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Behavioural Defences Against Parasites Across Host Social Structures

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Comments

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Abstract

(1) Animals exhibit a variety of behavioural defences against socially transmitted parasites. These defences evolved to increase host fitness by avoiding, resisting, or tolerating infection.

(2) Because they can occur in both infected individuals and their uninfected social partners, these defences often have important consequences for the social group.

(3) Here, we discuss the evolution and ecology of anti-parasite behavioural defences across a taxonomically wide social spectrum, considering colonial groups, stable groups, transitional groups, and solitary animals.

(4) We discuss avoidance, resistance, and tolerance behaviours across these social group structures, identifying how social complexity, group composition, and interdependent social relationships may contribute to the expression and evolution of behavioural strategies.

(5) Finally, we outline avenues for further investigation such as approaches to quantify group-level responses, and the connection of the physiological and behavioural response to parasites in different social contexts.

Introduction

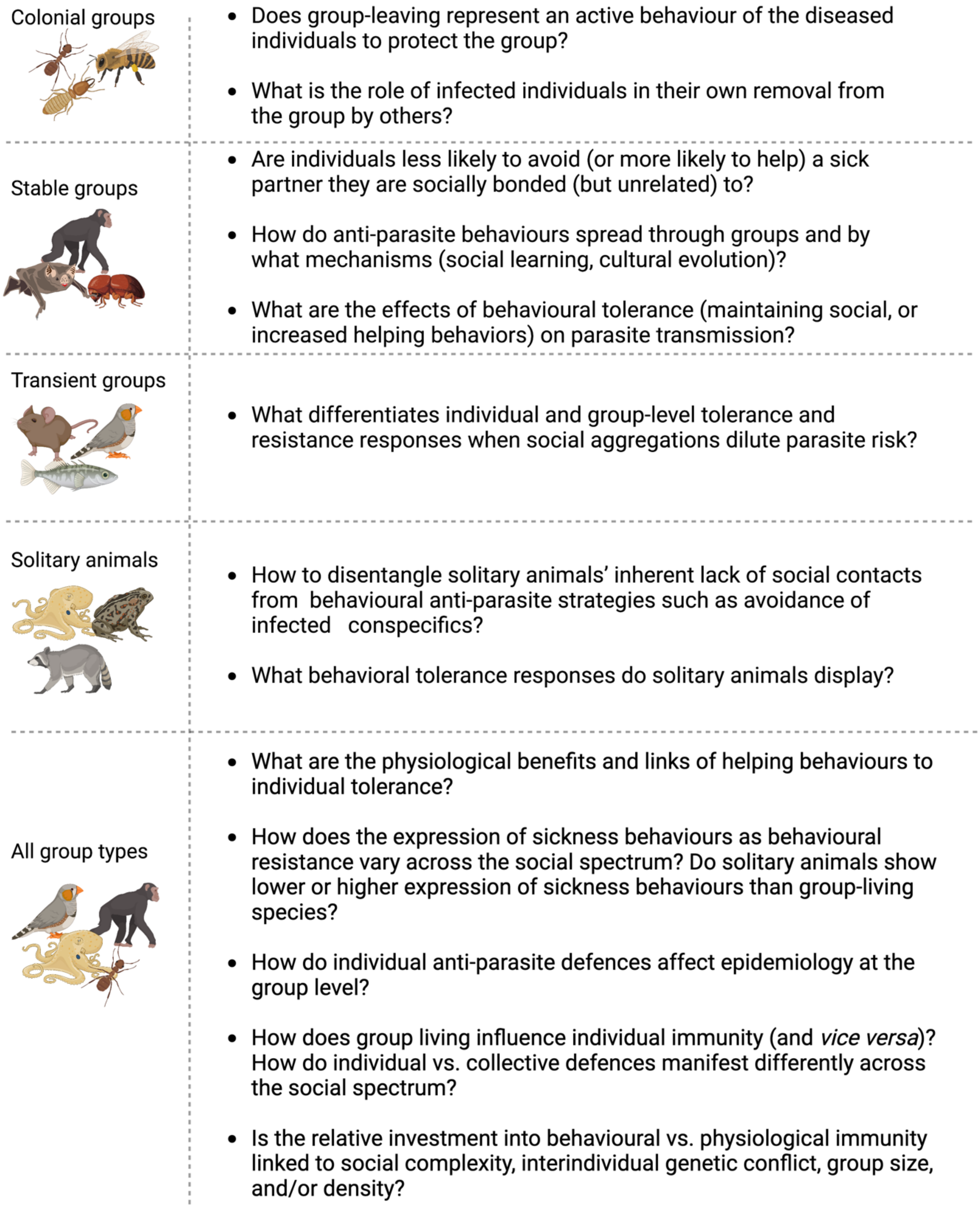
Parasites can drive the evolution of a variety of traits in host animals (Graham et al., 2011). Host behaviour is a fundamental component of parasite transmission, and often greater sociality correlates with greater rates of exposure – and therefore infection (e.g., Lucatelli et al., 2021, Schmid-Hempel 2021). However, animals can alter their behaviour in many ways that reduce their infection risk or modulate the outcome of an infection (Stockmaier et al., 2021, Lopes et al., 2022, Hart and Hart 2021), with important emergent consequences at the group or population level (Albery et al., 2020; Stroeymeyt et al., 2018).

