Social immunity and the evolution of group living in insects

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The evolution of group living requires that individuals limit the inherent risks of parasite infection. To this end, group living insects have developed a unique capability of mounting collective anti-parasite defences, such as allogrooming and corpse removal from the nest. Over the last 20 years, this phenomenon (called social immunity) was mostly studied in eusocial insects, with results emphasizing its importance in derived social systems. However, the role of social immunity in the early evolution of group living remains unclear. Here, I investigate this topic by first presenting the definitions of social immunity and discussing their applications across social systems. I then provide an up-to-date appraisal of the collective and individual mechanisms of social immunity described in eusocial insects and show that they have counterparts in non-eusocial species and even solitary species. Finally, I review evidence demonstrating that the increased risks of parasite infection in group living species may both decrease and increase the level of personal immunity, and discuss how the expression of social immunity could drive these opposite effects. By highlighting similarities and differences of social immunity across social systems, this review emphasizes the potential importance of this phenomenon in the early evolution of the multiple forms of group living in insects.

1. Introduction

The shift from a solitary life to group living is considered to be one of the major evolutionary transitions [1,2]. To date, group living can be found in almost all animal taxa, with its complexity ranging from simple mutual attraction between individuals, over temporary periods of parental care in family associations, to permanent societies with reproductive division of labour [3,4]. The ecological success of group living species is traditionally thought to rely on the fitness benefits social life provides to group members, such as improved protection against predators, increased reproductive success, enhanced foraging efficiency and higher survival rates [5]. However, group living also comes with major fitness costs. One of these costs is the increased risks of parasite infection (broadly defined to include bacteria, viruses, protozoans, helminths and fungi) [6–12]. These risks are particularly exacerbated in group living species, because frequent and intimate contacts between individuals are known to facilitate parasite transmission, and because the close genetic relatedness often exhibited by group members is likely to make them susceptible to the same parasites [6,7,13–15]. Hence, to gain a better understanding of the evolution of group living, we need to shed light on the mechanisms that limit the inherent risks of parasite infections for group living individuals [7].

Group living individuals are not only able to limit parasite infection using their personal immune system [16,17], but may also use their unique capability of mounting collective defences. This phenomenon, called social immunity (see below for a more detailed definition [6,7,18]), encompasses multiple mechanisms such as the use of antimicrobial substances as nest material and sanitation behaviours to eliminate corpses and waste products from the nest (figure 1). Over the last 20 years, eusocial insects, which mostly include ants, termites, as well as some bees and wasps, have provided one of the main biological models to study social immunity [7,19–21]. The resulting studies were of key importance, because they revealed the structural diversity of social immunity across eusocial species and...
2. Definitions of social immunity

The first definition of social immunity in an evolutionary context was offered in a landmark paper published in 2007 by Cremer et al. [7]. They defined social immunity as ‘collective action or altruistic behaviours resulting in avoidance, control or elimination of parasitic infections’. This definition, followed by the shorter one ‘collective defences against parasites and pathogens’ by Wilson-Rich et al. in 2009 [19], was coined to describe the group-level defences against parasites expressed in colonies of eusocial insects (and to some extent in groups of primates). These defences included allogrooming, a behaviour during which one individual grooms another individual to remove its external parasites, and hygienic behaviours, during which diseased brood are removed from the nest [7,19] (see also figure 1).

In an important review published in 2010, Cotter & Kilner [23] proposed to broaden the field of social immunity by applying the theory previously developed in the context of eusocial insects to other forms of group living. To this end, social immunity was defined as ‘any type of immune response that has been selected to increase the fitness of the challenged individual and one or more recipients’. One major benefit of defining social immunity in a broader context than eusocial insects was to allow the inclusion of anti-parasite defences that are not tightly linked to permanent social organization, such as parental care during family life (e.g. [24]) and to some extent herd immunity [25] (see also conclusion in [7]). Another benefit of the definition by Cotter et al. was that it clarified that social immunity refers to defences that have been selected for their collective anti-parasite protection, and not the ones that provide benefits to group members as a simple by-product of personal protection. This distinction is of key importance, because social immunity could otherwise encompass the strategies used by solitary-living individuals to fight their own infection, as these strategies somewhat reduce parasite exposure of the conspecifics they might encounter during their life cycle (e.g. during mating or competitive interactions).

