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The sociality–health–fitness nexus: synthesis, conclusions and future directions

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This theme issue has highlighted the links between sociality, health and fitness in a broad range of organisms, and with approaches that include field and captive studies of animals, comparative and meta-analyses, theoretical modelling and clinical and psychological studies of humans. In this concluding chapter, we synthesize the results of these diverse studies into some of the key concepts discussed in this issue, focusing on risks of infectious disease through social contact, the effects of competition in groups on susceptibility to disease, and the integration of sociality into research on life-history trade-offs. Interestingly, the studies in this issue both support pre-existing hypotheses, and in other ways challenge those hypotheses. We focus on unexpected results, including a lack of association between ectoparasites and fitness and weak results from a meta-analysis of the links between dominance rank and immune function, and place these results in a broader context. We also review relevant topics that were not covered fully in this theme issue, including self-medication and sickness behaviours, society-level defences against infectious disease, sexual selection, evolutionary medicine, implications for conservation biology and selective pressures on parasite traits. We conclude by identifying general open questions to stimulate and guide future research on the links between sociality, health and fitness.

1. Introduction

The papers in this theme issue address important and emerging links between sociality, health and fitness. Many of these links have epidemiological implications, resulting in increased spread of infectious diseases through social contact patterns [1–4] and effects of infectious disease on host behaviour [2]. Other links involve effects of sociality on buffering the stressors of social life, including the intense competition that is observed in some species [5], with resulting effects on susceptibility to infectious and non-infectious diseases when these support networks are unavailable. Some papers in this theme issue provide examples of the mechanisms that underlie predicted interactions, such as the effects of dominance rank, sex and stress on hormone production [6], their effects on immune function and parasitism [7], and the role of the sympathetic nervous system in mediating effects of social instability on immune function [5]. Other papers in this issue have investigated the fitness consequences of sociality and parasitism, for example in Columbian ground squirrels [8]. The papers also take a wide range of approaches, including broad-scale comparative and meta-analysis [3,7,9], long-term field research on food availability, stress and population density

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[10], social networks and disease spread in wild animals [4], and experimental studies of behaviour in captive primates [5].

The studies in this theme issue also cover a wide range of taxa, involving invertebrates and vertebrates, including humans. This breadth is important because, for many of these topics, clear implications exist for understanding human health and behaviour, for example in relation to social contact and various chronic diseases throughout the life course [11], or in terms of how disease influences individual psychology, which can have far-reaching population-level consequences [12]. Indeed, an important take-home message from this theme issue is that understanding the links between health, fitness and sociality in broad comparative perspective has important implications for understanding human health—a point that others have also made [13–15].

In this concluding chapter, we first synthesize the results of these diverse studies into some of the key concepts identified in the introductory paper of this theme issue [16]. In many cases, the studies in this theme issue both support pre-existing hypotheses, and in other ways challenge some of those expectations. With the maxim that 'the exception can prove the rule', we explore some of the unexpected findings, with the aim to place the results into a broader, synthetic framework.

In the second part of this paper, we shift gears to consider what is missing from this collection of papers. As with any edited contribution, we aimed to showcase a broad range of examples in our topic. However, we also experienced constraints, and thus had to focus on only a few of the topics and example systems. We therefore wish to highlight some topics that could have been included if space and time allowed, including more discussion on the evolution of behavioural defences to infectious disease that involve consumption of medicinal plants, sickness behaviours and even society-level responses to disease threat. We also consider sexual selection, evolutionary medicine, implications for conservation biology and the evolution of pathogen transmission mode and other characteristics.

Finally, we conclude with future research directions by considering several ways forward to better understand the links between sociality, health and fitness. The specific future directions that we consider involve additional studies of the fitness consequences of parasitism [8]; a greater understanding of behavioural and physiological responses to infectious disease, especially including their effects on individual health and spread of infectious diseases in populations [2,17]; and emerging links between sociality, the microbiome and health.

2. Synthesis and exceptions

(a) Synthesis

The introductory paper of this theme issue [16] provided a synthesis of key concepts. In that first chapter, the authors highlighted how transitions from a solitary lifestyle to group living resulted in new health-related costs and risks, and thus favoured the evolution of new counterstrategies to these costs that involve behaviour, physiology and immune responses. This evolutionary pattern is well illustrated by Meunier's [9] analysis of social immunity and group living in insects, where social immunity refers to collective anti-parasitic defences, such as systematic removal of dead animals from the nest. His review of the macroevolutionary patterns highlights the many diverse solutions that natural selection has discovered to control infection after group living evolves.