Behavioural anti-parasite defences, like other anti-parasite defences, can take three general forms: avoidance, resistance, and tolerance. We define *avoidance behaviours* as actions that reduce any type of physical contact between uninfected individuals and the infectious agent, whether the infectious agent is in the environment, in or on other hosts. Avoidance-induced contact limitation – whether driven by the infectious individual or by its group members – will contribute to reducing disease transmission within the group. *Resistance behaviours* reduce parasite load (Hall et al., 2017; Rigby et al., 2022). Some behaviours directly remove pathogens from the exposed individual, like grooming, which can be exerted by the individual itself (selfgrooming) or by its group members (allogrooming), and which will help to prevent establishment of the infection and transmission. Other behaviours support the immune system of individuals and reduce parasite load by creating unfavourable conditions for the parasite through, for instance, behavioural fever (Rakus et al., 2017) or self-medication (de Roode et al., 2013), or by freeing resources otherwise used for other tasks. The latter has been suggested for sickness behaviours – a set of behavioural changes in response to infection such as lethargy, loss of appetite, and reduced movement (Hart 1988). Finally, *tolerance behaviours,* (e.g., Adelman and Hawley, 2017; Burgan et.al., 2019)*,* reduce the negative impact of infection on host fitness without reducing parasite load (Medzhitov et al., 2012; Råberg et al., 2008). Group-living can support individual tolerance through beneficial social interactions (e.g., if mutual feeding allows sick individuals to maintain fitness) or can improve group tolerance by compensating for the lost workforce of sick individuals to maintain colony performance (Beros et al., 2015).

Different modes of behavioural defences are predicted to have vastly different consequences for parasite transmission and host-parasite coevolution (Råberg et al., 2008). For example, while resistance is expected to decrease parasite prevalence in a host population, tolerance is not, and may even increase population-level prevalence. Moreover, the same behaviour can contribute to multiple defence modes and can do so at different scales (e.g., individual vs. group level). For instance, sickness behaviours could (i) save resources that can then be redirected to the immune system to decrease pathogen load (Hart, 1998), thereby increasing individual resistance, (ii) increase individual tolerance, i.e. the individual's ability to reproduce or survive in the presence of a high pathogen load (Medzhitov et al., 2012), and (iii) contribute to avoidance if they cause social withdrawal in infected individuals, which in turn reduces transmission to other group members (Stockmaier et al., 2021).

Because these behaviours can affect not only the exposed or infected individual but also its conspecifics, the evolution and expression of these anti-parasite behaviours should depend on the social organisation and structure of the host groups. It is unclear, however, how the mode and strength of such defences vary along axes of sociality, and how elements of social "complexity" should affect their sophistication (Pull and McMahon, 2020). Here, we discuss how animals' social structures could influence the evolution and expression of avoidance, resistance, and tolerance behavioural defences against parasites that are socially transmitted (including both micro- and macroparasites). We outline studies that have examined behavioural responses to parasites in both invertebrate and vertebrate hosts, representing a range of social structures, which we loosely categorize as colonial groups, stable groups, transient groups, and solitary animals. It is important to note that for some social groups (like colonial groups), behavioural avoidance, resistance, and tolerance strategies likely evolved due to their benefits of protecting the group (i.e., social immunity; Cremer et.al., 2007), but not necessarily providing direct benefits to all individual group members. For less cooperative groups, behaviours likely evolved due to their direct benefits at the individual level but may still have some group-level effects (i.e., increase fitness of other group members). For instance, even if individuals avoid or resist infection for selfish reasons this might also reduce the likelihood of transmission to conspecifics (Albery, 2022). Ultimately, we hope to widen the diversity of study systems considered for the study of behavioural anti-parasite responses, in a framework for understanding how axes of sociality should influence the expression and evolution of behavioural parasite avoidance, resistance, and tolerance.