The definition proposed by Cotter & Kilner [23] also raised two potential issues. First, it frees the recipients from being a member of the donors’ group, so that social immunity might not be a product of social life, but simply the outcome of shared location between individuals (even from different species) [23]. For instance, this definition allowed social
immunity to encompass symbionts protecting their hosts, which is unlikely to reflect social life. The second potential issue comes from the strong emphasis on the fitness benefits for both donor and recipient(s). This may suggest that no cost is involved in social immunity, which in addition to being an unlikely scenario (e.g. [26]), would also raise the question of why not all anti-parasitic defences have evolved towards this universally beneficial state.

To circumvent the issues raised by the definition of Cotter & Kilner [23] while adopting their proposal to expand the field of social immunity beyond eusociality, I propose to define social immunity as ‘any collective and personal mechanism that has emerged and/or is maintained at least partly due to the anti-parasite defence it provides to other group members’. Readers interested in details of terminologies covering individual and social immunization are referred to the review by Masri & Cremer [22].

3. Social immunity in eusocial, non-eusocial and solitary insects

Inflicting multiple members of an insect group generally requires that parasites successively pass three steps [7,19]. The first one consists of the uptake of the parasite from the environment, the second is its successful transfer into the nest and the third one is its multiplication and transmission to other group members. Any individual or collective strategy reducing the success of parasites in at least one of these three steps thus possibly qualifies as a mediator of social immunity (given that its collective benefits are under selection). In their seminal study, Cremer et al. [7] reviewed the large diversity of anti-parasite mechanisms employed by eusocial insects to diminish the risks associated with each of the three steps of infection. Some of these mechanisms require traits that are specific to eusocial systems, such as division of labour, so that their expression is unlikely to exist in other forms of group living. However, many of them do not have such requirements, which offers scope for their expression in non-eusocial species, and even to find counterparts in solitary species [23].

In the following sections, I provide an up-to-date appraisal of the anti-parasite mechanisms involved in each of the three steps of group infection in eusocial insects (adapted from Cremer et al. [7]) and then determine whether they have known counterparts in non-eusocial and solitary insects. I summarize what is known in table 1, which is organized around the three steps to infection just described. Based on this information, I then discuss potential reasons for the presence/absence of these defences across the different forms of group living.

(a) Step 1: limiting parasite uptake from the environment

The most common strategies used by eusocial insects to limit parasite uptake from the environment encompass both collective and individual mechanisms that help to avoid infection after or during foraging activities. Collective defences are illustrated, for instance, by guards of the honeybee Apis mellifera, which prevent newly infected nest-mates from entering the hive [38] and ‘hitchhikers’ of leaf-cutter ants, which ride on leaf fragments to defend foragers against parasitoid attacks [37]. On the other hand, individual defences can be exhibited by foragers that avoid habitats containing entomopathogenic fungi and nematodes, such as in the termite Macrotermes michaelseni and the ant Solenopsis invicta [27,28], respectively, as well as by other ant species that refrain from the consumption of contaminated food or conspecifics [32,33].

The individual anti-parasite mechanisms reflected by avoidance behaviours are not specific to eusocial insects and can be found in many non-eusocial and solitary species. For example, gregarious individuals of the migratory grasshopper Melanoplus sanguinipes and the German cockroach Blattella germanica avoid the consumption of contaminated food/con-specifics [34,35]. In the subsocial burying beetle Nicrophorus vespilloides, females avoid degraded carcasses (covered with many microbes) if given a choice with fresh ones, a mechanism that could also have evolved to reduce post-hatching competition between juveniles and microbes over the carcass [30]. Finally, in the solitary-living Japanese beetle Popillia japonica and the seven-spot ladybird Coccinella septempunctata, individuals avoid soil contaminated with entomopathogenic fungi [31] and larvae inhibit their consumption of infected prey [36], respectively. Because avoidance behaviours provide direct fitness benefits to the actors, the importance of social interactions in the emergence and/or persistence of these behaviours in social species, and thus their qualification as social immunity, remains to be further explored [7].

(b) Step 2: limiting parasite establishment into the nesting habitat

Incorporating chemical/antimicrobial substances into the nest material and/or expressing nest sanitation behaviours are the two main processes reported in eusocial insects to prevent parasite establishment in their habitat. Chemical substances can be collected from the environment, such as in the wood ant Formica pantulagubris and the honeybee in which workers collect pieces of resin and incorporate them into nest structure (figure 1, [39,40]), or they may be synthesized by colony members through metapleural, sternal or venom glands [41–43,83] (reviewed in [84]). Sanitation behaviours involve eliminating waste material, such as conspecific corpses, left-over food or frass that could be used as a substrate by the parasites [54,55,85].