Increased risk of acquiring infectious disease appears to be one general consequence of living in groups [18–20]. However, effects are not always as strong or consistent among studies as one might expect [21], including in the taxonomic groups in which social life is often viewed as most elaborate, i.e. primates [22,23]. It is also important to consider transmission mode in assessing links between sociality and infectious disease (e.g. sociality may have different effects on exposure to vectors, intermediate hosts and water-borne diseases). As demonstrated in this issue, it is also crucial to incorporate social structure into studies of the sociality–health–fitness nexus, where social structure describes patterns of contact among individuals in a social group. One paper in this issue details, for example, how contact patterns can be critically important for understanding parasitism in primates [4], while another paper uses comparative analyses and meta-analyses to investigate a positive association between group size and subdivision of those groups [3]. The main point is that group size on its own is often insufficient to explain parasitism in all species; social contact within groups can provide significant traction on these important epidemiological questions, as suggested by previous researchers in the context of measuring network structure [24,25].

Another important aspect of the transition from a solitary lifestyle to group living concerns the origins of increased susceptibility to disease, arising from the stress of social competition for food, mates and other fitness-relevant resources. While we might expect that animals living in a group will experience some increased exposure to infectious disease [18,21], the same is not true of social stress, where heterogeneity in responses might be more marked (e.g. in relation to dominance rank, see [7], with possibilities for both positive and negative effects). The reasons for this difference in exposure and social stress effects are related to reasons given above: we only expect negative health consequences from chronic social stress in gregarious settings in which individuals have distinct social relationships [16]. In addition, of course, social stress may affect patterns of social contact (i.e. exposure to disease), and more stable bonds may reduce exposure to infectious disease if they limit the number of interactions. Thus, social structure is again an important element for understanding both infectious disease risk and chronic, stress-related diseases, highlighting the importance of new methods to quantify and analyse social interactions [1]. Similarly, dominance rank may have important predictive capacity for measures of health that translate into fitness.

Another major theme from the Introduction to this theme issue [16] involved life-history trade-offs, and the integration of sociality into frameworks in ecology and evolution that centre on these trade-offs. The foundation of many studies on trade-offs in evolutionary ecology is that the immune system, growth, reproduction and maintenance activities are costly for an organism, and that resources to sustain these activities are limited. An emerging appreciation—illustrated in this issue—is that sociality is an axis that is important for understanding these trade-offs. The role of sociality in life-history trade-offs arises in several ways. One involves simple effects of group size on risk of infectious disease at the individual level; this may generate selective pressure on gregarious animals to invest more in immune defences, creating trade-offs with growth and reproduction. Another way

that sociality affects life-history trade-offs involves the stress of competition in groups; competition for mates, resources and rank itself contributes to the costs involved in balancing these trade-offs, potentially favouring different outcomes. Finally, a good social position in a group—with reliable social support and cooperation—can enable both behavioural counterstrategies to some disease threats, such as greater allogrooming to reduce ectoparasite loads, and more effective immune defences. In general, the social environment modulates individual susceptibility to infectious and non-infectious diseases in numerous ways related to life-history trade-offs.

In summary, within highly social mammal species—including humans—social interaction appears to be associated with a health-related trade-off that is highlighted across several articles in this theme issue [5,11,12]. On the one hand, increased social contact may increase individual organisms' exposure to infectious diseases [12]. On the other hand, increased social contact with conspecifics is associated with more effective immunological and behavioural responses to infection and with better long-term health outcomes [5,11]. Similarly, in humans, individuals who are more socially connected are more resistant to viral infection, as are individuals who report a greater incidence of intimate physical contact [26,27]. It remains an important topic for future research to resolve exactly how this particular cost/benefit trade-off is resolved within highly social species, and to identify the conditions under which the potential costs of social contact outweigh the benefits and vice versa.

(b) Exceptions

As noted earlier, this theme issue also uncovered several unexpected patterns. Notable here is the experimental fieldwork by Raveh *et al.* [8], which examined the fitness consequences of ectoparasitism in Columbian ground squirrels. Based on theory and previous research [28], the authors expected to find that ectoparasitism had fitness costs for the squirrels, yet newer data and analyses suggested otherwise [29]. In a careful and rigorous analysis, the authors failed to find compelling evidence that ectoparasite loads covary with key fitness components that included body condition, survival, reproductive success and characteristics of dependent offspring. In other words, ectoparasite loads seem unrelated to fitness.

