

Opinion

# Unconditional versus condition-dependent social immunity

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**Socially living animals can counteract disease through cooperative defences, leading to social immunity that collectively exceeds the sum of individual defences. In superorganismal colonies of social insects with permanent caste separation between reproductive queen(s) and nonreproducing workers, workers are obligate altruists and thus engage in unconditional social immunity, including highly specialised and self-sacrificial hygiene behaviours. Contrastingly, cooperation is facultative in cooperatively breeding families, where all members are reproductively totipotent but offspring transiently forgo reproduction to help their parents rear more siblings. Here, helpers should either express condition-dependent social immunity or disperse to pursue independent reproduction. We advocate inclusive fitness theory as a framework to predict when and how indirect fitness gains may outweigh direct fitness costs, thus favouring conditional social immunity.**

## Unconditional social immunity in insect superorganisms

Living socially increases the risk of pathogen transmission and infection due to close spatial, temporal, and genetic proximity between society members [1–4]. To counteract this increased risk of disease, social animals can modulate their behaviour, and some lineages have evolved highly specific collective and cooperative disease defences [5–10]; these include joint disinfection, mutual grooming, treatment of infections, and social distancing. Together, such adaptations provide an additional layer of higher-level disease protection, termed ‘**social immunity**’ [6] (see [Glossary](#)), which goes beyond the separate hygiene behaviours and immune defences of each individual.

The study of social immunity has focussed predominantly on the immune system-like cooperative disease defences of superorganismal social insect colonies [7,10–12]. The ants, crown-group corbiculate bees, vespine wasps, and higher termites are all classified as superorganisms [13–15] because they exhibit permanent caste-differentiated reproductive division of labour: Queens are physically specialised for reproduction and cared for by workers offspring that, unable to reproduce, specialise in colony growth, maintenance, and protection. The evolution of obligatory interdependent queen and workers closely mirrors the germline–soma separation found in multicellular organisms, leading early evolutionary biologists to elevate caste-differentiated social insect colonies to a novel level of organismality, the **superorganism** [13,15]. The evolutionary origin of multicellular organisms from cooperating clonal cells and of colonial superorganisms from monogamous insect families with maximal sibling relatedness both represent major evolutionary transitions resulting in new higher levels of organisational complexity [16–18]. Each major transition is defined by adaptations that evolved to promote the fitness of the new higher-level entity, even though these adaptations might not be directly beneficial for the individual constituent parts when viewed in isolation. This is exemplified by the evolution of a barbed sting in honeybees, which causes the death of the bee when used [18,19]. In the cases of multicellularity and superorganismality,

## Highlights

Cooperation in social animals can lead to collective disease protection beyond individual-level defences, termed ‘social immunity.’

Social immunity is unconditionally expressed in superorganismal insect colonies with reproductive division of labour between queens and workers. Being obligate altruists, nonreproductive workers fully commit to colony-level disease defence, exhibiting highly specialised and self-sacrificial behaviours.

In families of cooperative breeders, all members can reproduce, but offspring delay reproduction to help parents. Here, cooperation, and thus social immunity, is condition-dependent and likely favoured only by high relatedness and low probability of independent reproduction.

Inclusive fitness theory is a useful framework to elucidate the relative importance of direct fitness costs of social immunity against indirect fitness benefits of promoting kin health.

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selection led to the evolution of a systemic, integrated immune system providing protection to the higher-level reproductive entity, involving, when needed, altruistic self-sacrifice by soma components [17,20–22].