Figure 1



Colonial groups

- Does group-leaving represent an active behaviour of the diseased individuals to protect the group?
- What is the role of infected individuals in their own removal from the group by others?

Stable groups

- Are individuals less likely to avoid (or more likely to help) a sick partner they are socially bonded (but unrelated) to?
- How do anti-parasite behaviours spread through groups and by what mechanisms (social learning, cultural evolution)?
- What are the effects of behavioural tolerance (maintaining social, or increased helping behaviors) on parasite transmission?

Transient groups

- What differentiates individual and group-level tolerance and resistance responses when social aggregations dilute parasite risk?

Solitary animals

- How to disentangle solitary animals' inherent lack of social contacts from behavioural anti-parasite strategies such as avoidance of infected conspecifics?
- What behavioral tolerance responses do solitary animals display?

All group types

- What are the physiological benefits and links of helping behaviours to individual tolerance?
- How does the expression of sickness behaviours as behavioural resistance vary across the social spectrum? Do solitary animals show lower or higher expression of sickness behaviours than group-living species?
- How do individual anti-parasite defences affect epidemiology at the group level?
- How does group living influence individual immunity (and *vice versa*)? How do individual vs. collective defences manifest differently across the social spectrum?
- Is the relative investment into behavioural vs. physiological immunity linked to social complexity, interindividual genetic conflict, group size, and/or density?

Figure 1: Open questions and future directions (illustrations from Biorender).

Colonial groups

We define colonial groups as permanent, obligate groups with very high levels of mutual dependence between group members. This mutual dependence often (but not always) stems from reproductive division of labour (i.e., the presence of non-reproductive helpers). These groups can exhibit varying levels of relatedness between group members, ranging from very high relatedness in clonal groups of some aphids and some ants; higher than normal full-sib relatedness, as between females in the social Hymenoptera like many bees, wasps, or ants; standard full-sib families like in termites; as well as lowered relatedness due to multiple reproductive individuals in the colony or multiple mating, as is typical in leafcutter ants and honeybees. Examples include all social insects (all ants and termites, and the social bees and wasps, Schmid-Hempel 1998), as well as some aphids (Stern and Foster, 1997), snapping shrimps (Hultgren et al., 2017), mole rats (Faulkes and Bennett, 2013), and colonial siphonophores (Dunn and Wagner, 2006). Based on group traits such as reproductive division of labour and close relatedness of group members, behavioural anti-parasite defences of colonial groups are expected, and often found, to be targeted at protecting the group rather than the individual.

(1) Behavioural avoidance in colonial groups: Compared to other social groups, classical avoidance behaviour displayed by healthy individuals to reduce contact with infectious individuals (Gibson and Amoroso, 2022) rarely occurs in colonial groups, even if examples exist where healthy colony members spatially separate infected nestmates, or move the location of the nest, leaving sick individuals behind (reviewed in Cremer et al., 2007). More frequently, healthy colony members do not avoid contact with pathogen-exposed individuals, but instead engage in sanitary actions to reduce their parasite load (see below).

Interestingly, however, it is often the infected individuals themselves that show contact reduction to their healthy colony members, particularly in species with complete reproductive division of labour (Boomsma and Gawne, 2018; Pull and McMahon, 2020) between the reproductive colony members and their sterile helpers. As the helpers in these species rely more on whole-colony health than on their own to pass on their genes to the next generation, infected individuals have an interest not to harm the colony and thus engage in behaviours that prevent transmission of parasites to others. When themselves infectious, social insects often reduce social contact with group members, e.g., by spending less time in the brood chamber (Ugelvig and Cremer, 2007) and in the nest (Stroeymeyt et al., 2018). Such 'altruistic avoidance behaviour' seems to be fully exerted by the infectious individual, in the absence of any observed aggression by colony members. Notably, while resulting in the same outcome, prevention of social contact between infectious and healthy group members in this case is not driven by the healthy but by the infectious individual (in contrast to classical avoidance of infected conspecifics, see Gibson and Amoroso, 2022). This contact reduction also occurs at non-infectious disease stages (Bos et al., 2012; Detrain and Leclerc, 2022, Conroy and Holman, 2022) and in generally moribund individuals (Heinze and Walter, 2010; Ruepell et al., 2010), where it has been suggested to result from impaired perception of social cues (Kralj and Fuchs, 2006; Leclerc and Detrain, 2017) or sickness behaviour. More work is needed to distinguish sickness behaviours such as reduced locomotion (Alciatore et al., 2021; Richard et al., 2008, but see Geffre et al., 2020) or reduced performance of colony tasks (Scharf et al., 2012) from altruistic self-removal, even though both may contribute to lower contact rates and parasite spread (Fig. 1). Importantly, contact-avoidance by infectious individuals in social insects can reduce the likelihood of disease transmission through the group, and therefore complements resistance behaviours that actively reduce pathogen load (see below).