Previous studies have found links between parasitism and fitness in wild populations (e.g. [30,31]), and ectoparasites are known to transmit infectious agents, such as the Lyme disease spirochete [32], which may negatively impact fitness. Why did Raveh *et al.* [8] fail to find support for their predictions in these ground squirrels? The answer may have to do with the other ecological conditions faced by these squirrels, and their ability to mount effective immune and physiological defences to the ectoparasites under different conditions. Given the variable conditions in which they live, for example, the effects of parasites may only be detectable at times of severe resource shortages [8]. In addition, neither parasitologists nor zoologists know much about the costs of parasitism, or whether organisms that are called 'parasites' are truly parasitic (meaning that they live in and on the host, at some cost to the host). Perhaps many of the organisms that are considered parasites should instead be viewed as mere hitchhikers, with negligible costs for the organisms that provide a home for them (i.e. commensals). Raveh *et al.*'s [8] paper therefore highlights how the effects of parasites on host fitness require careful consideration of the ecological context and its variability, life-history trade-offs across the yearly cycle, an understanding of each parasite's biology and awareness that different parasites may exert different costs on the host.

Habig & Archie's [7] meta-analysis of the effects of social status, immune response and parasitism in male vertebrates also failed to confirm predictions about the effects of stress on immune function. The authors focused on heterogeneity in immune function, and noted that two sets of predictions have been made concerning the links between dominance rank and immune function. On the one hand, the stress of maintaining high rank is expected to compromise immune function because dominant males divert much of their available energy to reproductive effort, creating a trade-off with immunocompetence and favouring investment in less energetically costly immune defence components. On the other hand, the chronic stress of low rank is also expected to compromise immune function, because low-status males are exposed to more unpredictable events or may be inherently less able to effectively cope with stressful situations. These perspectives are highly influential in the field of ecoimmunology, and one might expect that after decades of research, clear patterns would emerge for different components of the immune system. In their analysis of 77 studies, however, the authors failed to find compelling support for either paradigm, which made specific predictions for the immune components favoured in males of different rank. This is to some extent a disappointment; it indicates that different studies are finding different patterns, yet we currently lack an understanding of the variability in the results. The authors [7] note that many other factors, such as mating system, may be needed to understand the links between social status and immunity. In addition, they note that many of the studies in the meta-analysis were conducted on captive animals, thus calling for more research on wild animal populations.

Habig & Archie [7] did provide a stronger and very interesting finding: in a second meta-analysis, dominant males exhibited higher levels of parasitism with protozoan blood parasites, gastrointestinal helminths and ectoparasites. Given their other results that demonstrate similar immune responses between subordinates and dominants, this suggests that other factors are influencing the difference in parasitism. A plausible explanation given by the authors is that dominant individuals have different exposure to parasites, namely through priority of access to food, mates and conspecific social partners. Thus, social rank may have some health-related benefits involving susceptibility to parasites, such as more social partners or better access to resources, yet they also have costs in terms of greater exposure to parasites [33]. Thus, the relationship between sociality and health is clearly bi-directional and more complex than previously thought.

A final example of surprising results comes from Chapman *et al.*'s [10] contribution to the theme issue. In this paper, the authors investigated a series of predicted links involving food quality and availability, glucocorticoid levels as a marker of stress, and abundance of wild red colobus monkeys. While they found some evidence for links between food quality and stress levels and a decline in food quality over time, the population has remained relatively stable. One change that has occurred involves group size and number of groups, with larger but fewer groups existing today than in the recorded past. Overall, this study is valuable for connecting

individual-level phenomena, such as diet and stress, to population-level phenomena. In this case, however, the underlying mechanisms that drive the documented patterns remain unclear; the authors propose that some aspects of behavioural flexibility have played a role (e.g. avoidance of infected individuals), again highlighting areas for more focused future research on the sociality–health–fitness nexus.

In summary, many articles in this theme issue present novel findings that, in some cases, fail to match the authors' predictions. Some of these unexpected findings lead to new insights and predictions for future research, such as behaviours that may be associated with parasite avoidance, and the importance of investigating immune function in wild animals [34]. By bringing together field, comparative/meta-analyses, and theoretical approaches, many of the papers provide ways to assess generality, in some cases failing to find general patterns empirically (e.g. in meta-analysis of immune function, [7]). These studies provide ways forward for deepening our understanding of the links between sociality, health and fitness. In other cases, authors provide a combination of empirically and theoretically supported results, which offers more confidence in the strength and generality of the findings [2,3].

