



## Introduction

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# Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies

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This paper introduces a theme issue presenting the latest developments in research on the impacts of sociality on health and fitness. The articles that follow cover research on societies ranging from insects to humans. Variation in measures of fitness (i.e. survival and reproduction) has been linked to various aspects of sociality in humans and animals alike, and variability in individual health and condition has been recognized as a key mediator of these relationships. Viewed from a broad evolutionary perspective, the evolutionary transitions from a solitary lifestyle to group living have resulted in several new health-related costs and benefits of sociality. Social transmission of parasites within groups represents a major cost of group living, but some behavioural mechanisms, such as grooming, have evolved repeatedly to reduce this cost. Group living also has created novel costs in terms of altered susceptibility to infectious and non-infectious disease as a result of the unavoidable physiological consequences of social competition and integration, which are partly alleviated by social buffering in some vertebrates. Here, we define the relevant aspects of sociality, summarize their health-related costs and benefits, and discuss possible fitness measures in different study systems. Given the pervasive effects of social factors on health and fitness, we propose a synthesis of existing conceptual approaches in disease ecology, ecological immunology and behavioural neurosciences by adding sociality as a key factor, with the goal to generate a broader framework for organismal integration of health-related research.

## 1. Introduction

Life in permanent groups has been considered as one of the major transitions in evolution [1]. The evolutionary factors favouring the transition from a solitary lifestyle to sociality have been studied in depth [2]. However, the consequences of sociality for individual fitness have received comparatively less attention [3,4], even though variation in fitness in humans and several group-living animals has been linked to various aspects of sociality [5–8]. Health has been suggested to play an important role in mediating some of these links, with two main costs of group living playing important roles: enhanced social transmission of parasites, and increased susceptibility to disease and infection owing to chronic stress induced by social competition [9–14].

This theme issue aims to achieve the conceptual integration that is required for deeper understanding of these processes and to identify general mechanisms and processes that may also affect human health and well-being. To this end, the contributions to this theme issue offer a broad comparative perspective on the links between sociality, health and fitness in a wide array of taxonomic groups, ranging from insects to primates, including humans. We also open a new dialogue between theoreticians, field biologists and laboratory scientists working on a variety of taxa that, hitherto, have had limited

opportunities and incentives for interdisciplinary exchange. Specifically, by outlining a comprehensive framework that is firmly based on evolutionary principles and incorporates the effects of sociality, we aim to enhance integration of proximate and ultimate approaches and to overcome conceptual gaps owing to taxon-specific constraints or methodological limitations that have hampered integration across disciplines in the past. Moreover, only by studying these topics in a range of taxa and model systems can one identify the evolutionary roots of many human health problems related to these issues in today's world—and to offer evolutionarily informed solutions. Thus, research presented here also contributes to growing efforts in the emerging field of evolutionary medicine [15].

Two unavoidable costs of sociality are important in this context. First, disease transmission mediated by social contacts—either between conspecifics or between members of different species—has become a major issue in the world economy and in human health. Some infectious diseases such as influenza, HIV and Ebola are sweeping the globe, causing major trauma and economic damage [16,17]. In general, transmission of parasites across species is creating new challenges for public health, agriculture, transportation networks and the conservation of migrating or endangered species [18,19]. A better understanding of the relative importance of different types of social contacts and other behaviours for parasite transmission in a variety of species, as exemplified in this theme issue, may contribute to improved control of infectious diseases in all of these spheres, for example by improving the ecological validity of epidemiological models.

The second unavoidable cost of sociality involves competition and resulting social stress. Social stress is known to cause major health problems through increased susceptibility to infectious and non-infectious disease [20–22]. However, different social variables may elicit a stress response, and the same factors may evoke contrasting physiological responses in different species [23,24], highlighting the need for broad comparative approaches to identify general principles. Moreover, a less obvious aspect of sociality—social isolation—has been identified as a major determinant of human health outcomes [25,26], for which animal models provide opportunities for experimental studies and exact quantification of the relevant social factors. By summarizing research on a wide range of wild and semi-naturally housed social animals and humans, this theme issue broadens the scope of (clinical) research on social stress and isolation, thus providing an evolutionary perspective and a valuable comparative framework for future clinical studies in the spirit of evolutionary medicine.

