ELSEVIER
Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Insect Science

Social immunity: why we should study its nature, evolution and functions across all social systems

Sophie Van Meyel[1,3], Maximilian Körner[2,3] and Joël Meunier[1]

Mounting defences against pathogens is a necessity for all animals. Although these defences have long been known to rely on individual processes such as the immune system, recent studies have emphasized the importance of social defences for group-living hosts. These defences, called social immunity, have been mostly studied in eusocial insects such as bees, termites and ants, and include, for instance, mutual cleaning and waste management. Over the last few years, however, a growing number of works called for a broader exploration of social immunity in non-eusocial species. In this review, we summarize the rationales of this call and examine why it may provide major insights into our current understanding of the role of pathogens in social evolution. We start by presenting the original conceptual framework of social immunity developed in eusocial insects and shed light on its importance in highly derived social systems. We then clarify three major misconceptions possibly fostered by this original framework and demonstrate why they made necessary the shift towards a broader definition of social immunity. Because a broader definition still needs boundaries, we finally present three criteria to discriminate what is a form of social immunity, from what is not. Overall, we argue that studying social immunity across social systems does not only provide novel insights into how pathogens affect the evolution of eusociality, but also of the emergence and maintenance of social life from a solitary state. Moreover, this broader approach offers new scopes to disentangle the common and specific anti-pathogen defences developed by eusocial and non-eusocial hosts, and to better understand the dependent and independent evolutionary drivers of social and individual immunity.

Addresses
[1] Institut de Recherche sur la Biologie de l'Insecte, UMR 7261, CNRS, University of Tours, Tours, France
[2] Institute of Organismic and Molecular Evolutionary Biology, Johannes-Gutenberg University of Mainz, Mainz, Germany

Corresponding author: Meunier, Joël (joel.meunier@univ-tours.fr)
[3] Authors contributed equally to the work.

Current Opinion in Insect Science 2018, **28**:xx–yy

This review comes from a themed issue on **Social insects**

Edited by **Joël Meunier** and **Sandra Steiger**

https://doi.org/10.1016/j.cois.2018.03.004

Introduction

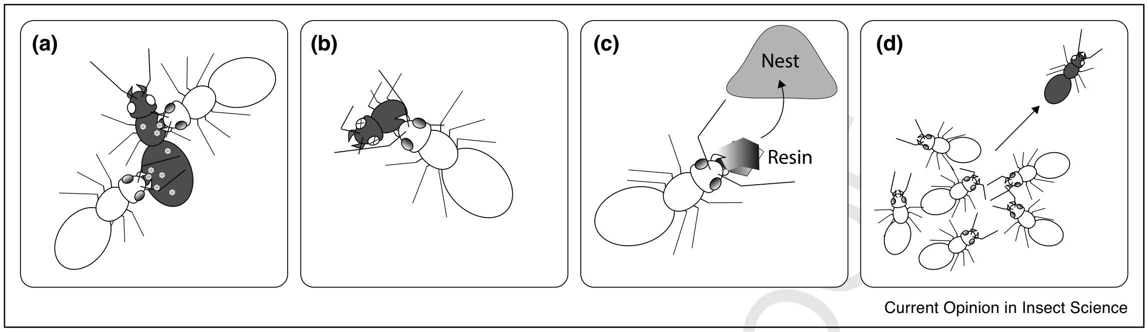
During its life cycle, every animal encounters large numbers of pathogens such as viruses, protozoans, bacteria, helminths and fungi [1]. Pathogen infections often have dramatic consequences in a host, ranging from premature death to the modification of a broad set of fitness-related physiological, morphological and behavioural traits [2]. To limit the costs of pathogen infection, hosts have thus developed a multitude of defences encompassed in the term individual immunity [2–4]. In insects, these defences typically rely on physiological changes limiting pathogen development into the host body (i.e. immune system) [2,5] and on behavioural processes reducing the risk of pathogen exposure and infection, for instance, by prophylactively or therapeutically consuming food sources with anti-pathogenic properties, a process called self-medication [4].

Over the last decades, a growing number of studies has revealed that protection against pathogens may not only rely on the defences exhibited by the host itself, but also on defences generated by its surrounding relatives [6–8]. Textbook examples of this *social immunity* typically come from eusocial insects such as bees, ants and termites (Figure 1) [6,8–10]. One of these examples is allo-grooming, a behaviour frequently reported in eusocial insects, during which workers groom each other to remove the pathogens present on the cuticle [11]. Another example encompasses sanitary behaviours, during which workers remove food waste and/or cadavers from their colony to prevent the development of microbial pathogens, as found in many bees, ants and termites [12–15]. Social immunity can also be illustrated by social isolation, during which infected individuals leave their colony [16,17] or reduce contacts to the brood [18,19] to limit the transfer of pathogens to colony members. Finally, ant and termite workers frequently use self-produced secretions to sanitize the nest walls and/or the brood [20–22], which is also a common form of social immunity (for an exhaustive list of all the classical forms of social immunity, please refer to [6,8]).