3. Other aspects of the health–sociality–fitness nexus

Several other obvious aspects of the health–sociality–fitness nexus could not be covered in this theme issue owing to limitations of space. We identify—and provide brief summaries of—some of those topics in this section.

(a) Society-level defences against infectious disease

In group-living species, it is thought that many behavioural strategies to reduce parasite transmission have evolved [3,9,35]. The basic principles underlying these 'social immunity' strategies serve as the basis for hypotheses linking parasitism to cross-species variation in the structure of social groups [3,19,36]. Analogous logic can be applied to within-species differences, too. In any species distributed across a range of different habitats, population-level differences in the endemic parasite load may exist. This ecological variation could lead to differences in behavioural anti-parasite strategies, which may have population-level implications. These implications remain virtually unexplored in wild animal populations, but a burgeoning body of research applies this reasoning specifically to the study of human cross-cultural variability.

Stimulated by a pioneering study on marriage systems in small-scale societies [37], some correlational evidence links ecological variation in 'parasite stress' to different population-level outcomes in human societies. This research typically treats countries and other geopolitical regions as units of analysis. Some of these studies have focused on individuals' behavioural traits (e.g. cross-national differences in extraversion [12,38]). Others have focused on formal institutions and informal social structures that help to define the nature of human societies [39]. For example, in geopolitical regions with higher levels of parasite stress, human societies are characterized by lower levels of philopatry, stronger family ties, stronger societal conformity pressures, more collectivistic value structures and more authoritarian government practices—all of which may provide structural buffers against the transmission of infections [39–41].

Although this line of research has been highly generative, the results are correlational and inferentially complicated. Ecological variation in parasite stress is highly correlated with other ecological and economic variables that may have conceptually independent implications for societal outcomes [42,43]. The most compelling correlates of parasite stress are those that persist even when statistically controlling for additional variables. Not all of the cross-national findings meet this standard of evidence, but many do [38,44,45]. Additionally, a subset of these outcomes—including societal conformity pressures, collectivistic value structures and authoritarian governance—are more strongly predicted by historical parasite stress than by contemporary parasite stress, a finding that renders a reverse causal explanation less plausible [44–46,38]. A further inferential complication arises because contemporary geopolitical areas are rarely independent of other areas [47,48]. For this reason, the most inferentially compelling correlations are those that emerge not only in cross-national analyses, but also in analyses of small-scale societies studied by ethnographers [49,50]. It remains for future research to more fully determine which societal outcomes are, or are not, influenced by parasite risks [47].

Even if ecological variation in parasite stress has played a unique role in the origin of human societal differences, it remains unclear which explanatory mechanisms might account for each specific outcome. Multiple mechanisms are plausible, including those associated with genetic evolution, developmental plasticity, context-contingent behavioural flexibility and cultural transmission [41]. These mechanisms may operate independently or in conjunction with one another.

(b) Sexual selection, mating systems and sexually transmitted diseases

Sexual selection has pervasive effects on all components of social systems. Behavioural traits subject to sexual selection are proximately involved in regulating access to mates, in actual mate choice and in defining mating patterns, and their evolutionary consequences impact a species' social organization [51]. Sexual selection acts through two main processes that also have downstream consequences for animals' health and, of course, for their reproductive success [52]. According to classical sex roles, competition among males is evaluated through intrasexual selection, whereas intersexual selection leads to non-random mating because females exercise mate choice to maximize direct or indirect benefits of choosing particular males [53,54]. However, it is now recognized that males are also choosy [55] and that females compete among each other as well [56,57].

Both inter- and intrasexual selection have several direct and indirect consequences for animal health. First, competitive interactions often involve fighting, for which an array of weapons has evolved to assist males in their struggle for reproductive success [58]. The use of horns, antlers, spurs, canines and the like is associated with a risk of injury, and the resulting wounds provide entry points for infectious agents so that even non-lethal injuries can lead to massive health problems or even death, and males are typically more often affected than females [59–61]. In the case of injury, wound healing is affected by stress and energetic costs [62], and also by the degree of social integration of the wounded individual [63], revealing

yet another functional relationship between sociality and health. In addition, competitive ability is also affected by health status, as demonstrated by experimental infections of males that compromise their investment into morphological traits used in competition [64].