The ‘somaticised’ workers [17] of superorganisms are normally unable to disperse and independently found colonies, so they propagate their genes to the next generation indirectly by enhancing queen reproduction. Somaticised workers are as committed to their colony as the soma of a multicellular organism and thus are considered to be obligate altruists. Consequently, workers in superorganisms express unconditional social immunity to ensure the survival and reproduction of the colony, even when this jeopardises their own survival. We thus see the evolution of care behaviours, such as grooming, provided by healthy colony members to pathogen-exposed or wounded individuals to prevent infection [20,23–27]. Additionally, infected individuals may engage in self-sacrificial hygiene behaviours, including self-removal or altruistically signalling to induce their own elimination, when they can no longer be cured and only represent a disease risk to the colony [20,28–32]. Suicidal **altruism** evolved in superorganisms because it increases colony fitness and, by extension, the infected individual’s own indirect fitness. Moreover, unconditional social immunity selects for worker specialisation and division of labour in collective disease defences [33,34], as well as highly coordinated, whole-colony organisational responses, which are comparable to immune cell specialisation and systemic immune responses in metazoan bodies [12,17,22,35].

### Condition-dependent social immunity may arise outside of superorganisms

The unconditional social immunity in superorganisms represents a major step change in social disease defence that provides colony-level protection [22]. However, outside of superorganisms, we still need to evaluate the individual-level benefits and costs of social disease defences [9,22]. Animal groups are hugely varied, ranging from aggregations of nonrelatives that live and breed together for ‘selfish-herd’ benefits of predator protection to discrete societies characterised by obligatory family life yet with incomplete reproductive division of labour, known as ‘**cooperative breeders**’ [17,36,37]. In cooperative breeders, helper individuals retain their individual reproductive independence but forgo reproduction, at least transiently, to help relatives reproduce. **Cooperation** is therefore facultative because individual engagement in collective and cooperative disease defences will vary according to relatedness between donors and recipients, the helpers’ **reproductive potential**, and aspects of local disease pressure (e.g., pathogen prevalence, virulence, and diversity).

The expression of social immunity is thus expected to be conditional outside of superorganisms; we can therefore use **Hamilton’s rule** and his theory of **inclusive fitness** [17,18,38] to predict when condition-dependent social immunity is selected for and when it should then be expressed. Using this Hamiltonian approach, we will first examine the costs and benefits of expressing conditional social immunity in animal societies where cooperation remains facultative. Then, we will formulate expectations under which circumstances conditional social immunity might occur or be suppressed; that is, when should helpers express facultatively altruistic social immunity and when should they rather disperse to avoid infection and pursue independent reproduction. Although these conditions are restrictive, the expectations that we outline are testable throughout.

### Costs and benefits of conditional social immunity

As with other forms of cooperation [39], cooperative disease defences can evolve when they provide a benefit to both the actor – either directly or indirectly – and the recipient of hygiene behaviour. The benefits of such behaviours towards others may be easily outweighed by their time and energetic costs [40] or by the risk of cross-infection for the actor. These cross-infection costs can range from low, if a pathogen is relatively benign, to severe, if infections reduce or eliminate future

### Glossary

**Altruism:** a behaviour that is beneficial to the recipient but costly to the direct fitness of the actor. Evolves because of the indirect fitness gain to the actor by providing help to others who share genes with the actor (i.e., genetically related kin). Workers in superorganisms are obligate altruists because they normally only gain their fitness indirectly via the queen’s reproduction; by contrast, helpers in cooperative breeders are facultative altruists who still have the potential for independent reproduction and can thus attain fitness both directly and indirectly. See also Glossary entries for Hamilton’s rule, Superorganism.

**Cooperation:** social behaviour that provides a benefit to the recipient of the action and evolves, at least partly, because of this benefit. Comprises both mutually beneficial and altruistic behaviours.

**Cooperative breeders:** social system with obligate family life and reproductively totipotent offspring helpers that transiently forgo reproduction to assist their parents in rearing additional offspring (usually siblings). Helpers may be altruists for life, but many eventually disperse to reproduce independently; they can also inherit a breeding position in their natal nest.

**Hamilton’s rule:**  $rB > C$ ; developed by William D. Hamilton, this rule explains how altruistic behaviours can evolve when the indirect fitness benefits ( $B$ ) of helping others, weighted by relatedness to recipients of help ( $r$ ), outweigh the costs ( $C$ ) to the actor’s direct fitness. See also Inclusive fitness.

**Inclusive fitness:** an individual’s total lifetime fitness, comprising both the direct fitness obtained through offspring production and the indirect fitness acquired by aiding kin in producing additional offspring. See also Hamilton’s Rule.