This introductory paper will set the scene for these major goals by first outlining the evolutionary perspective underlying our approach, along with common terminology necessary for effective interdisciplinary communication. We then characterize and define the main factors, processes and mechanisms that link sociality, health and fitness, distinguishing between individual- and group-level phenomena. Because various aspects of these links have been investigated previously in research on social immunity, ecological immunology, disease ecology and behavioural neurosciences, we also attempt to compare these approaches in the quest for a unified theoretical framework. Throughout this Introduction, we integrate the main questions addressed by the contributions to this theme issue.

## 2. Sociality, health and fitness: evolutionary perspective

A key assumption of the conceptual approach advocated here is that the effects of sociality on health ultimately lead to tangible fitness consequences in terms of differential reproduction and survival. A comprehensive understanding of the underlying processes requires (i) establishment of causality, (ii) identification of the specific links between sociality and health and (iii) identification of behavioural and physiological mechanisms mediating these links. First, correlations between aspects of sociality and various fitness measures have initially been identified in humans and primates [5,7], but causality was hard to discern; it was initially unclear whether a lack of social integration leads to unfavourable health outcomes, whether sick individuals are less likely to establish social relationships, or whether social variables and health are jointly driven by a third variable. Experimental exposure of patients and monkeys with a harmless flu virus eventually demonstrated the causal effect of sociality, however, because individuals with low social network diversity (humans) or low social rank (monkeys) exhibited infection significantly more often than study subjects in other social categories [27,28].

Second, in studying the links between aspects of sociality and health, it is important to distinguish between two fundamental types of health outcomes. Non-communicable diseases are the result of systemic or organic failures, whereas communicable diseases are the result of successful infection by infectious microbial agents, such as viruses, bacteria, fungi, protozoa or multicellular organisms; hereafter, we refer to all of these organisms as parasites (following Nunn & Altizer [29]). In this context, it is also important to acknowledge the feedback between individual health and condition and aspects of sociality, because sick individuals may behave or be treated differently than healthy conspecifics. Moreover, changes in susceptibility to diseases may also affect the likelihood of successful transmission of pathogenic agents, creating complex dynamics.

Finally, the behavioural and physiological mechanisms are important components for many papers in this theme issue. For example, the distinction between infectious and non-infectious disease is crucial for the study of underlying mechanisms, because altered susceptibility (i.e. physiology) to disease also affects non-infectious disease outcomes, whereas altered rates of social contact (i.e. behaviour) primarily affect the spread of infectious diseases. Moreover, the links between individual health status and fitness outcome can be mediated by either physiological and nervous processes altering probabilities of reproduction and survival, on the one hand, or direct negative impacts on these fitness determinants by parasite infection, on the other hand.

To integrate perspectives from diverse disciplines, including psychology, evolutionary biology, physiology, veterinary medicine and wildlife and disease ecology, an agreement on common definitions is indispensable, given that some key terms are being used differently in different disciplines. Thus, additional terms require definition and explanation before we explore the links among sociality, health fitness, and the proximate and ultimate mechanisms underlying them in more detail. We then discuss the health-related costs and benefits of sociality in this section before exploring fitness outcomes that should and can be measured in different disciplines.

### (a) What is sociality?

Sociality and 'social' are used in several, often not explicitly defined ways in different disciplines. To make matters worse, additional qualifiers, such as 'highly' social or 'social complexity', are increasingly being used in the vertebrate literature often without explicit definition, whereas researchers studying invertebrates have been using categories such as parasocial, subsocial, semisocial and quasi-social to distinguish certain taxa from the eusocial Hymenoptera and termites. These categories cannot be easily transferred to most vertebrates, because the latter lack many of the traits (e.g. reproductive division of labour and cooperative brood care) underlying this classification scheme [30–33]. Psychologists and others studying human behaviour, on the other hand, are mainly referring to particular patterns of social relationships when qualifying aspects of social behaviour; this was used, for example, in an influential definition by Wilson [34], who characterized a species as social if it was group living and exhibited 'reciprocal communication of a cooperative nature'. Thus, studies on social evolution in the broadest sense are still lacking a unified terminological and conceptual framework.