Second, dominance relationships are thought to have evolved as another mechanism to reduce the costs of intersexual strife. Whenever access to mates and other contested resources is mediated by ritualized signals rather than overt fighting, the individual risk of injury is reduced [65]. It has long been assumed that being dominant or subordinate comes with physiological costs that enhance susceptibility to certain types of disease and parasites [14,66], but the meta-analyses by Habig & Archie [7] in this theme issue revealed no consistent differences in immune function and parasitism between these two classes of males. As noted by the authors, however, the majority of studies available for their analyses came from captive animals; additional research on wild animals is sorely needed.

Third, in the context of intersexual selection, the functional relationships between sociality and health largely run in the reverse direction. Theoretical and empirical evidence suggests that members of the choosy sex are likely to carefully evaluate the health and condition of potential mates [67,68]. By discriminating against obviously parasitized males, females can obtain direct benefits of mate choice by reducing their individual risk of having parasites transmitted to them through social contacts with males [69]. This risk may also affect the rules of mate sampling, i.e. whether females make their choice based on a certain threshold that potential mates must exceed or whether they first sample a certain number of potential mates before deciding with whom to mate [70,71].

Fourth, healthy males may also be favoured in mate choice because their condition indicates superior immunocompetence, which can create indirect benefits of female choice if the underlying immune genes can be acquired for their offspring. In this context, it has been suggested that females might be looking for mates with absolutely good major histocompatibility complex genes, but the empirical evidence tends to favour the interpretation that each female attempts to find the best complementary genotype for her immune genes [72]. These perspectives have been applied to human mate preferences, for example, by investigating the hypothesis that people strategically prefer mates who are likely to produce offspring characterized by strong immune systems. Empirical evidence has tested—and supported—many specific hypotheses that focus on preferences for mates characterized by specific phenotypic cues that are likely to be honest signals of immunocompetence [52].

Although the production of highly immunocompetent offspring is likely to have generally beneficial implications for fitness, these benefits are likely to be greater under ecological conditions in which infectious diseases pose a more substantial threat to health and fitness. One implication is that the selective preference for highly immunocompetent mates may vary depending on the threat posed by infectious diseases. Research on humans provides some support for this hypothesis. For instance, several experiments have manipulated the temporary psychological salience of infectious diseases, and examined its effects on people's subjective preferences for symmetrical faces. Results reveal that facial symmetry is especially attractive when the threat of infectious diseases is highly salient, and that this effect shows up primarily when judging opposite-sex faces [73,74]. The results of these experiments are complemented by correlational results from cross-national comparisons of mate preferences. Compared to countries characterized by relatively low levels of infectious diseases, people place a relatively higher priority on a mate's physical attractiveness in countries characterized by higher levels of infectious diseases [75].

Finally, inter- and intrasexual competition also influences the spread of disease directly by affecting patterns of mating, i.e. who mates with whom. In particular, individuals with the greatest number of mating partners and high mating rates are at greatest risk of contracting sexually transmitted diseases (STDs) and will also contribute disproportionately to STD spread in a population [76–79]. A number of studies have investigated the link between STDs and aspects of mate choice and mating systems [78–80]. For example, Thrall *et al.* [77] examined disease spread in the context of a polygynous mating system. The authors used a simulation model to investigate the spread of STDs in males and females with respect to variance in male mating success, dispersal of females among groups and mortality rates. Analyses of the simulations revealed that increasing variance in male mating success resulted in higher STD prevalence for both males and females. In addition, STD prevalence tended to be higher in females than males, and this difference increased with greater variance in male attractiveness. An intuitive explanation for these latter findings is that as sexual selection increases, a smaller percentage of males in the population actually mate, generating lower prevalence among males than females. These highly successful males also act as super-spreaders for disease, highlighting the role that social network analysis [1] can have in understanding STD risk.

(c) Sickness behaviours affect sociality and disease spread

Sick animals act differently from healthy animals, and this can have implications for disease spread. Most obviously, when vertebrates mount immune responses to parasites, they exhibit reduced motor activity, including reduced grooming and social interaction. Rather than a simple by-product of infection, this pattern of 'sickness behaviour' may actually comprise an adaptive response to infection [81,82]. For example, a reduction in motor activity conserves caloric resources, which can be redirected to immunological responses that fight off infection. In group-living animals, the reduction in social interactions may have the further benefit of inhibiting transmission of infection to others within the group, but the difficulties of assessing health in wild animals have hampered studies of sickness behaviour in natural ecological and social contexts. Physiological responses are also important, such as fever; one recent paper took an epidemiological perspective on fever and proposed, via a model and knowledge of how fever reduces viral shedding, that suppression of fever results in higher numbers of influenza cases in human populations [17].