**Reproductive potential:** the likelihood of an individual to survive and reproduce in the future. Important determinants are an individual’s physiological level of totipotency and the likelihood of successfully achieving reproduction either within the natal nest or independently, after dispersal and founding a new nest.

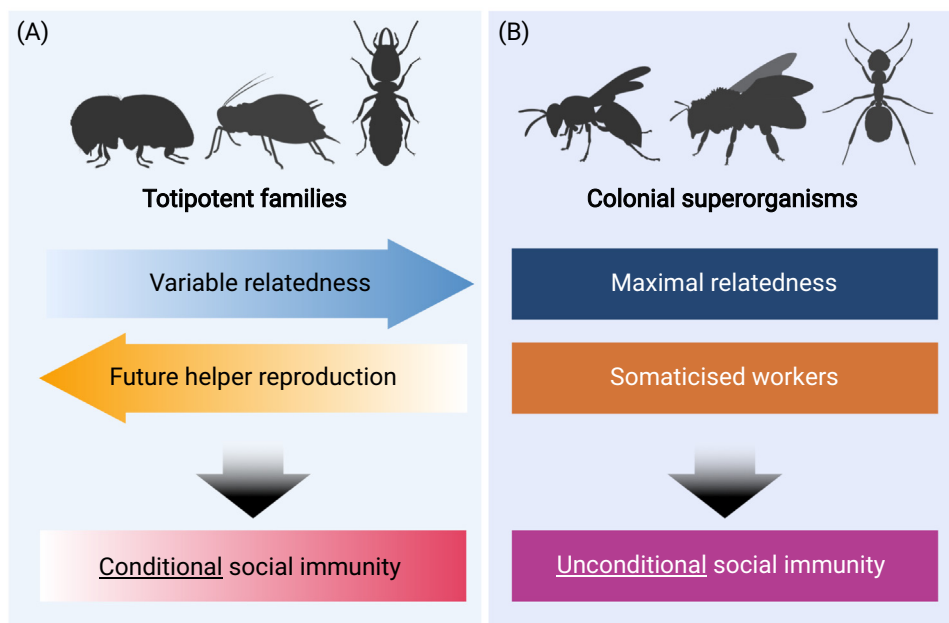
**Social immunity:** an additional level of disease protection arising from collective and cooperative behaviours in social animals; the resulting total protection is thus greater than the sum of each individual’s defences. Somaticised

independent reproduction [41]. Cross-infection risks are thus expected to raise the cost of hygienic altruism significantly compared with the mere altruistic provisioning of siblings. Consequently, unlike other forms of altruistic or mutualistic cooperation [39], we therefore expect that social disease defences will not be selected for in many social settings, because even mild infections can have substantial negative fitness effects [41]. These costs should particularly constrain hygienic cooperation in aggregations of nonrelatives, where cooperation can emerge only through direct mutual benefits [39]; accordingly, at best, we expect simple forms of prophylactic hygiene or nonrisky caregiving in these aggregations. Instead, we predominantly expect and observe self-centred behaviours by which animals avoid sick conspecifics to minimise individual-level infection risk [42,43] and where sick individuals attempt to conceal disease symptoms to remain part of the group [4,42–45].

The benefits of performing conditional social immunity increase, however, when there is substantial relatedness between actors and recipients (Figure 1, Key figure [11]). Relatedness is typically

### Key figure

#### Conditional and unconditional social immunity



Trends in Parasitology

**Figure 1.** (A) In families with totipotent helpers, such as cooperatively breeding ambrosia beetles, aphids, and lower termites, relatedness levels tend to be significant but often do not stay at their highest possible levels. Most if not all helpers retain the ability to reproduce at some later point in life, either by dispersing or by inheriting a breeding position within their parental nest. Social immunity in these social clades is thus expected to be expressed in a condition-dependent manner, provided Hamilton's rule for the expression of social immunity is satisfied: when the benefits of helping kin outweigh the direct fitness costs. (B) By contrast, in colonial insect superorganisms, somaticised workers ancestrally evolved to be obligate altruists and thus gain all their fitness indirectly. For major evolutionary transitions to superorganismality to occur, workers had to be as related to their siblings as they were to their own offspring, giving predictably maximal sibling relatedness (of 0.5, the mean of 0.75 and 0.25 in haplodiploid Hymenoptera). Workers in superorganisms thus evolved to express unconditional social immunity, protecting their colony at great sacrifice, including hygienic suicide of infected individuals. Figure created with BioRender.