The use of chemical/antimicrobial substances and sanitation behaviours can also be found in many non-eusocial species [84]. For instance, adults of the group living beetle Dendroctonus rufipennis exude oral secretions in their galleries to inhibit the growth of colonizing fungi [44]. Subsocial females of the beewolf Philanthus triangulum cultivate Streptomyces bacteria on their antenna and apply them to brood cells to protect cocoons from fungal infection [45]. Frass removal occurs in the subsocial cockroach Cryptocercus punctulatus [57], the group living beetle Trachysus ghanensis [58] and the subsocial cricket Anuragryllus muticus [59]. Frass removal can even be found in solitary insects exhibiting high site fidelity, such as the grasshopper Atractomorpha lata and in Epargyrus clarus caterpillars, in which frass pellets are ballistically ejected by the producing individuals [56,60].

Interestingly, an alternative strategy to frass removal is to imbue frass or anal exudates with antimicrobial properties and use them in the nest to limit parasite establishment. This process occurs in both eusocial (termites) and non-eusocial (cockroaches and burying beetles) species, in which the use
Table 1. Personal and collective mechanisms shaping social immunity in eusocial insects, and their counterparts in non-eusocial and solitary species. Requirements for their expression are listed for each mechanism. The mechanisms can be absent/not reported (?) or not expected to occur in the given system (x). Table adapted from Cremer et al. [7], which also contains information on whether these defences are prophylactic or induced. References [113–219] are given in the electronic supplementary material.

<table>
<thead>
<tr>
<th>defence mechanisms</th>
<th>requirements</th>
<th>eusocial</th>
<th>non-eusocial (group living)</th>
<th>solitary</th>
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<tbody>
<tr>
<td><strong>Step 1. Limiting parasite uptake from the environment</strong></td>
<td></td>
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<tr>
<td>only a small proportion of group members forage</td>
<td>stable habitat (e.g. nest) division of labour</td>
<td>(113)</td>
<td>x</td>
<td>x</td>
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<tr>
<td>avoidance of contaminated habitats (incl. oviposition</td>
<td></td>
<td></td>
<td>[27 – 29, 114 – 116]</td>
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<td>places)</td>
<td></td>
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<td>[30, 117]</td>
<td>[31, 118 – 120]</td>
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<tr>
<td>avoidance of consumption/contact with infected food/</td>
<td></td>
<td></td>
<td>[32, 33, 121 – 124]</td>
<td></td>
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<tr>
<td>conspecifics (incl. cannibalism)</td>
<td></td>
<td></td>
<td>[34, 35]</td>
<td>[36, 119, 120, 125 – 127]</td>
</tr>
<tr>
<td>guarding of foraging trails</td>
<td>stable habitat (e.g. nest) foraging trails division of labour</td>
<td>[37]</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>guarding of nest entrance</td>
<td>stable habitat (e.g. nest) division of labor</td>
<td>[38, 128]</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><strong>Step 2. Limiting parasite establishment into the nesting habitat</strong></td>
<td></td>
<td></td>
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<tr>
<td>collection of antimicrobial substances</td>
<td>stable habitat (e.g. nest)</td>
<td>[39, 40, 129, 130]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>use of self-produced chemical secretions on habitat</td>
<td>stable habitat (e.g. nest)</td>
<td>[20, 41 – 43, 131 – 134]</td>
<td>[44, 45, 135]</td>
<td>x</td>
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<tr>
<td>surface (e.g. metapleural or sternal glands, venom,</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>other)</td>
<td></td>
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<tr>
<td>faecal material/anal exudates with antimicrobial</td>
<td>stable habitat (e.g. nest)</td>
<td>[46 – 48]</td>
<td>[26, 49 – 53, 136, 137]</td>
<td>x</td>
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<tr>
<td>properties cover the nest</td>
<td></td>
<td></td>
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<tr>
<td>corpse removal</td>
<td>stable habitat (e.g. nest)</td>
<td>[54, 138 – 144]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>garbage and frass removal/separated waste dump</td>
<td>stable habitat (e.g. nest)</td>
<td>[55, 56, 145 – 150]</td>
<td>[56 – 59, 151 – 154]</td>
<td>[60] [56]</td>
</tr>
<tr>
<td>cover/encapsulate corpses or parasites within the nest</td>
<td>stable habitat (e.g. nest)</td>
<td>[33, 143, 155 – 157]</td>
<td>?</td>
<td>x</td>
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<tr>
<td><strong>Step 3. Limiting parasite transmission between group members</strong></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>(a) From adults to brood</td>
<td></td>
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<td></td>
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<tr>
<td>mechanical removal by allogrooming (adults-to-brood)</td>
<td>parental/sibling care</td>
<td>[20, 158]</td>
<td>[24, 159, 160]</td>
<td>x</td>
</tr>
<tr>
<td>application of antimicrobial secretion on the brood/</td>
<td>parental/sibling care</td>
<td>[61, 161 – 163]</td>
<td>[24]</td>
<td>x</td>
</tr>
<tr>
<td>the eggs</td>
<td></td>
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<td></td>
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<tr>
<td>feed the brood with anti-parasitic components</td>
<td>parental/sibling care</td>
<td>[62, 164 – 166]</td>
<td>[63, 167 – 172]</td>
<td>x</td>
</tr>
<tr>
<td>infected individuals do not tend the queen/brood</td>
<td>communal breeding or precocial species</td>
<td>[64, 65]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>trans-generational immune priming</td>
<td></td>
<td>[68, 175]</td>
<td>[69]</td>
<td>[176 – 180]</td>
</tr>
<tr>
<td>(b) From adults to adults</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>mechanical removal by allogrooming (adult-to-adult)</td>
<td>behavioural interactions</td>
<td>[20, 33, 64, 70, 71, 158, 181 – 192]</td>
<td>[72]</td>
<td>x</td>
</tr>
<tr>
<td>social fever</td>
<td></td>
<td>[73, 193]</td>
<td>[74]</td>
<td>[74]</td>
</tr>
<tr>
<td>spatial compartmentalization of the nest/digging area</td>
<td>stable habitat (e.g. nest) complex nest architecture</td>
<td>[13, 113, 194 – 198]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>infected individuals leave the group/limit contact to</td>
<td></td>
<td>[65, 75, 199, 200]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>group members</td>
<td></td>
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</table>