In recent years, our understanding of the mechanisms that underlie sickness behaviours has improved. As expected given the proposed role of sickness behaviour in mediating adaptive responses to infection, the immune system plays a part in these mechanisms, particularly involving pro-inflammatory cytokines [81,83]. When infection is detected, the innate immune system produces an inflammatory response mediated by the

production of cytokines. The physiological impact of these cytokines is not limited to the local area of infection; via multiple pathways, they also affect the nervous system and thus cause patterns of motor activity that characterize sickness behaviours [84]. Experimental research shows that the artificial induction of a pro-inflammatory response leads to characteristic patterns of motor inactivity and social withdrawal among many species of animals, including humans. For instance, compared to placebo controls, people exposed to an endotoxin—which triggers the release of pro-inflammatory cytokines—reported a decreased desire to be with other people [85].

Although sickness behaviour may typically be characterized by the inhibition of social interaction, this is not always the case [83]. For instance, a study of male song sparrows revealed that, while inflammation led to reduced activity during the non-breeding season, no such effect was observed during the breeding season [86]. In an experimental study of finches with conjunctivitis, uninfected males preferentially attended food sources on sides of the cage associated with sick individuals, probably owing to their lower competitiveness [87], suggesting that sickness behaviours may not always lead to less contact. In general, the tendency for social withdrawal may be eliminated under circumstances in which the fitness benefits of specific forms of social behaviour—such as mating—outweigh the benefits of conserving caloric resources during illness.

While cytokine-induced sickness behaviour is typically characterized by decreased sociality, it may also be characterized by specific kinds of increased sociality, such as an increase in approach-oriented attitudes towards potential carers. In one experiment, the induction of cytokine-mediated inflammation led laboratory rats to spend more time in close contact with familiar cage-mates [88]. Analogous results have been observed in humans. Compared to placebo controls, people injected with endotoxin report greater desire for contact with supportive friends or family members, and also show greater activity in a brain region—the ventral striatum—that is associated with feelings of social connection in close relationships [89].

(d) Self-medication and social learning

Self-medication has been identified in a wide array of animals [90], and can be seen as one of several mechanisms that promote non-immunological defences to infectious disease [91]. Self-medication has been studied intensively in the African great apes [92], where two self-medication behaviours, bitter pith chewing and leaf swallowing, have been observed widely among chimpanzee, bonobos and lowland gorilla populations [92]. While it might seem that social learning is limited to highly intelligent animals, such as primates, it may play a role in self-medication in other species, too [93]. In fact, evidence indicates the potential generality of this behaviour among other taxa [33,94,95] including fruit flies, where females respond behaviourally to parasites by 'medicating' their offspring [96].

An important question in the context of this theme issue on the health–sociality–fitness nexus concerns whether these behaviours are learned socially. Young wild chimpanzees have been documented to carefully observe self-medication behaviours by others, typically their mothers, and then attempt such behaviours immediately after [97]. These and other observations suggest the potential for social learning of health-promoting behaviours that have fitness consequences. However, experimental studies have found that naive captive chimpanzees are capable of initiating key aspects of self-medication behaviours without the benefit of social learning [98,99]. Such incongruent findings highlight the need for integrated natural and manipulative experiments to examine the importance of social learning in the acquisition of self-medication behaviours.

Interestingly, our understanding of the role of social learning in the initiation and propagation of most population-specific ape behavioural patterns remains largely unexplored despite the major focus on 'culture' in the study of ape behaviour [100,101]. This process is further complicated by recent evidence that genetic dissimilarity cannot be eliminated as playing a major role in generating group differences in chimpanzee behaviour [102]. Testable hypotheses for learning have been developed in relation to social contact patterns, emulation, social and local enhancement, and trial-and-error learning [103–106], and researchers have begun to identify how imitation might facilitate the propagation of animal culture, while not explaining its stability [107]. Thus, rapid improvements in our understanding at this interface are expected. In addition, with growing evidence of self-medication beyond cognitively advanced animals [108,109], any concept of self-medication based solely on learning is inadequate. Mechanisms such as innate response and adaptive plasticity will need to be examined as we re-evaluate our assumptions concerning the importance of social learning in the acquisition of self-medication behaviours [90].