workers in superorganisms show unconditional social immunity, including self-sacrificial hygienic suicide. By contrast, totipotent helpers in nests of cooperative breeders are expected to express condition-dependent social immunity if it benefits the indirect component of individual inclusive fitness, and to a degree that trades off with their future independent reproduction, making it likely that they will eventually disperse.

**Superorganism:** a colonial state of organisational complexity distinctly higher than a single metazoan body or a society of such bodies; superorganismality evolved as an irreversible major transition in evolution in the ants, corbiculate bees, vespine wasps, and higher termites with strict lifetime parental monogamy as a necessary condition and physically differentiated queen and worker castes as convergently evolved consequences. Owing to strict monogamy, selection during these major transitions shifted to the colony level, so that traits for the exclusive benefit of the colony (e.g., suicidal social immunity) could evolve.

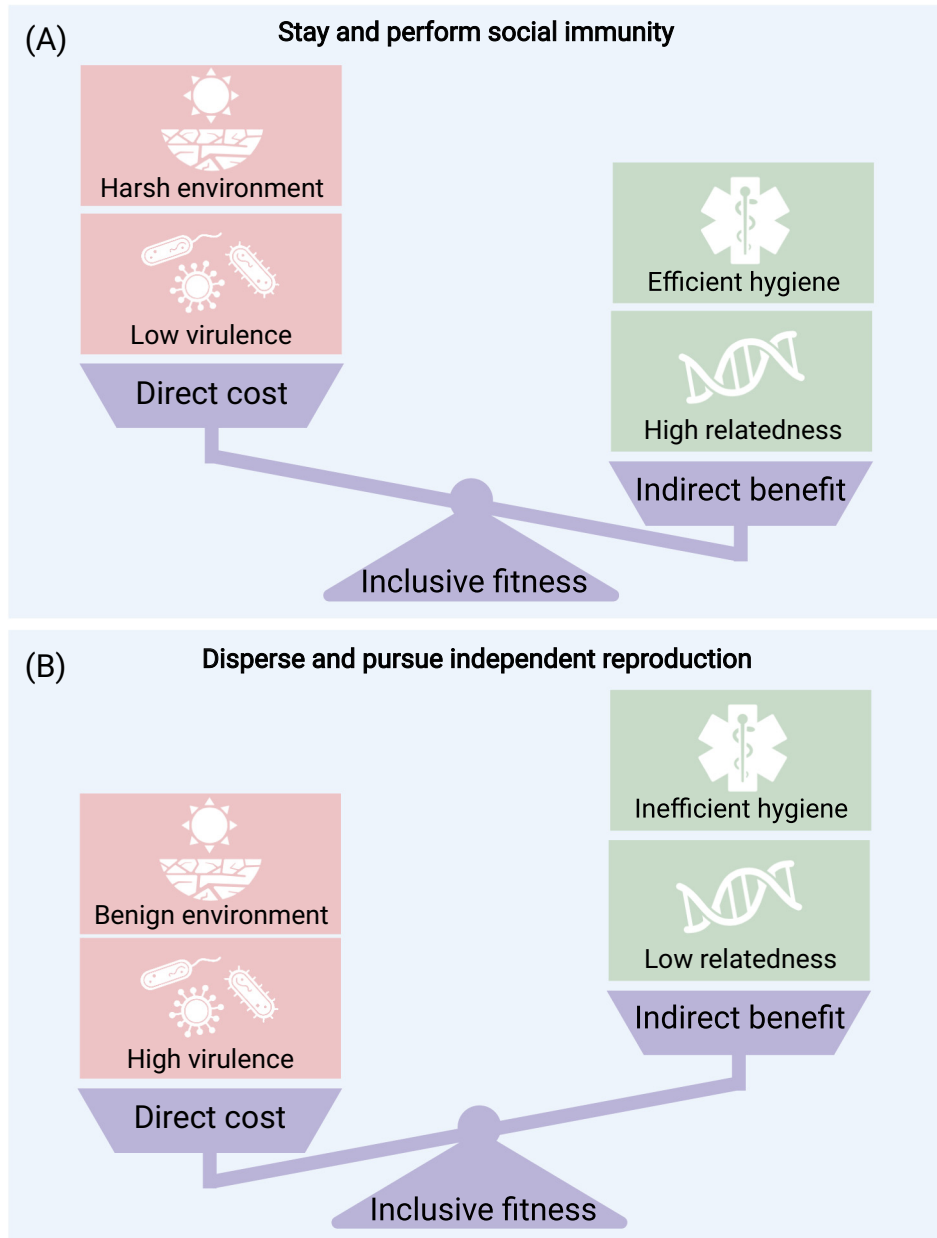
high between family members when levels of parental promiscuity are low, such as in the monogamous log-dwelling lower termites [17] or in clonal social aphids or inbred social thrips and ambrosia beetles [46–49]. Here, helping kin might enhance an actor's indirect fitness by improving the likelihood that relatives survive and reproduce [18,38,39]. Consequently, the probability of risky hygienic care evolving in family groups may increase because of kin-selected benefits, despite potential direct fitness costs for the actor. Risky care may thus be favoured outside of superorganisms when it enhances an individual's overall inclusive fitness [11,12,22], but the conditions remain more restrictive than for noninfectious altruistic behaviours.