To better characterize sociality, it is first useful to consider its opposite, namely the millions of species that lead a largely solitary life. Individuals in many solitary species develop from eggs that their mothers have deposited or released somewhere in the environment, but only a fraction of them enjoys any form of post-natal care by parents or other conspecifics [35]. In taxa with obligate parental care, such as certain bees, lactating mammals or mouthbrooding fish, offspring may associate and interact with a parent for longer periods of time, but these associations typically do not persist beyond independence [36]. Crucially, in solitary species, adults do not habitually associate with other adults. Aggregations of adult conspecifics are only temporary and either accidental (e.g. due to drift by wind or water currents) or due to joint attraction to a temporary resource (e.g. vultures to a carcass or colonially breeding birds to a suitable breeding site) [37]. Interindividual encounters among solitary animals are often characterized by a lack of individual recognition and the exchange of agonistic behaviour. Mating is the only context in which adults of species with sexual reproduction seek the temporary vicinity of potential mates [38,39]. Other contacts with conspecifics may be indirect and limited to the exchange of visual, acoustic or olfactory signals. Thus, despite quantitative and qualitative differences, solitary species also exhibit social behaviour, making the use of 'social species' misleading and self-defeating for referring to non-solitary species.

One of the major transitions in evolution involved changes in association patterns of adult individuals, resulting in the formation of permanent groups of variable size, composition and stability [2]. Favoured by factors such as reduced predation risk and increased opportunities for cooperation, e.g. in jointly defending resources, individuals of group-living species are permanently associated with each other and actively maintain group cohesion [40–42]. Pair-living species, which often live in small family groups with their offspring [43,44], can be classified together with group-living species when considering these two costs of sociality.

Some species are so flexible in their social behaviour or life histories that they form groups temporarily or facultatively [45–47]. Yet, the categorical distinction between solitary and group-living species is sufficient and practically meaningful

for two reasons. First, for questions related to the social transmission of parasites through any kind of interindividual close contact [48,49], group living is the key criterion for classifying different species into types of social organization (with the caveat that the probability of social transmission of parasites is, of course, also enhanced in temporary associations or during extended periods of parental care). Second, the other health-related costs of sociality accrue only in a subset of group-living species, and not in solitary species. Among group-living species, there is not only great variation in group size, sex ratio, relatedness and other aspects of their social organization, but also in crucial aspects of interindividual relationships among group-members. These social relationships develop through repeated interaction between individually known conspecifics and may result in dominance relations or social bonds of variable quality, with the latter being apparently limited to birds and mammals [4,50]. The frequency of social interactions can be used to quantify one dimension of social integration. The nature of interactions, whether they are primarily amicable or agonistic, determines the quality of dyadic relationships, which, in combination with their frequency and the extent of social support by third parties, has physiological consequences that are detailed below.

An important prediction emerges from these considerations. Specifically, we expect that the risk of social transmission of parasites is enhanced in any species, regardless of whether it lives in temporary aggregations or stable groups, whereas the risk of suffering from negative health consequences due to social stress are mainly found in group-living species with individualized social relationships. We consider these costs further in §2b.

### (b) Health-related costs of sociality

Because not all species are group living, being solitary must be advantageous for some taxa, and certain costs of group living may outweigh the benefits of sociality for others. The two costs of sociality in the present focus have direct consequences for individual health and condition because they ultimately impact an individual's energy balance. From a life-history perspective, individuals vary in fitness, because the trade-offs among basal organismal functions (growth, maintenance and reproduction) are played out in ever-changing ecological and social contexts, so that there is no single optimal solution for the allocation of available energy [51]. In adults, a key trade-off exists between reproduction and immune function [52]. Proximately, total energy available for these functions is a result of various ecological (e.g. food and water availability, weather, predation risk) and intrinsic (e.g. age, sex, genotype) variables [53]. However, individuals in group-living species additionally have to mitigate the consequences of competition with group members for access to food and mates at higher frequency or intensity than animals in solitary species.

