

Forum

Personal immunity versus social immunity

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Many organisms defend their fitness against attack from parasites and pathogens by mounting an immune response. Most physiological immune responses are internal and targeted at organisms that have invaded the body. For example, invertebrates show innate responses to parasites by producing antimicrobial peptides and lysozymes that either inhibit the growth of microorganisms or kill them. Similarly, their blood cells phagocytose single-celled parasites, whereas larger invaders are encapsulated in a layer of blood cells that are melanized, sealing off the invader from the host's body (Rolff and Reynolds 2009). Vertebrates additionally have an adaptive immune response comprising lymphocytes that respond to antigens on the surface of the parasite, and these provide a targeted response with immunological memory (Janeway et al. 2001). In addition to this typical internal response, some defenses are deployed externally to overcome microorganisms in the environment. For example, the uropygial secretion with which birds preen their feathers has been shown to have antimicrobial activity and is used to protect the feathers from feather-degrading bacteria (Shawkey et al. 2003; Martin-Vivaldi et al. 2010).

These are examples of personal immunity in which the challenged individual is the main beneficiary of the immune response. However, there is increasing evidence that immune systems can also provide fitness benefits to others, besides the individual mounting the response. In the evolutionary literature, when behaviors have fitness consequences for both the actor and a recipient, they are described as "social" (e.g., West et al. 2006). Applying the same logic to immune function, we suggest that any type of immune response that has been selected to increase the fitness of the challenged individual and one or more recipients should be classified as social immunity. According to our definition, therefore, social immunity includes the immune services provided for others in animal families, subsocial insects, and social microbes as well as the social insects, some group-living primates, and other kin-structured populations.

SOCIAL IMMUNITY IS SEEN IN DIVERSE CONTEXTS

Our definition of social immunity is significantly broader than the current use of the term (e.g., Cremer et al. 2007; Cremer and Sixt 2009; Wilson-Rich et al. 2009). In a landmark paper, "social immunity" was first coined to describe the group level immune function exhibited by social insects and group-living primates (Cremer et al. 2007). Specifically, it describes immune defenses that are mounted by a collective for the benefit of themselves and others (e.g., Cremer et al. 2007; Cremer and Sixt 2009; Wilson-Rich et al. 2009). It includes, for example, the antifungal fecal pellets that termites use to coat the inside of their chambers (Rosengaus et al. 1998), antimicrobial sternal gland secretions in termites (Rosengaus et al.

2004), and metapleural gland secretions in leaf-cutting ants, which are deployed against fungi and bacteria that compete with their symbiotic fungus (Nascimento et al. 1996) as well as against pathogenic microorganisms (see Cremer et al. 2007 and references therein). It also encompasses the behavioral social fevers triggered when individuals huddle to raise temperatures beyond those optimal for pathogens (Wilson-Rich et al. 2009). The key idea is that by acting collectively, individuals are better able to mount a defense than is possible were they to act independently. According to this definition, it is the collective nature of the immune response that puts the social into social immunity rather than the fact that it is being mounted for the benefit of others as well. We suggest using the term "collective immunity" to describe these immune services, so as to free up the use of social immunity for the more broadly defined acts of social immune function that we outline below. As we illustrate in Figure 1, acts of collective immunity are nested within our broader definition of social immunity.

Our broader definition of social immunity encompasses immune services performed for others in at least 3 new contexts. The first of these is the animal family, which is effectively a transient animal society in miniature. Parental investment in offspring (Trivers 1972), a social behavior at the heart of animal family life, is a kin-selected form of cooperation (Dawkins 1989; Komdeur 2006) that is analogous to worker care of larvae seen in the eusocial insects: it involves individuals sacrificing future fitness for the benefit of others, to whom they are not genetically identical, for their mutual benefit. Parental care can therefore be treated just like any other kin-selected social behavior (Kilner and Hinde 2008). Just like the social insects and group-living primates, parents mount immune defenses for their own benefit and the benefit of others. Many of these immune services are externally produced. For example, 2 species of blenny produce antimicrobial mucus in their anal glands, which they rub over the nest surface and directly on to eggs during egg guarding (Giacomello et al. 2006). The sperm duct gland secretions of the grass goby show similar antimicrobial activity (Giacomello et al. 2008) as does the epidermal mucus of the fringed darter, which is applied to protect eggs from microbial contamination (Knouft et al. 2003). The three-spined stickleback uses antimicrobial mucus to glue together his nest, protecting the eggs inside from microbes (Little et al. 2008), and the foam with which tungara frogs cover their eggs contains a cocktail of chemicals that protect the eggs from microbes (Fleming et al. 2009).

