates facilitate the

Figure 2



In the ant, *Lasius neglectus* **(a)**, social contact between naïve individuals and those exposed to the fungus *Metarhizium anisopliae* **(b)** causes low-dose infections in naïve ants that confer pathogen resistance. Social contact between bumblebees **(c)** facilitates the transmission of commensal gut microbes that confer protection against the parasite *Crithidia bombi* **(d)**. Group living in wolves **(e)** improves the survival of individuals infected with mange, *Sarcoptes scabei* **(f)**. Images are from Wikimedia Commons.

establishment of the normal gut microbiome in newly pupated bees, and second, that a normal gut microbiome is essential in defense against a virulent parasite, *Crithidia bombi* [35] (Figure 2). More recent studies on both bumblebees and honeybees confirm that social contacts between nest mates are crucial for development of a normal gut microbiota [36,37]. The importance of social transmission for structuring the gut microbiome is also supported by recent studies of wild vertebrates. For example, a longitudinal study of a group of wild chimpanzees found that the amount of time individuals spent together was a key predictor of both the similarity between individuals' gut microbial communities and the richness of their individual microbiomes [38••]. Although not quantified, the authors suggest that these microbial patterns likely reflect increased direct or indirect (e.g. via feces) contacts occurring between individuals who spend time together. Of course, evidence that group living confers benefits to individuals via microbially-mediated pathogen resistance requires demonstrating both social transmission of microbes and microbially-mediated resistance. Few studies aside from Koch and Schmid-Hempel [35] have been able to link these two lines of evidence, but a growing number of studies supporting social transmission of commensal microbes [38••,39–41] and microbially-mediated pathogen resistance [42–44] highlights the need for more work focused on testing the potential linkages between the two.

Tolerance benefits of group living

Pathogen tolerance involves any mechanism that can reduce the health or fitness impacts of pathogen infection. As such, there are a variety of ways in which group living could enhance tolerance. For example, tolerance-related benefits of group living may arise from social interactions that improve individual physical condition through improved resource acquisition or increased social support [4]. These by-products of group living could enhance an individual's ability to mitigate the impact of a given infection. In a fascinating example of this, [45••] showed that wolves in Yellowstone National Park benefit enormously from group living when it comes to surviving sarcoptic mange (*Sarcoptes scabei*) infection (Figure 2). Using data on pack size, infection status, and individual survival collected over eight years, the study showed that mange infection significantly increased mortality risk for solitary wolves, however, this elevated risk declined sharply with increases in pack size. In fact, an infected individual could almost completely offset the added mortality risk of mange infection by having five pack mates [45••], suggesting that sociality strongly mediates the fitness consequences of mange in wolves. Increasing pack size also reduced mortality risk for uninfected individuals, although the survival benefit for infected wolves was substantially greater [45••]. This discrepancy between infected and uninfected wolves suggests that for infected individuals there is added value to being in a group. The authors posit that this effect might be driven, in part, by improved hunting success in larger groups. Their own work linked park-wide food availability (measured as elk-to-wolf ratios) to improved odds of surviving infection thereby implicating resources as an important factor shaping the fitness costs of mange. Intriguingly, the tolerance benefit of group living for infected wolves appeared to level off at a pack size of 8–10 animals [45••], which is suspiciously close to the pack size (9–13) at which the success of capturing difficult prey levels off in Yellowstone wolves [46]. More generally, increased access to food is a major benefit of group living in many species. For example, social animals can benefit from information about food sources [47], by participating in cooperative hunting [46], or by simply having more time to forage [48]. Since resource availability has also been linked to pathogen tolerance in other systems [e.g. 49,50], social effects on pathogen tolerance arising from differences in resource acquisition may be common.