In particular, caloric intake is reduced for individuals with inferior competitive abilities when food is limited [54,55]. Furthermore, for some group members, repeated defeat in agonistic interactions, subordinate social status or low rank in a hierarchy are the possible outcomes of incessant conflict with group-mates. If persistent, these social variables will result in chronic stress for some individuals [56–58]. The resulting chronic elevation of glucocorticoids and other stress hormones has several detrimental effects, including reduced

immunocompetence, muscle breakdown and osteoporosis, detrimental effects on memory and vigilance, anovulation and (in juveniles) delayed sexual maturation [21–23].

These physiological consequences of social stress—in combination with compromised resource access—ought to affect individual susceptibility to both communicable and non-communicable disease, which, in turn, compromises individual survival and reproductive success, i.e. fitness. A meta-analysis across male vertebrates revealed similar immune responses in dominant and subordinate males, but dominants exhibited consistently higher parasitism [59]. A behavioural consequence of social competition and stress may be social isolation, which can be due to either ostracism or self-withdrawal, and which has costs in terms of challenging homeostasis but benefits in terms of lowering the risk of social transmission of parasites [60–62]. Thus, one type of cost of group living should lead to a net increase in the risk of developing some non-communicable disease by compromising individual condition.

Moreover, group living also creates unavoidable costs at the group level in the form of increased risk of social transmission of infectious agents [9,10,63], which are often specialized on a particular host species [64]. In addition, many animal groups include clusters of related individuals that, owing to their immunogenetic similarity, face an additional risk of correlated susceptibility to infection by particular parasites that increases with the degree of genetic homogeneity [65]. While the actual transmission route is parasite-specific and depends on the type of social contact [48,49], the fundamental risk of social transmission is elevated in group-living species compared with solitary ones because of the spatio-temporal concentration of potential hosts. Because group-living species exhibit tremendous variation in group size, frequency and type of physical contacts, mating systems and dispersal patterns, there is great inter- and intraspecific variation in the probabilities of social transmission of parasites. It has been suggested that susceptibility to parasite transmission depends on group size [66], but group size only explains a small amount of variance [67], so that characteristics of a species-typical social network might be more important in controlling social transmission of parasites [49,68,69]. For example, the frequency of contacts among Tasmanian devils predicts their probability of contracting facial cancer through biting conspecifics [70], whereas the type and direction of the contact is more important for predicting the spread of tuberculosis among meerkats [71], the spread of infectious fungi in ant colonies [61] and for explaining the prevalence of gastrointestinal helminths in brown howler monkeys [72].

The predicted costs of sociality related to enhanced parasite transmission can also be examined by comparing levels of infection with parasites between group-living and solitary species. The few systematic comparative studies, indeed, reported higher infection levels in group-living mammals, birds and insects than in solitary species [73,74]. Intraspecific variation in certain aspects of sociality can also be used to test this hypothesis. For example, gorillas in groups appear to be more susceptible to Ebola than solitary males [75]. Other parasites are vector-borne, but individual susceptibility to their infectious stages may also be influenced by social factors, e.g. when vectors are attracted to or better able to find aggregations of host individuals [76]. Finally, even the transmission of parasites from the environment can be affected by social variables of their hosts, because species differ, for

example, in the degree of territoriality, which determines the extent to which conspecifics share the same space over time [73,77,78]. In addition, faecally transmitted infectious agents may accumulate differently in the territories of groups with different size. Thus, living in groups and several social factors of group-living species enhance the *a priori* probability of contracting communicable diseases that results from the presence of parasites.

### (c) Health-related benefits of sociality

Group living is not only advantageous because of several well-known benefits related to reduced *per capita* predation risk, joint resource defence and other collaborative activities, but also because the two main costs of group living discussed above are partly offset by benefits that only accrue in group-living species, and which therefore contribute to the maintenance of group living. These benefits can also be separated into those related to reduced disease susceptibility, which mainly arise at the level of individuals, and those related to parasite transmission, which are played out at the level of the group.