Hamilton's rule [18,38] formalises the factors important for the evolution of conditional altruism and thus also for the evolution of conditional social immunity: the relatedness to the recipient of the action, typically siblings or other nonoffspring ( $r$ ), the indirect fitness gain from helping ( $B$ ), and the direct fitness cost incurred by not instead raising one's own offspring ( $C$ ). Hamilton's rule is satisfied and helping behaviour is expected to evolve when  $rB - C > 0$ . A more nuanced version of Hamilton's rule [17,50] measures helping in terms of own offspring loss and indirect offspring gains, which together produce an individual's inclusive fitness. Here,  $r_x$  represents the relatedness to the recipient's kin, whereas  $r_o$  represents the relatedness to own offspring. The rule is expressed as  $r_x B - r_o C > 0$ , meaning helping evolves when the genetic gain from helping nonoffspring kin, adjusted for relatedness, exceeds the genetic loss of not investing in own offspring. Hamilton's rule clearly shows that only noncostly, mutually beneficial caregiving can evolve in aggregations of nonrelatives, because the relatedness to the recipient is zero. However, when caregiving is directed to kin, it can be beneficial to perform for an individual even in the presence of direct costs, when the indirect fitness gained results in higher overall inclusive fitness, depending on the specific conditions affecting the Hamiltonian  $B/C$  ratio.

### Conditions for the expression of social immunity under facultative cooperation

Cooperative breeders are good models for the study of condition-dependent social immunity [9,22]; they comprise a diverse range of societies where family life is obligate and a single mother or mated pair usually monopolises reproduction, assisted by helper offspring that retain their reproductive totipotency but do not currently breed themselves [36,37]. These helpers may eventually disperse to attempt independent nest foundation or stay to potentially inherit the breeding position within their extended family [36,37,51,52]. Examples of cooperatively breeding insects include some ambrosia beetles, thrips, aphids, certain wasps, and lower termites [36,37,53–55]. Helpers in cooperatively breeding groups must individually weigh the indirect benefits of assisting their kin against the costs this imposes on their direct fitness [40,51,53,56]. Conditional helping should thus end when future reproductive potential is jeopardised and/or when indirect fitness benefits drop below some threshold [46,56].