(Continued.)
of frass as nest material has been shown to limit parasite development [46,47,49–51]. The maintenance of frass in the nest may also provide immune benefits by allowing exchanges of endosymbionts and other immune factors among group members. For instance, in the bumblebee *Bombus terrestris*, individuals obtain bacterial microbiota by feeding on conspecific faeces, which improves their resistance against the protozoan parasite *Crithidia bombi* [48]. To date, this latter benefit remains unexplored in non-eusocial insects.

(c) Step 3: limiting parasite transmission between group members

When a parasite has successfully passed the two first steps of group infection, the expression of mechanisms limiting its transmission among group members is required. Eusocial and non-eusocial species share most of the mechanisms known to limit the transmission of parasites from adults to offspring (including eggs and juveniles). This is expected as many group living species with non-eusocial systems are characterized by various forms of parental care, which possibly include anti-parasite defences [86]. These mechanisms include adults grooming the brood to remove external parasites [20,24], applying antimicrobial secretions to the brood [24,61], providing food with antimicrobial properties to the brood [62,63] or transferring immune components to their eggs (called trans-generational immune priming [68,69]). The mechanisms solely present in eusocial insects consist of workers eliminating infected brood (hygienic behaviour, [66,67]) or of infected individuals avoiding contact with the brood [64,65]. Nevertheless, these two mechanisms could be expected in subsocial (and precocial) species.

Limiting parasite spread between group members is not only important for the brood, but also for adults. In eusocial species, multiple processes are known to limit parasite spread among adults, such as building nest architecture with small chamber areas [13], abandoning infected nests [78], boosting personal immunity by social contacts [70] or consuming infected group members [77] (table 1). Individuals of the dampwood termite *Zootermopsis angusticollis* also express pathogen alarm behaviours when encountering infected conspecifics [71] (but also infected environments [76]), a behaviour that prevents pathogen spread among individuals by triggering avoidance behaviours. Infected individuals may also be isolated from the group either through exclusion, such as in the subterranean termite *Reticulitermes tibialis* [29], or through self-driven desertion (due to their moribund state), as in the ant *Temnothorax unifasciatus* [75]. Although the above processes do not necessarily require traits that are specific to eusocial systems (table 1), only allogrooming has been found in non-eusocial and/or solitary species. This behaviour is ubiquitous in eusocial insects [87], in which it reduces the presence of external parasites on the receiving individual, as well as improving the immune response of the donor through low dose infection [70]. Allogrooming has also been reported in non-eusocial insects, such as earwigs and cockroaches [72,88], but its importance in reducing parasite infection remains unclear. Note that the mediator of social fever is also not specific to eusocial systems. Social fever is a collective defence during which group members adaptively and temporarily increase their immune response of receiving individuals by low dose infections [70].