Another way that group living might confer tolerance is through commensal microbes. As previously described, social transmission can be an important way hosts obtain their normal microbiota [35,36,38••]. Importantly, commensal microbes not only enhance pathogen resistance [32], but also pathogen tolerance. This was recently shown in a mouse model, where a specific member of the gut microbiota, *Escherichia coli* O21:H was shown to prevent muscle wasting associated with *Salmonella* serotype Typhimurium and *Burkholderia thailandensis* infection [51•]. Interestingly, the study showed that *E. coli* did not alter wasting via changes in host metabolism or caloric uptake, but rather by promoting signaling pathways in skeletal muscle that were directly involved in the prevention of wasting [51•], revealing the diverse ways by which pathogen tolerance can occur. Importantly, social transmission of *E. coli* strains has been documented in wild mammals. For example, [52•] used a network approach to explore the relative importance of social versus environmental factors in explaining the transmission of *E. coli* among wild giraffe. The study found that social interactions played a much stronger role than environment in shaping patterns of microbe transmission. Similarly, in brushtail possums, direct contact between individuals was a better predictor of *E. coli* strain sharing than was spatial proximity [11]. These findings raise the possibility that the exchange of common commensal microbes among group members may be essential for promoting pathogen tolerance. However, future work is needed to directly test the hypothesis that social transmission of commensal microbes influences pathogen tolerance in group living animals. Ultimately, what is most intriguing about tolerance benefits of group living is that animals living in larger groups may have higher pathogen burdens than those living in smaller groups on one hand, yet still experience lower fitness costs of infection. This means that in many situations simply quantifying asymmetries in infection status that are due to variation in social behavior may be insufficient to fully understand how group living translates into pathogen-related fitness costs.

Concluding remarks

In understanding the pathogen-related costs of group living it is clear that pathogen context matters — while contact-transmitted pathogens can spread faster in larger groups, mobile parasites typically do not [6,8]. Likewise, any anti-parasite benefits of group living likely depend on pathogen context. Social immunization, for instance, might only be a viable benefit of social contact if low-level transmission of the focal pathogen is associated with limited morbidity or mortality risk, as is the case for the entomopathogenic fungus, *Metarhizium anisopliae* [31]. In the case of socially-mediated tolerance, group living individuals might only derive an advantage if pathogen prevalence is relatively high and infection is chronic. Under these conditions most individuals face a high probability of being infected for a potentially significant portion of their lives, so behaviors that reduced the fitness impact of these pathogens might be under strong selection. Pathogens like chronic and common intestinal worm infections harbored by most vertebrates, and *Sarcoptes scabei* in wolves [45••] may fit this profile. Potentially, animals may face conflicting pressures where group living imposes costs related to some pathogens and benefits related to others. Indeed, seminal work on the effects of contact-transmitted versus mobile parasites in shaping group size in animals [53,54] has shown that grouping might simultaneously confer parasite costs and benefits, with both ultimately influencing optimal group size. These classic studies, coupled with new insights about the role of infectious diseases in natural populations, suggest that conflicting pressures of parasitism may play an as yet underappreciated role in the evolution of sociality.

Finally, the way in which anti-parasite benefits accrue may have profound effects on pathogen dynamics with further implications for host social behavior. Animal biologists have only recently turned significant attention to studying pathogen tolerance empirically in natural populations [20,22,55]. However, theory predicts that resistance and tolerance strategies should have very different outcomes for pathogen epidemiology. Resistance, because it reduces parasite fitness should decrease parasite prevalence at the population level, whereas tolerance, because it does not reduce parasite fitness, can actually increase population-level prevalence [56,57]. In situations where the anti-parasite benefits of group living improve tolerance rather than resistance, enhanced transmission of pathogens in groups coupled with a longer duration of infectiousness of infected individuals (e.g. via reduced pathogen-induced mortality as in the case of wolves and scabies) could serve to drastically increase pathogen transmission and prevalence. Intriguingly, under such circumstances, higher pathogen prevalence could reinforce selection for group living, if social individuals maintain higher fitness in the face of infection. Of course, specific outcomes will depend strongly on the shape of the relationship between tolerance benefits and group size. More generally, given emerging research in animal behavior, infectious disease ecology, microbial ecology, immunology and other fields, the time is ripe to revisit questions about group living and pathogen infection from a new perspective.

Conflict of interest

Nothing declared.

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- •• of outstanding interest

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