First, with respect to the costs of chronic stress, group living also provides unique opportunities for social support and cooperation that may partly offset these costs. Individuals may receive agonistic support in conflicts with third parties from other often related individuals, alleviating individual costs due to physical inferiority or low rank in contests over access to resources, ultimately contributing to an improvement of the physical condition of the beneficiaries [79–83]. Social support may also be manifest in the form of social bonds that form through regular association and positive interactions [4,84]. The documented fitness benefits of social bonds in vertebrates [7,8] may proximately be due to a reduction of chronic activation of the hypothalamic–pituitary–adrenal axis and sympathetic nervous system activity [58,85]. Other social mechanisms of potential social buffering remain more obscure, e.g. where only the presence of a particular class of individuals, like fathers, has a positive effect on individual health and development [86]. Development of new physiological and genetic markers, also including non-invasive methods, may contribute to better characterization of the physiological and genetic mechanisms underlying these effects. Such research on proximate mechanisms linking behaviour and physiology may also contribute to answering the big question in this context, i.e. what is the relative importance of social, ecological, physiological and genetic factors in shaping individual disease susceptibility?

Evidence from comparative studies also suggests that the higher *per capita* risk of social transmission of pathogenic agents is partly offset by enhanced personal immune response capabilities [87]. Several studies comparing the anti-microbial efficiency of body surface secretions between solitary and social species found higher efficiency in the more social bees [88], wasps [89] and thrips [90]. Such improved individual ability of members of group-living species to resist pathogenic agents may arise from individual mechanisms, such as increased investment into personal immunity as a response to the increased risk of disease transmission, described as density-dependent prophylaxis [91], in temporal aggregations of otherwise solitary species. Improved personal immunity could also be the result of an interaction with other group members, such as the described phenomenon of social immunization [60,92–94]. Increased personal immunity of group

members can be achieved either by transfer of protective immune effectors (passive social immunization [93]), or by spread of low numbers of infectious agents through social contact that may stimulate the immune system without leading to disease (active social immunization [94]), similar to the effects of variolation in early human medicine [95]. Such transfer of immunity in social groups can increase the proportion of well-protected or resistant group members [96], allowing for the beneficial effect of herd immunity [97,98].

Moreover, many behavioural mechanisms to control parasite transmission are only available to group-living species because they require social interaction or coordination. Whereas behaviour plays a role in reducing individual risk of parasite acquisition in all species from invertebrates to humans [87,99] through various avoidance and hygienic behaviours, as well as through self-medication [19,100], regular opportunities for social interactions with a hygienic function exist only in group-living species. Conspecifics can, for example, remove ectoparasites from the body surface of conspecifics through grooming, a widespread behaviour in invertebrates and vertebrates [101–103]. Group members may also reduce or avoid interactions and contact with obviously infected individuals, collectively generate heat that kills off parasites (a type of behavioural fever), or they may share anti-microbial compounds and apply them to infected conspecifics (reviewed in [104–106]). Social contacts, especially but not exclusively between parents and offspring, also facilitate vertical transmission of microbiota, which are being recognized as an important source of well-being [107]. Similarly, social interactions may also lead to contact immunity in humans after immunization with live attenuated vaccines [108], or in social immunization in ants and termites [94].

Animals can acquire parasites not only through social interactions with conspecifics, but also directly from the environment or from various vectors. Infection directly from the environment may result from contact or ingestion of infectious stages in water, food or substrate, whereas vector-borne infections are mediated by contacts with intermediate hosts, such as blood-sucking insects. These sources of infection with infectious agents are principally identical for solitary and group-living species, with the caveat that the probability of infection via these conduits can also be affected by social factors. For example, intraspecific variation in group size among neotropical primates is associated with the risk of infection with mosquito-borne malaria [76], and encounter rate was non-linearly related with home range overlap in female elk [109]. The big question in this context is therefore about the relative importance of social transmission compared with other routes of parasite acquisition. However, many of the existing epidemiological models do not take social structure of their hosts into account [68,78,110]. Moreover, the relative importance of interspecific social transmission [111], either in mixed-species communities or in multiple-host parasites, needs to be better understood for a comprehensive assessment of the relative importance of social transmission of parasites.