### Table 1. (Continued.)

<table>
<thead>
<tr>
<th>defence mechanisms</th>
<th>requirements</th>
<th>eusocial</th>
<th>non-eusocial (group living)</th>
<th>solitary</th>
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</thead>
<tbody>
<tr>
<td>behavioural structuring (castes/age)</td>
<td>overlapping generations</td>
<td>[6,201,202]</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>indirect interaction with garbage workers</td>
<td>stable habitat (e.g. nest)</td>
<td>[145]</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>pathogen alarm</td>
<td>division of labour</td>
<td>[71,76]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>isolation of infected individuals</td>
<td>stable habitat (e.g. nest)</td>
<td>[29]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>remove/cannibalize infected individuals/brood from the group</td>
<td>[66,67,77,158, 174,203 – 207]</td>
<td>?</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>abandon infected nests</td>
<td>stable habitat (e.g. nest)</td>
<td>[20,78,124]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>immunity transfer by social interactions</td>
<td>behavioural interactions</td>
<td>[65,70,208]</td>
<td>?</td>
<td>x</td>
</tr>
<tr>
<td>(c) Genetic adaptations</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>increased genetic diversity (multiple mating, multiple queens)</td>
<td>stable group</td>
<td>[66,79,80, 209 – 216]</td>
<td>but see [81]</td>
<td>x</td>
</tr>
<tr>
<td>increased recombination rates</td>
<td></td>
<td>(82,217,218)</td>
<td>?</td>
<td>x</td>
</tr>
</tbody>
</table>

*a* In burying beetles, this mechanism could help mothers and offspring to limit competition with microbes over the carcasses.

*b* Frass ejection.

*c* Application of cuticular hydrocarbons on the brood.

*d* Could also be considered as a form of parental care [219].

*e* Role against parasite infection still unclear.

*f* Behavioural fever.
own temperature (behavioural fever) to increase nest temperature (then called social fever) to a level that is detrimental for parasites. This collective defence has only been reported in honeybees [73], but behavioural fever is a common anti-parasite defence in non-eusocial and solitary species (reviewed in [74]). Whether behavioural fever can be elevated to social fever in non-eusocial insects remains unknown.

Finally, the increase in genetic diversity within a group is also known to help prophylactically in reducing the risk of parasite spread between group members, including both adults and juveniles [89,90]. In eusocial insects, this resistance can be achieved by increasing the number of queens and/or of the queen’s mating partners, as revealed by the higher survival rates of ant and honeybee workers living in infected colonies headed by multiple compared to single queens [79] or by multiply compared to singly mated queens [80], respectively. The benefits of increased genetic diversity have also been proposed to result from genomic recombination, which occurs at high rates in several eusocial species [82] (but see [91]). Somewhat surprisingly, the importance of group genetic diversity for parasite resistance remains poorly studied in non-eusocial insects. To the best of my knowledge, only a single study (indirectly) tested this effect in a gregarious insect, caterpillars of the moth Malacosoma californicum pluviale, but reported inconclusive results [81].

(d) Ubiquity of collective immunity across group living insects?

Although several mechanisms of social immunity are common to eusocial and non-eusocial species, others are unexpectedly absent in non-eusocial insects living in nests (e.g. during family life). This is the case, for instance, for corpse removal from the nest, abandoning of infected nests, increase in group genetic diversity to prophylactically resist against parasite infection, isolation of infected individuals or group desertion by infected individuals (table 1). One potential explanation for this lack of evidence is the very limited number of studies investigating social immunity in non-eusocial insects, even if a growing number of studies recently have started to fill this gap (e.g. [24,52,53]). Another possible explanation is that the emergence of these mechanisms depends on traits that are specific to eusocial insects, but not directly associated with their social system. For instance, colonies of eusocial insects are mostly composed of non-reproductive individuals, for which social immunity is the only way to protect the queen’s brood and thus to favour their own (indirect) fitness under parasite attack [19]. Similarly, eusocial colonies may contain a large number of individuals, which could increase the efficiency and thus the use of collective anti-parasite defences compared with smaller groups [19]. Further research should thus be conducted to (i) enlarge the number of studies testing the expression of social immunity in non-eusocial species and to (ii) determine the importance of eusocial-derived traits on the emergence and expression of these collective defences.