Insects with parental care exhibit similar external immune defenses. Bark beetles tunnel chambers into living wood in which to lay their eggs, and they coat the inside of these chambers with oral secretions that contain a fungus-inhibiting bacterium (Cardoza et al. 2006; Adams et al. 2008). Without the protection of this secretion, eggs would be killed by invasive fungi (Cardoza et al. 2006). Similarly, houseflies that lay their eggs in manure cover the surface of their eggs with bacteria that inhibit the growth of fungi, which can affect larval development (Lam et al. 2009). Burying beetles exhibit elaborate pre and posthatching parental care, one aspect of which involves preparing a vertebrate carcass for their offspring by covering it with anal exudates that have potent antibacterial activity (Cotter and Kilner 2010). This defends the resource

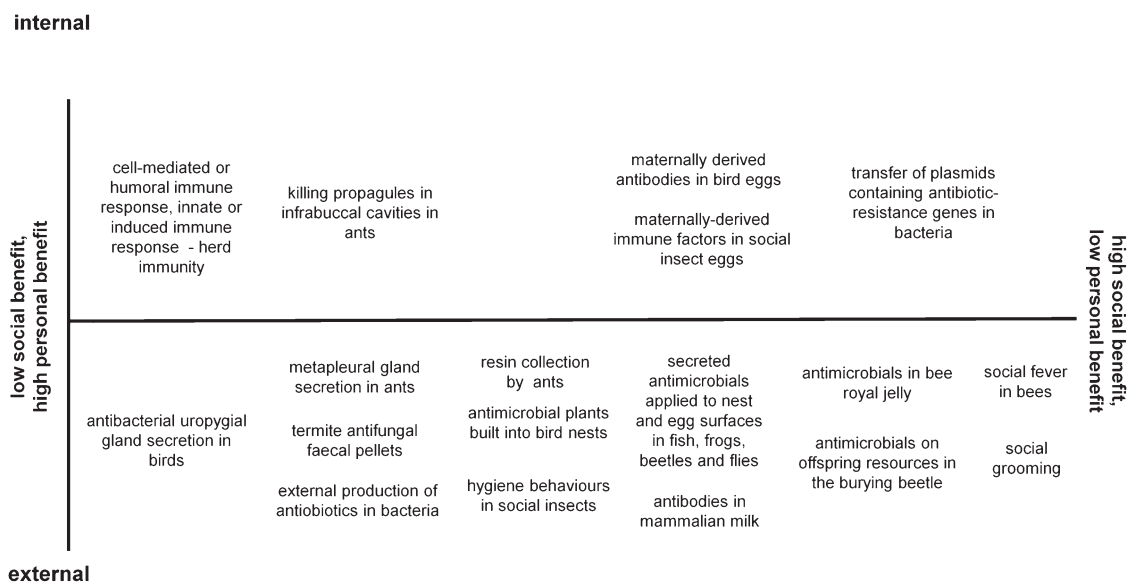


Figure 1

Examples of immune function are classified in 2 dimensions: according to whether they are internal or external, and according to the extent of cooperation, where cooperation is judged by the magnitude of the benefits they bring to others, relative to personal gain.

from microbial attack and thus improves the survival of the offspring (Rozen et al. 2008).

Parents can also endow immune defenses for their offspring internally. For example, invertebrates, fish, reptiles, mammals, and birds provide their young with maternally derived antibodies (vertebrates) or other immune factors (invertebrates) either directly in the egg or in the milk (see Grindstaff et al. 2003 and references therein). Another option is to collect material from the environment to aid in immune defense. For example, some bird species line their nests with aromatic plants as a prophylactic immune defense (e.g., Lafuma et al. 2001; Gwinner and Berger 2005).

Each of these examples qualifies as an instance of social immunity, according to our definition, although the nature of the resulting benefit varies from case to case. In the simplest scenario, such as the fish examples, a single parent provides an immune service for its offspring and the other parent benefits as well, simply through the offspring's improved fitness. Where there is biparental care, such as in the burying beetle, and both parents contribute to social immunity (Cotter and Kilner 2010), then each potentially gains additional benefits, in some cases this may be because there is increased genetic diversity in the immune service, which may well make it more effective (e.g., Sherman et al. 1988) and partly because the cost of investing in social immunity is shared. These benefits increase in magnitude if several adults breed together on a resource, as in the bark beetles and burying beetles, and if all the breeding adults contribute to social immunity.

Immune defenses mounted on behalf of other individuals can also be found among the social microbes. It might seem peculiar to suggest that microbes have immune systems, but perhaps this appears less odd if we consider that immune systems function to provide resistance to external agents that damage the body and that they have coevolved with those agents for precisely this purpose. Mechanisms of antibiotic resistance might justifiably then be regarded as microbial immune systems because there is good evidence that antibiotic resistance has coevolved with the organisms that produce the antibiotics themselves (Davies 1994). Furthermore, the organisms that thrive as a consequence of producing antibiotics presumably then go on to attack more susceptible bacteria,

in much the same way as pathogens thriving within a host go on to attack another susceptible host. The dynamics of this interaction could therefore be very similar to those involving more conventional examples of immunity.