#### (d) Fitness consequences

The links between sociality, health and fitness are being studied in different experimental systems and with a diversity of methodological approaches, each of which has its own strengths and weaknesses. One major difference exists

between studies of humans and animals because in clinical studies, various health outcomes can be studied in great detail and in large samples, but variation in social variables mostly relies on self-reports rather than direct quantification, often with the goal to control for these effects rather than study them directly. Field studies of wild animals, in contrast, can take advantage of natural variation in several aspects of sociality within and among study species, and individual variation in survival and reproductive success can be determined in an ecologically meaningful context, but measures of health correlates and outcomes are cumbersome and rely largely on non-invasive methods. In addition, field studies offer ecologically valid opportunities to study the mechanisms and consequences of social transmission of parasites directly, whereas this is not meaningful or possible in most vertebrate laboratory animal systems. For social insects, the opportunities for studying the social transmission of parasites in the field versus the laboratory are reversed [61,94]. Animal laboratory studies can elegantly control some social variables and also obtain detailed physiological data on health outcomes, but they typically lack meaningful or practical fitness proxies because laboratory animals are efficiently buffered from ecological causes of extrinsic mortality. Finally, quantitative comparative studies can address evolutionary hypotheses about broad patterns while statistically controlling for confounding variables, but they cannot establish causality. Thus, a combination of approaches, as represented by the contributions to this theme issue, is required for a comprehensive understanding of the complex inter-relationships among health, fitness and sociality.

The different types of studies also face different opportunities and constraints with respect to the fitness correlates or determinants they can measure. In long-term field studies of most vertebrates, it is challenging but possible to measure direct components of individual lifetime reproductive success [112], but it is less clear how to analyse fitness consequences of sociality in species with reproductive division of labour, because reproduction is highly skewed, individual worker mortality has little impact on colony fitness, and inclusive fitness is more difficult to measure [113–115]. Variation in survival is relatively straightforward to determine, provided individuals can be recognized and followed, but survival estimates are generally complicated by dispersal, and causes of mortality must be separated into those due to extrinsic causes (primarily predation) and those attributable to infection and non-infectious diseases. For example, Chapman *et al.* [116] use demographic data collected over decades to make inferences about the effects of stress and new parasites on population dynamics in red colobus monkeys, and recent studies revealed that survival is affected by social relationships in female baboons [117] and male bottlenose dolphins [118].

Because of the fundamental trade-off between maintenance and reproduction, variation in reproductive success provides a second important fitness component. Depending on species-specific details, interindividual variation in fecundity and fertility can often be estimated, e.g. by counting clutch or litter size. Again, variation in reproductive success may be influenced by other factors that are not or only weakly related to individual health condition, such as age, parity and rank, which need to be controlled for. Nonetheless, several field studies reported positive relationships between measures of social connectivity and measures of reproductive success, including studies of male long-tailed manakins [119], female

horses [120], female bottlenose dolphins [121] and male Assamese macaques [122]. Some field study systems are also amenable to experimental manipulation of parasite load, typically by experimental removal or addition of parasites [123,124], measuring the treatment effects on proxies of health and condition or on direct fitness components. For example, Raveh *et al.* [125] examined the effects of ectoparasite removal on body mass, number and size of offspring at weaning in ground squirrels. However, only a few established vertebrate study systems, such as striped mice or racoons [45,126], are amenable to studies of the health and fitness consequences of natural intraspecific variation in sociality, for the simple reason that field studies have limited experimental control over relevant aspects of sociality.

Studies with human subjects yield detailed data on a number of health outcomes related to social variables, such as depression, cognitive performance, immunocompetence or cardiovascular function [62]. The same holds true for measurement of specific physiological variables related to immune function. Because most clinical studies are conducted with WEIRD subjects [127], i.e. from 'Western, educated, industrialized, rich and democratic societies', which exhibit limited variation in natural fertility, variables reflecting reproductive success are normally not being recorded. However, longitudinal clinical studies can and do study effects on mortality [6,128]. Controlled experiments with model laboratory species can also produce insights into endocrine and immune responses to variation in social variables, but face limitations in terms of generating meaningful predictors or even estimates of survival and reproduction [25,85,129]. Finally, comparative analyses allow testing of the fundamental hypothesis that variation in sociality affects health and fitness outcomes by contrasting solitary and group-living species while taking potential other variables, such as shared phylogenetic history, into account, provided sufficient data on the same health or fitness variables are available from a range of species [78,130,131].