The discovery of social immunity rapidly led to major advances in our understanding of why and how eusocial insects are efficiently protected against pathogens [6,9,23]. It also gave rise to two evolutionary scenarios on the role of social immunity in the evolution of group living. The first scenario posited that social immunity is a phenomenon that has secondarily derived from eusocial systems and thus only plays a role in the consolidation of complex, permanent and obligatory forms of group living

Please cite this article in press as: Van Meyel S, et al.: Social immunity: why we should study its nature, evolution and functions across all social systems, Curr Opin Insect Sci (2018), https://doi.org/10.1016/j.cois.2018.03.004

Figure 1



Four classical examples of social immunity that can be found in ant colonies. **(a)** Two workers groom an infected nestmate (grey) to remove external pathogens. **(b)** A worker carries a corpse (grey) away from the nest. **(c)** A worker collects a piece of resin with antimicrobial properties and brings it back to its nest. **(d)** An infected worker (grey) isolates itself from the group to limit the risk of pathogen spread. References can be found in [6,8].

exhibiting reproductive division of labour (thereafter called the *eusocial framework*) [6,24,25••]. The other (more recent) scenario postulates that social immunity is an ancestral phenomenon that can be found in many forms of group living and thus, that social immunity also plays a key role in the early emergence and maintenance of group living from a solitary state (thereafter called the *group-living framework*) [7,8].

In this study, we review recent empirical data across eusocial and non-eusocial (i.e. group living species that do not exhibit a eusocial organisation) insects to emphasize why it is now time to study the nature, evolution and functions of social immunity across all social systems. Specifically, we first present the origin and implications of the eusocial framework in our current understanding of anti-pathogen defences in eusocial insects. We then discuss the rationales of the recent call for a switch from a eusocial to a group living framework by shedding light on three major misconceptions that can be fostered by the eusocial framework. In a final part, we stress that understanding social immunity requires boundaries in its definition and thus propose a newly defined group-living framework detailing three criteria that could allow discriminating what is a form of social immunity, from what is not. Overall, we argue that expanding the number of studies on social immunity in a broad taxonomical spectrum of non-eusocial species would provide novel major insights into our general understanding of the common and specific solutions developed by each type of social host to counteract infections and thus, into the role of pathogens in social evolution.

The eusocial framework of social immunity

The eusocial framework of social immunity emerged at the beginning of the 21st century as the result of works conducted by researchers investigating how eusocial insects limit the inherently high risks of pathogen exposure and transmission between colony members [6,9,10,26]. The central idea of this framework is that social immunity mimics the individual immunity of multicellular organisms when the unit of selection has shifted from the individual to the colony [23,27]. In other words, social immunity has ‘evolved in convergence with individual immunity to protect the entire reproductive entity (i.e. the superorganism [28•]) and maximize its fitness’ [25••]. Three examples typically illustrate this parallel between personal and social immunity in eusocial insects. First, wood ants, honeybees and stingless bees collect and incorporate plant resin with antimicrobial properties into their nests to limit the development of microbial pathogens [29–31], a process mimicking individuals’ self-medication process to fight an infection [32]. Second, honeybee workers can fan their wings simultaneously to increase the temperature of their hive and thereby eliminate heat-sensitive pathogens [33], a process mimicking the fever exhibited by a body to fight an infection. Finally, workers of the ant *Lasius neglectus* administer antimicrobial poison inside infected cocoons to prevent pathogen replication and establishment within the colony, just like the individual immune system targets and eliminates infected cells from host body [34••].

The accumulation of results supporting the parallel between individual and social immunity in eusocial insects rapidly led to the adoption of the eusocial framework by researchers interested in collective defences against pathogens. This adoption then fostered the claim that social immunity is ‘necessary and essential to eusocial systems’ [25••] and thus, that social immunity should be considered as a major and unique social parameter once eusociality has emerged [6,9,24,25••].

The limit of the eusocial framework

One pillar of the original eusocial framework is thus that all collective defences against pathogens employed by

Please cite this article in press as: Van Meyel S, et al.: Social immunity: why we should study its nature, evolution and functions across all social systems, Curr Opin Insect Sci (2018), https://doi.org/10.1016/j.cois.2018.03.004