(2) Behavioural resistance in colonial groups: When the first line of defence provided by avoidance fails, resistance behaviours reduce individual or colony-level parasite load, either by removing the infectious agent itself, by reducing parasite replication, or by removing infected hosts, which would otherwise present a risk of spreading the parasite within the group. Specific resistance strategies vary depending on the biology of the parasite and the infection stage. At the individual level, selfgrooming is an efficient way to clean the body surface from infectious particles (Hughes et al., 2002; Reber et al., 2011; Zhukovskaya et al., 2013). Similarly, self-medication using antimicrobial compounds can reduce infection from contaminated food (Tragust et al., 2020), and ants exposed to contamination with a fungal pathogen ingest otherwise harmful reactive oxygen species to fight the infection (Bos et al., 2015; Rissanen et al., 2022). At the group level, allogrooming of infectious individuals by their healthy colony members is widespread in social insects (Hughes et al., 2002; Reber et al., 2011; Rosengaus et al., 1998; Zhukovskaya et al., 2013). Allogrooming is particularly effective against, but not restricted to (see Beros et al., 2021) parasites that infect from the body surface (and can thus be mechanically removed and disinfected by grooming, Tragust et al., 2013a) and it can dramatically increase the survival of fungus-contaminated hosts (Hughes et al., 2002; Rosengaus et al., 1998), with low risk for the groomers (Konrad et al., 2012). The sophistication of resistance behaviours in social insects suggests that healthy colony members often do not need to avoid infectious others (Theis et al., 2015), but instead engage in collective resistance behaviours, such as grooming (Alciatore et al., 2021; Hughes et al., 2002; Reber et al., 2011; Rosengaus et al., 1998).

In addition to cleaning one another, individuals in colonial groups should also perform high levels of nest hygiene. While it was suggested that antimicrobial use increases with sociality in bees (Stow et al., 2007), it is unknown how common this pattern is and with what precise axes of sociality it correlates (Fig 1): is hygiene linked to the complexity of social organization, to genetic interindividual conflict, or simply to group size or density? Colonial animals often have permanent nests in which parasites can build up over time, which raises the question of whether hygiene is less important in social groups without permanent nesting locations (e.g., nomadic army ants).

When individual resistance or collective grooming or disinfection fails, so that hosts develop advanced infections and can no longer be cured, these individuals are commonly targeted by antagonistic behaviours that reduce colony-level pathogen load and thus increase colony-level resistance by preventing the replication and spread of infectious particles through the colony (Pull et al., 2018). For example, virus-infected honeybees are attacked by their nestmates (Drum and Rothenbuhler, 1985; Waddington and Rothenbuhler, 1976) or evicted from the nest altogether (Baracchi et al., 2012). Other antagonistic responses include shifts from grooming to cannibalization as fungal infections progress in termites (Davis et al., 2018), the removal of infected brood in bees and ants (Rothenbuhler, 1964; Tragust et al., 2013b, but see Drees et al., 1992), and even destructive disinfection in ants (Pull et al., 2018), which results in the brood's death. Because this sacrifice prevents pathogen transmission from the infected individual to other group members, it benefits the whole colony, and thereby also indirectly the sacrificed individual. We therefore expect infectious individuals in colonial groups not to hide their infection status, or even to actively signal it (Rosengaus et al., 1999; Cremer, 2019). Yet, the mechanisms involved and the role of the sick individual in triggering these behaviours are still underexplored (Fig. 1).

(3) Behavioural tolerance in colonial groups: In colonial groups, tolerance has been suggested as an important mechanism acting at both the individual and colony level, particularly because the care and stable access to resources provided by group members might allow infected individuals to function despite high parasite loads (Cremer et al., 2018; Kurze et al., 2016). Examples of behavioural responses that may promote group-level tolerance include behavioural shifts (e.g., in task allocation) by uninfected workers of social insect colonies that compensate for the reduced work performance by the infected workers, such as in cestode-infected ants (Scharf et al., 2012); such tolerance may however come at a cost, such as increased mortality in nestmates taking over tasks of the missing workforce (Beros et al., 2015).