(e) Evolutionary medicine

The emerging field of evolutionary medicine (or 'Darwinian medicine', as it is sometimes called) addresses questions about the ultimate origins of disease in humans and animals [110–113]. Evolutionary medicine involves both understanding disease, such as past selection pressures that make humans prone to obesity, and treating disease, including new solutions to halt the evolution of drug-resistant pathogens and the creation of novel cancer therapies. Research in evolutionary medicine investigates the full gamut of diseases and disorders that impact humans, including injury, sleep disorders, emerging infectious diseases, psychiatric disorders, autoimmune diseases, obesity, addiction and infertility.

We see many areas where research in this theme issue may contribute to evolutionary medicine in the future. One of these involves the ways that social contact relates to many of the major mental health disorders in humans, such as depression. Hidaka [114] provides one such perspective in a review of depression from an evolutionary perspective (see also [115–117]). He presents evidence of increasing rates of depression over time, and an association between population prevalence of a mood disorder over the lifetime and gross domestic product, with countries as the level of analysis. Hidaka [114] then points to several lifestyle correlates of modern societies, such as diet and exercise, as contributing to higher rates of depression. Important among these factors is the social environment; specifically, 'contemporary populations may now be more susceptible to depression because of greater inequality, low social support, intense individual competitiveness, and increased social failure' (p. 210). The research in

this theme issue and elsewhere provides insights to the evolutionary origins of these drivers [11,15].

Another element of evolutionary medicine involves the importance of comparing different species, as illustrated with the many different organisms covered in this theme issue. 'Comparative medicine' emphasizes the importance of collaboration between veterinary medicine and human medicine. Comparative approaches have been used, for example, to investigate associations between body mass and rates of cancer; the lack of such an association across species is termed 'Peto's Paradox' and suggests that larger-bodied animals have more effective cancer suppression mechanisms [118]. We propose that whenever comparisons are made, it is essential to bring in a phylogenetic framework to understand species differences, for example through use of comparative methods that control for phylogeny in understanding the adaptive basis of traits [119]. In other words, in addition to veterinarians and doctors, evolutionary biologists, ecologists and behavioural biologists have much to offer comparative medicine.

(f) Implications for conservation biology

Links between health, sociality and fitness also have important implications for conservation biology, as highlighted by the contribution to this theme issue by Chapman *et al.* [10]. Conservation biologists often consider the problems that arise in small populations, which of course is characteristic of endangered species. Habitat loss, climate change, overexploitation, invasive species and environmental pollution are among the important drivers of species extinctions; the compounding effects of health, specifically infectious disease, are now considered as an additional driver [120]. Infectious diseases threaten conservation of biodiversity through both local and global extinctions [121–123], and health and disease should be considered in population viability analysis and species conservation planning [124,125], as well as in reintroductions of species of conservation concern [126].

The Allee effect represents one effect of sociality that is also relevant to conservation biology. The Allee effect occurs when 'under-crowding' leads to a decrease in survival or reproduction, and can be thought of as inverse density dependence at low densities [127]. When there are fewer individuals in a social group, a decrease in interspecific cooperative interactions can trigger the Allee effect [128]. Infectious diseases can reduce population numbers below a critical group size, thereby starting a cascade of negative fitness impacts via the Allee effect. This effect has been posited as a reason for added challenges in conserving social wild animals. Obligate cooperative breeding species, such as the African wild dog and Ethiopian wolf, might be especially vulnerable to disease-mediated extinctions involving the Allee effect [129,130].

(g) The parasites' perspective: sociality and selective pressures on parasites

Sociality might also conceivably influence the evolution of pathogen traits, such as transmission mode and virulence. First, with regard to transmission mode, is it possible that living in larger groups would favour the evolution of close-contact transmission, when compared with other transmission modes that involve less close contact? While plausible, only a handful of studies have considered this question. One study used a theoretical model to investigate the evolution of sexual- versus non-sexual transmission [131]. On the basis of the model, the authors proposed that STDs would be more common relative to other infectious diseases in species living solitarily or at low density. The reason for this is that mating provides one of the few opportunities for disease transfer among largely solitary individuals. The authors also proposed 'a social–sexual crossover point', or SSCP. Increased sexual transmission is favoured when the population size was less than the SSCP, highlighting the advantages for sexual contact transmission at low host density; above the SSCP, non-sexual (close contact) transmission is favoured, given that increased social contact is expected at higher population size. Applying this model to group size variation might be possible, although it assumes that population size in the model is equivalent to group size, which may be problematic if between-group rates of migration (dispersal) are high.