When helper cooperation is condition-dependent, Hamilton's rule allows one to predict that social immunity should be expressed when indirect fitness benefits of improving the health of kin, weighted by relatedness, outweigh the costs to the helper's direct fitness. Because performing social immunity may compromise the helpers' future reproductive potential – if it results in infection or is expensive to perform – we generally expect less risky/expensive hygienic altruism in cooperative breeders than in superorganisms with somaticised workers that have no or negligible direct fitness to lose and hence engage in high-risk caregiving. For the same reason, self-sacrifice by infected individuals via hygienic suicide should not evolve in cooperatively breeding helpers, whereas it has evolved in superorganisms [28,29,31,32]. When the costs of social immunity increase, we expect helper offspring to disperse for independent reproduction sooner, an option that is not available for superorganismal workers. However, when helpers can lay their own eggs in the maternal nest while also providing sibling care, as in some ambrosia



**Trends in Parasitology**

Figure 2. Factors determining whether conditional social immunity should be expressed in totipotent families. Helpers must balance the indirect fitness costs of protecting their kin now versus the direct fitness costs on future reproduction incurred by possible infection. (A) When family relatedness is high, hygiene measures to improve kin health are effective, the probability of independent nest founding and reproduction is low (harsh environment), and the virulence of a focal pathogen in the nest is also low, the expression of conditional social immunity will likely be selected for. (B) By contrast, when social hygienic measures are not very effective, relatedness is relatively low, the likelihood of independent nest-founding and reproduction is improved (benign environment), and pathogen virulence is high, a disease outbreak in the maternal nest will favour dispersal. Figure created with BioRender.

beetles [48], improving the overall health of the group will also benefit their direct fitness, so dispersal may be delayed. Similarly, direct fitness benefits could drive investment into social immunity if it results in a larger, more productive group that the helper later inherits and then assumes the breeder position [51,57,58]. In both these cases, what may seem to be altruism can thus, in part, be selfish behaviour to promote the helper's direct fitness.

Whether helpers stay and perform health care or disperse from the nest when it is under parasitic pressure will depend on many factors, such as (i) relatedness to recipients, (ii) a focal parasite's virulence, (iii) the effectiveness of social immunity to improve kin health, and (iv) the likelihood of future helper reproduction, either within the nest and/or after dispersal and nest founding, where success will be affected by ecological and climatic conditions. High relatedness, low parasite pressure/virulence, and a low likelihood of successfully founding a new nest should all promote staying to help over early dispersal (Figure 2) [55], but there will likely be considerable variation within and between species and across host–parasite systems. Notably, even a slight chance for future independent reproduction should counteract the evolution of self-sacrificial social immunity behaviours and irreversible social immunity specialisation [13,22], whereas such cost constraints do not apply to somaticised workers of superorganisms. Interestingly, some cooperative breeders, namely most species of Hormaphidinae aphids, several species of *Kladothrips*, and essentially all species of lower termites have evolved a nondispersing, physically differentiated soldier caste that appears to have reduced or zero direct reproductive potency [47,54]. In thrips and some termites, these soldiers have been shown to play important roles in hygienic nest defence, producing antimicrobial secretions [59,60]. Detailed studies asking whether the loss of totipotency in such soldiers has enabled the evolution of specialised caste-specific social immunity behaviours could therefore be worthwhile. More generally, a large body of work on lower termites has revealed especially well-developed collective immunity, including grooming, hygienic cannibalism, social immunisation, and the use of antimicrobial secretions and faeces [10,61–66]. In these termites, Hamilton's rule is satisfied as long as parents remain monogamous, and the chance of helpers successfully founding colonies is tiny [54]. Consequently, the necessary conditions for facultative social immunity to evolve and be expressed appear to have been met [22]. However, future work should assess how their reproductive flexibility constrains expensive social immunity and if engagement in social immunity versus rates of dispersal change when relatedness in colonies collapses (e.g., during colony fusion events [67]).