Stable groups

We define stable groups as mostly permanent where individuals nonetheless retain the ability to move between groups (e.g., fission-fusion dynamics). In these groups, there is often high interdependence between specific subsets of individuals due to cooperative relationships, and reproduction can be skewed towards a few individuals (e.g., cooperative breeding), but who reproduces might change. Social investments are often directed towards certain individuals that, for instance, increase indirect fitness through kin selection, or confer fitness benefits through other mechanisms of cooperation such as reciprocity. Examples include vampire bats (Stockmaier et al., 2020, Stockmaier et al., 2018), mandrills (Poirotte et al., 2017; Poirotte and Charpentier, 2020), banded mongoose (Fairbanks et al., 2015), meerkats (Smyth and Drea, 2016), or cooperatively breeding ambrosia beetles (Nuotclà et al., 2019). Because relationships between individuals strongly differ (e.g., between socially bonded animals), behavioural anti-parasite behaviours are expected to depend on whom an individual interacts with (Stockmaier et al., 2020, Poirotte and Charpentier, 2020). For instance, conspecific avoidance might only be beneficial for an individual if it doesn’t lose fitness benefits from an existing relationship with a diseased conspecific.

(1) Behavioural avoidance in stable groups: Avoidance of parasitized conspecifics in stable groups is generally present (e,g., Poirotte and Charpentier, 2020) but can be modulated by inter-individual relationships, likely reflecting the fitness benefits gained from these privileged relationships. For instance, mandrills avoid grooming others that have high loads of orofecal parasites (Poirotte et al., 2017), but this avoidance is suppressed towards kin (Poirotte and Charpentier, 2020). Conspecific avoidance might also be absent as shown in banded mongoose that continued allogrooming their tuberculosis infected groupmates (Fairbanks et al., 2015), illustrating that avoidance could be absent in stable, highly social groups that continuously interact and that individuals might even choose to help others (see more details below in tolerance section, Loehle 1995; Fairbanks et al., 2015; Hart 1990).

Social withdrawal as a result of sickness behaviours has been observed in species that live in stable groups and in some cases, infected individuals reduce contact with others (Stockmaier et al., 2018; Stockmaier et al., 2020, but see Willette et al., 2007). While such a reduction in contacts can also benefit conspecifics (e.g., Shakar and Shakar 2015), there is relatively little evidence that sickness behaviours have evolved as a mechanism to protect others (e.g., based on kin relationships, Lopes et. al., 2021). On the contrary, sickness behaviours can be suppressed to engage in important, partner-specific interactions. For instance, sick vampire bat mothers keep grooming their offspring potentially because the mother-pup relationship in this species is an important and lasting social bond (Stockmaier et al., 2020). As such, sickness behaviours thus far seem to benefit the infected individual more than others in stable groups. Research has mainly focused on how behavioural avoidance can vary across kin relationships (Poirotte and Charpentier, 2020; Stockmaier et al., 2020) and not on other, non-kin, relationship types (Fig. 1). Are individuals less likely to avoid (or more likely to help) a sick partner they are socially bonded (but unrelated) to? Would infected individuals suppress their sickness behaviours only when interacting with some, but not other group members based on the strength of their social relationships?

(2) Behavioural resistance in stable groups: Self-medication is a resistance behaviour that has been observed in species that live in stable groups. For instance, bonobos self-medicate with hispid whole-leaves when infected with gastrointestinal parasites (Fruth et al., 2014). Similarly, self-grooming can reduce parasite load (Hart, 1990). While such resistance behaviours benefit the individual, they might also benefit the group, if they spread through social learning (Kavaliers and Choleris, 2018; Poirotte and Charpentier, 2023) or if they reduce transmission to others. However, the group-wide epidemiological effects of individual parasite resistance behaviours and how they could potentially spread and evolve through mechanisms such as cultural evolution within stable groups are understudied (Fig. 1). In addition to individual resistance, group-level resistance behaviours such as allogrooming occur in stable groups (Hart, 1990), such as in ambrosia beetles (Nuotclà et al., 2019).

Cannibalism (Nuotclà et al., 2019) and other forms of aggression towards sick individuals (McFarland et al., 2021), have been documented in stable groups and could increase group-level resistance by reducing infection of more group members if the infectious individuals are excluded from interacting with others. However, like grooming, such aggressive behaviours in stable groups often serve social functions (e.g., gain in dominance status, McFarland et al., 2021) and their potential role in decreasing the parasite load within the group are unclear (Fig. 1).