Even if many studies reveal the occurrence of social immunity in eusocial species, it is important to note that others have failed at providing relevant support. For instance, queens of the wood ant F. paralugubris are specifically attracted to (instead of repelled from) habitats contaminated by entomopathogenic fungi [92]. Similarly in the pharaoh ant Monomorium pharaonis, colonies preferentially move into infected nests when presented with the choice between an infected and an uninfected one [93]. Finally, workers of the termite Z. angusticollis do not discriminate between infected and non-infected conspecifics [94], and parasite infection does not increase the expression of all-against-the-infant Formica selges [95]. Overall, these results provide important insights into the link between group living and social immunity because they (i) reveal that not all the mechanisms of social immunity are necessarily expressed during group living and (ii) shed light on the potential role of other factors, e.g. parasitic strategies and life-history costs, in the expression of collective defences. Furthermore, these results suggest that social immunity is not always the most efficient defence against parasite infection, which raises questions about the importance of personal immunity in group living individuals.

4. Personal immunity and group living

The early evolution of group living and its associated risks of parasite infection may not only have favoured the emergence of social immunity, but may also have selected for higher effort in personal immune responses. This higher effort would help group living individuals both to prophylactically limit a greater per capita risk of infection (density-dependent prophylaxis hypothesis, called DDP [96]) and to benefit from herd immunity, which is generated by the accumulation of resistant individuals within a group [97]. A series of three studies recently provided empirical support for DDP’s prediction of a positive association between group living and efforts in personal immunity [98–100]. In these studies, authors compared the level of personal immunity across six species of bees, nine species of wasps and six species of thrips exhibiting a gradient of sociality ranging from solitary to eusocial. Each of these three studies showed that the antimicrobial secretions present on individuals’ cuticles were significantly more efficient in eusocial compared with solitary species. Empirical support for this prediction also comes from within-species comparisons. For instance, in the desert locust Schistocerca gregaria, individuals in the gregarious phase showed higher antimicrobial activities and survived infections better than individuals in the solitary phase [101] (see other examples in [96]).

By contrast, it has been proposed that the emergence of social immunity could reduce the expression of personal immunity due to investment trade-offs between these two processes [7,23,90]. Three genomic and two physiological studies conducted with eusocial and non-eusocial insects supported this prediction. The genomic analyses showed that (i) the number of gene families implicated in immunity was three times lower in honeybees than in two solitary insects [90,102], that (ii) experimentally isolated Bombus terrestris workers up-regulated the expression of immune-related genes [103] and that (iii) the number of immune-related genes expressed in infected S. gregaria individuals was higher when they lived in the solitary compared with gregarious phase [104]. Moreover, the physiological studies revealed that across 12 Lepidoptera species, the caterpillars feeding solitarily had higher levels of personal immunity than the ones feeding gregariously [8]. Finally, in the Australian plague locusts Chortoicetes terminifera, the level of personal immunity was negatively correlated with population densities, while experimental isolation of individuals marching in bands yielded an increase in their personal immune levels [105].
The discrepancy between these positive and negative associations sheds light on the two main assumptions required to expect a negative effect of group living on personal immunity. The first one is that group living is associated with the expression of social immunity, which is not necessarily the case in all group living insects (see above). The second one is that mounting a collective immune response is costly for the producers. To the best of my knowledge, only one study investigated this cost in a (sub)social insect. In particular, Cotter et al. [26] showed in the burying beetle *N. vespilloides* that increased investment in wound repair (personal immunity) caused a temporary decrease in the antibacterial activity of anal exudates (social immunity) of mothers. These exudates are used by the parents to limit microbial development on the carcass hosting their developing offspring [30]. This important finding raises questions about the general costs of social immunity across social systems and thus of its importance in the expression of personal immunity. Both questions call for further studies addressing this issue in a large number of eusocial and non-eusocial species. It is important to note, however, that the expression of such costs may depend on the intrinsic quality of the individuals, so that high-quality individuals could afford relatively high investment into both personal and social immune responses [106]. As a result, any variation in individual quality within a population could have the potential to prevent detection of the trade-off between the two types of immunity, or even to transform it into a false-positive association at the population (or species) level [107]. Future studies on the costs of mounting forms of collective immunity should therefore control for individual quality, e.g. by experimentally upregulating the social or personal immune response of a given individual and then looking for downregulation in other areas (e.g. [26]).