### Concluding remarks

Social immunity describes the additional level of disease protection that arises through cooperative defence actions. We here distinguished between unconditional social immunity present in superorganismal insect colonies and facultative social immunity that is expected to evolve outside of superorganisms under specific conditions. In superorganisms, the loss of reproductive totipotency in helpers has resulted in obligately altruistic, somaticised workers, which engage in disease defence at great self-sacrifice, including hygienic suicide [11, 13,20,22,32,35]. Consequently, social immunity in superorganisms can be conceptualised as an elaboration of the major transitions to superorganismality, leading to a highly specialised, organisationally complex, and integrated defence system, analogous to metazoan immune systems [12,17,22,68]. Outside of superorganisms, the expression of condition-dependent social immunity can be expected to vary with relatedness and an individual's likelihood of future independent reproduction, which is conditional on each species' unique natural history and ecological conditions, as well as on parasite virulence [40].

We here identified Hamilton's rule and inclusive fitness theory as a powerful framework to generate testable predictions about when, and to what extent, an individual helper should engage

### Outstanding questions

Prophylactic defences should be less costly than treating active infections, because only the latter carry the risk of cross-infection. Do cooperative breeders show greater expression of prophylactic rather than reactive defences relative to superorganisms?

Helpers in cooperative breeders must balance the benefits of providing health care to kin against the risk to their own future independent reproduction. Can the 'tipping point' between indirect fitness gain and direct fitness loss be determined by experimental manipulation of (i) the costs of social immunity, including the risk of severe infection, by altering parasite virulence; (ii) the magnitude of indirect fitness gains by varying group relatedness; or (iii) the independent founding success of dispersing offspring by varying nest site availability or abiotic factors?

In several cooperative breeders, such as in social thrips and lower termites and some social aphids, a soldier caste has evolved while other offspring remained totipotent. Soldiers are specialised for physical defence and often forgo independent reproduction. How similar is the investment into social immunity between soldiers in these facultatively cooperative breeders compared with somaticised workers in obligately altruistic superorganisms?

In some cooperative breeders, such as several wasps and lower termites, offspring can gain direct fitness benefits through nest inheritance as an alternative to dispersal and founding of a new nest. These 'hopeful reproductives' would benefit from inheriting a healthy nest. Do cooperative breeders with possible nest inheritance show higher investments in social immunity than those where helpers can reproduce independently only upon leaving the nest? Do individuals most likely to inherit a nest help more (to inherit a 'better' nest) than their nestmates, or do they help less to protect their chances of independent breeding after nest inheritance?

in social disease defences outside of superorganisms, where indirect fitness gains by caring for relatives need to outweigh the direct fitness loss such behaviour may have for the actor. Condition-dependent social immunity requires Hamilton's rule to be satisfied; yet, the risk of a helper becoming infected will often be a major constraint and hence restrict the conditions under which it can evolve. Notably, applying Hamilton's rule to superorganismal social immunity is obsolete because somaticised workers are obligate altruists [13], which means that they are fully committed to the colony and hence show unrestricted 'motivation' for self-sacrifice. We recommend cooperatively breeding insects with obligate family life and reproductively totipotent helpers to be studied explicitly with manipulative experiments to validate whether their varying degrees of social immunity match Hamiltonian expectations. We generally expect that helpers (i) should accept greater levels of risk during altruistic health care when relatedness to recipients is higher, yet (ii) do so only when these behaviours do not compromise their likelihood of independent future reproduction [40,53]. This implies that even low prevalences of reproductive totipotency should preclude that self-sacrificial hygienic suicide can evolve in these social systems. Finally, even though joint sanitary prophylaxis and mutually beneficial hygiene can evolve in the absence of indirect fitness gains between nonrelatives, any more elaborate forms of social immunity will likely be prevented by the costs of infection, implying that commitment between interactants is key to the evolution of social immunity. We hope that new studies on cooperatively breeding insects, such as social ambrosia beetles, aphids and thrips, *Polistes* wasps, and lower termites, using Hamilton's inclusive fitness framework will advance our understanding of the conditions that both select for and constrain the evolution of social immunity (see [Outstanding questions](#)).

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### Declaration of interests

The authors declare no competing interests.

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