(3) Behavioural Tolerance in stable groups: In stable groups, behaviours that promote disease tolerance might not only manifest via maintenance of social behaviours (Adelman and Hawley, 2017), but also increased, cooperative behaviours (i.e., helping behaviours, Stockmaier et al., 2021). Cooperative behaviors include individuals providing food (Loehle, 1995) or territory defence (Almberg et al., 2015) to support to sick group members, all of which contribute to maintaining the fitness of parasitized individuals, with potential feedback benefits for the individual providing help if sick individuals reciprocate after they recover (Albery, 2022). Currently, these helping behaviours in stable groups are understudied, potentially because the physiological benefits and the clear link of helping behaviours to parasite tolerance are often challenging to quantify (Fig. 1). Notably, any tolerance behaviours like maintenance of social behaviours or increased cooperative behaviours towards infected group members could also lead to greater levels of transmission. While this will not necessarily affect the health of the group members receiving benefits from others and therefore being tolerant to the disease, it will affect pathogen prevalence and epidemiology (Fig. 1)."

Transitional groups

We define transitional groups as fluid, non-permanent groups with some level of interdependence based on individual needs. Aggregations are often driven by predator avoidance, food availability, seasonal reproduction, or shelter availability. Generally, individuals gain intermediate fitness benefits from joining groups or aggregations for certain periods. Examples include but are not limited to den-sharing in Caribbean spiny lobsters (Behringer et al., 2006), seasonal aggregations of birds (Bouwman and Hawley, 2010; Zylberberg et al., 2013), shoaling of tadpoles or fishes (Kiesecker et al., 1999; Stephenson, 2019; Stephenson et al., 2018; Tobler and Schlupp, 2008), or communal nesting of mice (Lopes et al., 2016). For animals in transitional groups, we would expect anti-parasite behaviours to primarily benefit the individual. Compared to animals that rely on stable group living, transiently social animals present promising study systems to understand the expression of anti-parasite behaviours in social contexts because of the plasticity they express in joining social situations (Jog et al., 2022, Hawley et al., 2020). Group-level avoidance, resistance, or tolerance effects might result from individual behaviours, but these likely do not represent behavioural strategies that have evolved to protect the group.

(1) Behavioural avoidance in transitional groups: Avoidance of infected conspecifics is often observed in transitional groups. For instance, Caribbean spiny lobsters avoid den-sharing with virus-infected conspecifics (Behringer et al., 2006), Trinidadian guppies avoid infectious, parasitized conspecifics (Stephenson, 2019; Stephenson et al., 2018), and bullfrog tadpoles avoid shoaling with yeast-infected conspecifics (Kiesecker et al., 1999). Importantly, these behaviours are plastic in many systems, depending on factors such as infectiousness of the conspecific (Stephenson et al., 2018), sex (Stephenson, 2019), or individual immune status (Stephenson, 2019; Zylberberg et al., 2013). In some cases, individuals might even choose not to avoid infectious conspecifics to gain individual benefits. For example, male house finches preferably feed next to infected conspecifics, potentially because infected individuals are less aggressive, and, hence, competitive (Bouwman and Hawley, 2010).

(2) Behavioural resistance in transitional groups: Behaviours that increase resistance have also been observed across transitionally social species. Sickness behaviours like lethargy, which could increase resistance by diverting energy to the immune response (Hart, 1988), have been observed in several such species (Lopes et al., 2021, 2016). They are often suppressed in social situations to avoid loss of social status (Lopes et al., 2012), loss of mating opportunities (Lopes et al., 2013), or continued parental care (Aubert et al., 1997; Weil et al., 2006). As such, the expression of sickness behaviours most likely depends on trade-offs between individual benefits (e.g., conserving energetic resources) and loss of social opportunities (Lopes, 2014). Because they gain little from specific relationships with other individuals, animals in transitional groups may also undertake selfish actions to reduce their own parasite load at the expense of others: for example, Trindiadian guppies with high ectoparasite load increase contacts with uninfected conspecifics, potentially allowing them to offload parasites to others (Reynolds et al., 2018).

(3) Behavioural tolerance in transitional groups: When infected, animals in more fluid group settings might gain fitness benefits such as predator avoidance or access to food (particularly in larger group sizes), thereby ameliorating the cost of infection (individual tolerance, e.g., Ezenwa and Worsley-Tonks 2018). However, this may lead to parasite transmission to others. Infected animals could also decrease social tendencies to increase their own tolerance. In western mosquitofish, parasite-infested fish reduce their shoaling tendencies, potentially allowing them to reduce food competition with others (Tobler and Schlupp, 2008, also leading to avoidance/contact-reduction).