Second, we can also consider how sociality influences virulence, defined here as the harm that a parasite or pathogen causes to its host [132]. Understanding the evolution of virulence requires a brief review of some key variables that influence pathogen transmission in typical epidemiological models; these variables include the per-contact probability of transmission, mortality owing to infection (i.e. virulence), and clearance rate owing to the immune system or physiological and behavioural responses. Factors that positively influence disease spread, such as per-contact probability of transmission, are counterbalanced by correlated negative effects on virulence and clearance, as proposed by the 'trade-off theory' of virulence [132]. For example, a pathogen with a higher per contact probability of transmission may have higher virulence, with the link driven by how increased pathogen replication rate positively influences both transmission probability and mortality owing to disease (i.e. a mechanistic link producing a positive association between transmissibility and virulence). With these considerations in mind, a simple association between group size and virulence is not forthcoming. While it might seem that living in a larger, more interconnected group might favour higher virulence, mathematical models show that simple predictions are not always possible, as the solutions depend on demographic and epidemiological parameters [132,133].

4. Conclusion and future directions

The authors of the papers in this theme issue provide many ways forward for understanding the links between sociality, health and fitness, especially in the context of their particular systems and questions. Here, we amplify these suggestions by identifying opportunities for future research in four main areas.

First, there is a great need for more research on the effects of parasites on hosts. This of course includes host fitness, but also involves related effects on fitness, such as activity levels, fecundity, vigilance and fat reserves. We actually know very little about how parasites impact host fitness, or about the parasite types that have the greatest effects in different host taxa. Important parasite distinctions could be investigated, such as viruses versus helminths, or ectoparasites versus endoparasites. Equally important are aspects of co-infection, in which infection with two or more parasites can have synergistic effects on host fitness [134–136]. Moreover, as raised by

Raveh *et al*. [8], it is important to investigate fitness in relation to ecological conditions in wild populations.

A second major area involves behavioural counterstrategies to infectious disease. Interesting new angles on this question were raised in this theme issue, including social immunity in insects [9] and the behavioural immune system in humans [12]. Yet other questions arise. To what extent are some of the behavioural responses in humans to disease risk, such as the disgust response [137], also found in non-human primates? How effective are behavioural defences in vertebrate systems, in terms of both individual recovery from infection and the epidemiological consequences of an introduced infection? How plastic are social networks? And, does the association between modularity and group size [3,24] represent an adaptive response to greater disease risk in larger groups, versus the alternative hypothesis that it results from limited time budgets in larger groups? These and many other questions will be important for future research.

It is also important to appreciate that 'health' can include central nervous system processes, with mental states such as loneliness or sadness having implications for effective physiological function. In this regard, it will be important in the future to develop new measures to assess these mental states in other animals, along with research paradigms to investigate these questions across human and non-human animals (e.g. [138]).

Finally, more research is needed on the links between the microbiome, health and sociality. The organisms making up the gut microbiota have multiple effects on host behaviour and fitness [139], including benefiting the host through various metabolic functions and assisting in pathogen defences [140]. The community structure of gut microbiota is responsive to several intrinsic host characteristics [141] and at the same time also influences host behaviour and cognitive functions [142,143], as demonstrated by transplantation experiments [144]. The bidirectional signalling between the gut and the brain mediated by the vagus nerve is vital for maintaining host homeostasis [145,146] and may therefore play an important role in coping with stress [147]. Furthermore, as with some infectious agents, gut microbiota are also socially transmitted among group members under natural conditions [148], providing a counterbalancing benefit to the increased risk of social disease transmission. As particular gut microbiota compositions are also related to various health outcomes [144,149], their interactions with host genotype, behaviour and fitness should make interesting topics for future research, especially in wild animals [150–152].

In conclusion, this theme issue has highlighted state of the art research on the links between sociality, health and fitness. We covered many exciting emerging areas on these links, yet we also had to be selective in the topics covered. In addition to synthesizing some of the findings in this theme issue, here we have highlighted major areas that also deserve further research attention, including specific directions that amplify and add to the future research suggested by authors in this issue. Clearly more research remains, and we anticipate productive findings along many current and future trends in research in biology, psychology and medicine.

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