5. Discussion

Better understanding of whether social immunity is a driver or a by-product of the evolution of complex forms of group living first requires data on its occurrence across social systems [23]. This review reveals that out of the 30 individual and collective mechanisms known to mediate social immunity in eusocial insects and listed in table 1, 10 have counterparts in non-eusocial and four in solitary species. The distribution of these mechanisms across social systems is compatible with a scenario placing social immunity as a prerequisite for increased complexity in the nature and frequency of social interactions (i.e. in the evolution of group living). In particular, eusocial insects express the individual mechanisms used by solitary species to limit parasite uptake from the environment (first step of parasite infection), to which they add the collective ones used by non-eusocial species to limit both parasite establishment in the nest (second step of parasite infection) and parasite transmission to the brood (first part of the third step of parasite infection), as well as specific ones that limit parasite spread between adult group members (second part of the third step of parasite infection). Note, however, that this scenario does not exclude that (at least) some collective mechanisms are secondarily evolved in eusocial systems.

The second step to establish an important role for social immunity in the early evolution of social life is to show that its personal and collective mechanisms are at least partly selected for their collective benefits. To date, however, this important step lacks experimental evidence. One possible reason is that some of the mechanisms of social immunity are known to mediate other key processes in insects, so testing their immune benefits while preventing the expression of their other properties is experimentally difficult. For instance, frass removal can serve to limit parasite establishment in the nesting habitats, but also to eliminate chemical cues used by parasites to detect host presence, or simply to free space from confined areas [56]. Allogrooming not only helps individuals to remove ectoparasites, but also to share chemical compounds with other nest-mates and consequently to improve the accuracy of nest-mate recognition by homogenizing chemical signatures among group members [108]. Finally, increasing genetic diversity prophylactically limits the spread of parasites among group members, but also shapes the level of social conflicts (e.g. between queens and workers over male production [109]) and improves the efficiency of division of labour [110].

Another reason for this lack of empirical evidence is that most of the currently available data come from eusocial insects, which is not ideal to determine whether social immunity is a driver or a by-product of the evolution of group living [23]. Testing this question indeed requires researchers to disentangle the fitness of the donor individual from that of the recipient, which is experimentally difficult (if not impossible) when the vast majority of group members is sterile or never reproduces, as in eusocial insects. To circumvent this difficulty, one option is to study the benefits of collective forms of immunity in queens that found a new colony (e.g. [111]). However, the specificity of the foundation phase might not properly reflect the selection pressures shaping ancestral eusocial colony life. Another option is to study the benefits of collective forms of immunity in non-eusocial species [23], as their group members traditionally express full reproductive capabilities and thus have experimentally quantifiable individual fitness. Compared to eusocial species, the non-eusocial ones can also be used to investigate temporal trade-off between social and personal immunity, as their group members possibly experience solitary and group living phases during their life cycle. For instance, solitary phases alternate with group living phases in the migratory locust, solitary life takes turns with family life in sub-social insects such as burying beetles, and juveniles even have the capability to choose between family or solitary life in the European earwig *Forficula auricularia* [112]. Finally, increasing the number of studies on social immunity in non-eusocial species would permit phylogenetic studies that are balanced across taxonomic groups and social systems, and, thus, to properly trace the early evolution of collective defences in insects.

In conclusion, using an up-to-date appraisal of the multiple forms of collective immunity reported in group living insects, this review highlights the fact that collective immunity is not limited to eusocial species (see also [23]). The distribution of these mechanisms across the continuum from solitary to eusocial insects suggests that social immunity is a tenet of social evolution, even if some collective mechanisms could be by-products of derived forms of group living. This review also emphasizes that the vast majority of studies on social immunity have focused on eusocial taxa, which calls for future empirical and theoretical research investigating its occurrence across a broader spectrum of group living species. Such additional studies would be particularly interesting, as they would allow conducting phylogenetic studies to reconstruct the evolutionary pathways and timing of collective defences and would more generally offer a novel framework to better
understand the role of parasite pressures on the emergence, transformation and/or disruption of social life.

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