Predominantly solitary animals

We define solitary animals as those that generally do not come together in social aggregations, except in rare occasions such as mating or for periods of joint parental care. Often, these species are characterized by lack of individual recognition and more frequent aggressive interactions (Kappeler et al., 2015). Examples of solitary or mostly solitary species include desert tortoises (Aiello et al., 2016), sleepy lizards (Bull et al., 2012), and octopuses (Locatello et al., 2013). Fundamentally, solitary animals will rarely interact directly relative to more social species. They do not have access to the many disease-related and general benefits of sociality (Ezenwa et al., 2016; Kappeler et al., 2015) and instead will more often be competing with their conspecifics. As such, we expect higher focus on direct benefits to the individual in their expression of behavioural anti-parasite behaviours and minimal group-level effects.

(1) Behavioural avoidance in solitary animals: Because of its direct benefits to the individual and the lack of social benefits to be gained from others, we expect that avoidance of infectious conspecifics could be common, however, because of their sparse contact patterns, this will often not translate into significant social interaction changes. Concurrently, solitary animals' tendency to remain asocial for other reasons may make infection-related avoidance difficult to discern empirically (Fig. 1). In mating contexts, conspecific avoidance has been demonstrated in solitary species of lizards (Martín et al., 2007) and birds (Borgia and Collis, 1989). We predict that avoidance in a mating context may also more broadly depend on the risks and costs associated with finding a mating partner (e.g., less avoidance shown in solitary species where individuals are sparsely distributed). Since solitary animals rarely meet – and do not rely on – conspecifics, it is also unlikely that they will retract from social interactions when infectious, unless retracting benefits them directly. For instance, immune-challenged octopuses will avoid interacting with conspecifics, potentially because they are unable to engage in competitive interactions (Locatello et al., 2013). Likewise, solitary animals may actively suppress symptoms of infections such as sickness behaviours that result in social withdrawal if it increases their fitness.

(2) Behavioural resistance in solitary animals: Given that evidence to date suggests that sickness behaviours are in part caused by the inflammatory response, controlled by specific neuronal populations (Lopes et al., 2021; Osterhout et al., 2022), and could have direct benefits for individuals as they could increase their resistance (Hart, 1988), we predict that solitary animals will express sickness behaviours. Solitary animals might, however, show less intense sickness behaviours than non-solitary animals potentially because of the absence of social buffer mechanisms (i.e., behaviours that increase tolerance or resistance of the sick individual) that could protect sick individuals from, for instance, increased predation. Instead, solitary animals would need to prioritise pursuing resources to replace those lost to the parasite on their own. Contrary to this expectation, however, a recent review of sickness behaviours across vertebrates found that the solitary species that have been studied show sickness behaviours comparable to group-living species, potentially because solitary animals experience fewer social costs of behaving sick (Lopes, 2014; Lopes et al., 2021). This pattern remains to be validated with more comparative studies of sickness behaviours across the social spectrum, especially in closely related species that vary in their social organization (Fig. 1). Infected solitary animals might also suppress sickness behaviours and their positive effects on parasite resistance if this suppression strongly benefits them such as in the context of parental care. For instance, when infected, burying beetles will continue to care for their young despite high costs to themselves (Ratz et al., 2021).

(3) Behavioural tolerance in solitary animals: We are not aware of any incidences of behavioural tolerance in solitary animals; it is very likely that they express them, but perhaps due to the field's tendency to focus on more-social animals rather than more-solitary ones, there have been few documented examples (Fig. 1).

Open questions across all social group structures

(1) Group-level responses to parasite infection: A vital element of further investigation will involve measuring how anti-parasite behaviours expressed by certain group members affect disease risk for other group members (Fig 1). For most social species, there is a lack of studies linking individual behaviours such as aggregation, avoidance, social isolation, hygiene (e.g., grooming), or self-medication to group-wide transmission dynamics. Parasites could also be diluted over the group, which is known to happen in transitional groups of juvenile sticklebacks (Poulin and FitzGerald, 1989) or Galapagos marine iguanas (Wikelski, 1999), as well as in colonial groups of ants (Konrad et al., 2012) and termites (Liu et al., 2015). In principle, such parasite dilution could lead to multiple scenarios. If individuals "offload" parasites to other group members (i.e., by choosing to be near others) their own resistance should increase. In colonial organisms, parasite dilution may promote group-level tolerance if colony health is maintained by diluting parasite load across more individuals compared to having the same load concentrated in fewer individuals, as individuals can often cope with lower infection doses and maintain their health (Konrad et al., 2012). Similarly, group-level resistance might arise if dilution reduces parasite replication, as fewer individuals fall sick and shed pathogens. Whether the same mechanism is at play in non-colonial social groups remains largely unexplored and deeper knowledge of the exact mechanisms will further help to demarcate group-level tolerance and resistance (Fig. 1). Answering some of these questions necessitates monitoring all group members simultaneously, which has become easier due to new tracking and computational tools (Mersch et al., 2013; Geffre et al., 2020; Walter and Couzin 2021). These approaches may help to understand collective behavioural responses to parasites and have to date been prominently used on social insects (e.g., Stroeymeyt et al., 2018; Geffre et al., 2020, but see Jolles et al., 2020) to reveal group-level responses to parasite infections in the form spatial and behavioural compartmentalization of contact networks, which provides a form of organisational immunity (e.g., Stroeymeyt et al., 2014). Achieving further crosstalk between researchers working across forms of sociality in the animal kingdom may allow us to apply these methodological advances to achieve greater integration and a more unified theory of behavioural immunity.