### 3. Conceptual integration

Three decades ago, the vertebrate immune system was considered as a closed system, whose response to challenges by antigens is solely controlled by lymphokines and cytokines [132,133]. Similar views prevailed about the autonomy of the endocrine and nervous systems [134]. The multitude of relationships between the immune system of an individual and various internal and (biotic and abiotic) external factors have been identified and integrated only more recently [135,136]. Here, we argue that, in contrast to human medicine, existing integrative concepts in ecology and evolutionary biology do not fully acknowledge the diversity of effects of social factors on health outlined above. We therefore briefly sketch existing frameworks and propose a synthesis that incorporates the costs and benefits of sociality.

Studies exploring the mechanisms determining human health outcomes first realized that the nervous and endocrine systems are in constant functional dialogue with the immune system. Accordingly, the emerging field of psychoneuro-immunology acknowledged that input from social factors affects immune function via neural and endocrine mechanisms [132]. A growing body of research in social neuroscience has since established both molecular and physiological

mechanisms as well as health outcomes of the various social influences individuals are exposed to in their daily lives [26,133]. More recently, proponents of Hamiltonian medicine suggested that not only details of the social relationships of patients but also the interactions among parasites, genes and cells need to be taken into consideration [137].

An important conceptual breakthrough in evolutionary ecology led to the recognition not only that the immune system of wild animals is integrated with other physiological processes within individuals, but also that individual variation in immunity across individuals and species exists as a result of interactions with ecological and evolutionary pressures [136,138]. Explaining the evolution of, for example, immune-mediated sexually selected traits [139,140] required the acknowledgement of costs of immunity and the existence of physiological trade-offs [141] that led to the establishment of a research agenda called ecological immunology. However, the focus of eco-immunological studies remained on traits of hosts that impact variation in immunity, neglecting the social environment of the focal subjects [142]. Disease ecology seeks to explain the emergence and transmission of disease at the population level, but its exclusive focus is on infectious diseases [143]. Similarly, it was recognized that collective interactions among group members may lead to avoidance, control or elimination of parasitic infection at the group level. Research on the mechanisms underlying this social immunity [104] initially showed a strong focus on the collective defences displayed in colonies of social insects, yet recently it has also been appreciated as a valuable concept for non-eusocial societies [97], allowing elaboration of their importance for the evolution of group living [87].

Last, but not least, we should also consider how medical perspectives have been influenced by perspectives in evolutionary biology and knowledge of our evolutionary history. The emerging field of evolutionary medicine aims to understand human health from an evolutionary perspective, by considering, among other things, how our modern lives are mismatched to the environments in which we evolved. Thus, evolutionary medicine views some mental health disorders, such as anxiety or depression, as representing at least partly maladaptive responses to modern pressures and exacerbated by lack of social networks with family and long-term friends [144]. Similarly, the causal agent of peptic ulcers, *Helicobacter pylori*, is also shown to play a crucial role in the development of the immune system, leading to lower levels of asthma [145]. However, *Helicobacter* is going extinct, at least partly through smaller family sizes and fewer opportunities for acquiring the bacterium from close kin [146]. Finally, the complexities of human birth are thought to require assistance, unlike in other primates, leading to recent movements to have increased midwifery and doula support [147]. The perspectives above can and should be better integrated with other evolutionary perspectives on human health.

Thus, current research on the determinants and consequences of health and immunity remains conceptually fragmented, despite tremendous recent progress towards integration, and there remains little dialogue between studies on humans and animals in terms of acknowledging the role of social factors in influencing infectious and non-infectious disease risks. We therefore stress that the social environment plays an important role in modulating individual susceptibility to both infectious and non-infectious disease, that these effects can have profound consequences for survival and reproduction, and that

most underlying mechanisms are identical in invertebrates and vertebrates, including humans [138,148]. The contributions to this theme issue underscore the possibility and necessity of such an integrative approach.

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