(2) Interplay between behavioural and physiological defences across social structures: Behavioural and physiological responses to parasitism can be connected; for example, sickness behaviours are partly a result of the inflammatory response (Lopes et al., 2021; Osterhout et al., 2022). The way animal physiology changes upon perception of parasitism risk (discussed in Lopes, 2022) may likewise lead to behavioural avoidance of parasitism and even potentially prepare animals for infection, leading to increased physiological resistance or tolerance. Indeed, immune status affects the way that social insects perform sanitary care (Konrad et al., 2018), revealing the tight interplay between physiological immunity and the expression of hygiene behaviour. It has long been debated whether collective anti-parasite behaviours expressed in highly social species such as mutual hygiene in ants and termites (Hughes et al., 2002; Rosengaus et al., 1998) or collective fever in honeybees (Starks et al., 2000) reduce the need for individuals to invest into their own immune system (Evans et al., 2006). Yet, there is no evidence for such a pattern when comparing the immune gene repertoire of solitary vs. social bees (Barribeau et al., 2015), maybe because the beneficial effects of group-level hygiene are counteracted by the higher transmission probability arising from frequent close social interactions (and/or that the former evolved to compensate for the latter). Interestingly, when animals forming transitional groups, such as migratory locusts, are exposed to crowding conditions, they upregulate their individual immune systems in a form of density dependent-prophylaxis (Wilson et al., 2002; but see Wilson et al., 2003) instead of displaying collective hygiene. It remains to be determined how the investment into individual versus group-level immunity manifests differently across hosts varying in social structure (Fig. 1).

Concluding remarks

Animals' behavioural responses to infection are a cornerstone of their behavioural immune system, and they vary substantially across the animal kingdom. We have identified a suite of such responses across a variety of social systems, with some suggested trends of divergent investment in individual- versus group-level responses according to the species' social organization. *Colonial groups* are characterized by a high level of cooperative disease defences between colony members because their fitness arises through performance at the level of the group rather than the individual colony member. *Stable groups* are characterized by interindividual relationships, and the degree of behavioural anti-parasite defences can be modulated according to the social setting, yet a link between relationship strength and these behaviours has not been clearly established and additional studies are required to test our prediction. Animals in *transitional groups* seem to show stronger tendencies for behaviours that benefit themselves (e.g., avoidance), if the benefits of such behaviours outweigh those of joining groups. This makes them excellent model systems to explore the cost-benefit trade-offs of anti-parasite behaviours. Finally, while *solitary animals* do show some forms of anti-parasite behaviours directed at conspecifics, the lack of research on these behaviours makes it hard to draw more general conclusions. One avenue to study these behaviours in predominantly solitary animals is within the context of their few social interactions such as mating or joint parental care interactions.

Overall, many questions have so far only been thoroughly studied in the most social groups, like the colonial groups of social insects. Extending these efforts equally to other animals that show different degrees of sociality would allow deeper understanding of the interplay between sociality, behaviour, and physiological responses to parasites. Insight could be gained by comparing phenotypes of the same or closely related species that vary in sociality, like solitary and social populations of halictid bees (Yagi and Hasegawa, 2012) or raccoons (Hirsch et al., 2013), or monogamous versus non-monogamous voles (McGraw and Young, 2010). Similarly, species that fluctuate in their degree of sociality over time, such as slime moulds with transient multicellularity (Wayne, 2010), or the solitary colony-founding phases in some social insects (Casillas-Pérez et al., 2022; Cole and Rosengaus, 2019; Manfredini et al., 2016) offer promising study systems. Moving forward, rigorously testing how anti-parasite behavioural defences vary with degree of sociality will provide a fuller understanding of behaviour as an integral component of immunity.

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Figure legends

Figure 1: Open questions and future directions (illustrations from Biorender).

Author contributions

All authors contributed equally

Data accessibility

The manuscript has no data

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