Work on *Staphylococcus aureus* has demonstrated that these bacteria exhibit antibiotic resistance that is socially acquired. In other words, they show social immunity. When *S. aureus* cells are grown in the presence of an antibiotic, some members of the population switch to an antibiotic resistant phenotype that also confers protection to the nonresistant wild-type cells (Massey et al. 2001). The resistant cells lower the pH of the medium thus rendering the antibiotic ineffective for the entire population, whether the cells themselves are resistant or not (Massey and Peacock 2002). Growth of wild-type cells starts to increase after the proportion of resistant cells reaches 10% of the population (Massey et al. 2001). This type of social immunity is therefore analogous to the social fever exhibited by bees in that several individuals must participate for the defense to be successful. It is unclear why only some individuals switch to becoming antibiotic resistant, but there is some indication that they benefit through selection acting at the group level. By promoting the survival of nonresistant wild-type individuals, the antibiotic resistant microbes maintain genetic diversity in the population and effectively store up a genetic reserve for countering new environmental conditions or antibiotic treatments, which they (or their descendants) may benefit from in the future (Dugatkin et al. 2005). This is not the only mechanism by which microbes share immune defenses. In other species, for example, defenses are shared through the transfer of plasmids containing antibiotic resistance genes, thereby providing susceptible neighbors (commonly kin) with the means to defend themselves against an attack (Davies 1994).

The third form of social immunity that falls within our broader definition is a form of herd immunity (Frank 1998) that arises from investment in personal immunity (see Figure 2), through the consequent reduction in the force of infection felt by neighboring susceptible individuals. Just as with any investment in a public good, herd immunity is vulnerable to cheats who seek the benefits it confers without contributing to the costs involved (Frank 1998). Nevertheless,

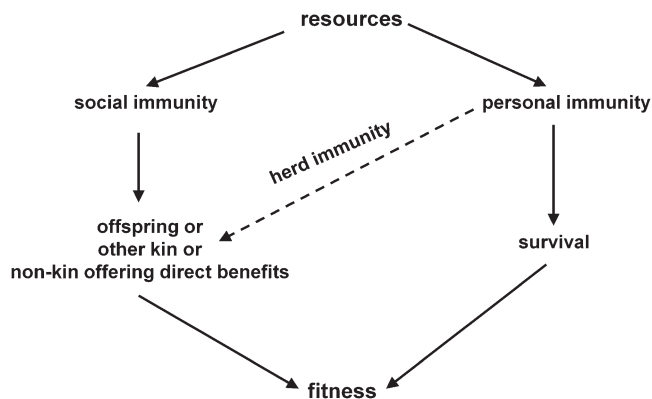


Figure 2
Resource allocation to personal immunity and social immunity, illustrating their respective roles in defending lifespan and the transmission of genes to the next generation (after Figure 1a in Stoehr and Kokko 2006).

theoretical analyses suggest that contributions to herd immunity are favored when individuals live in kin-structured populations (Frank 1998). Consistent with this idea is the evidence that cooperatively breeding adult African birds mount a stronger immune response than equivalently immune-challenged pair-breeding African birds (Spottiswoode 2008), perhaps because this reduces the levels of infection that their nestling kin then experience. Herd immunity in populations with limited dispersal might even be considered a form of niche construction, if it persists through overlapping generations, and this too could be kin selected (Lehmann 2007). In future work, it would be interesting to determine the extent to which herd immunity influences levels of investment in personal immunity. In species with sex-biased dispersal, for example, we might expect the dispersing sex to exhibit lower investment in personal immunity when it joins a new group because it stands to gain fewer herd immunity benefits than the philopatric sex that remains near kin. Sex-biased dispersal could thus offer a novel explanation for the sexual dimorphism in immune investment that is commonly observed and that is more usually attributed to resource-based life-history trade-offs (Zuk and Stoehr 2002; Stoehr and Kokko 2006).

Herd immunity could also be attributed to external immune responses. Flour beetles produce a quinone-rich secretion that reduces microbial growth in the flour in which they live (Prendeville and Stevens 2002). Flour beetles gain personal benefits as a result, but their actions could also potentially advantage other beetles living in their proximity. However, whether or not this actually constitutes a form of social immunity is yet to be determined. In general, when individuals gain immune benefits simply as a by-product of someone else's personal immunity rather than as a consequence of selection, this is not an instance of social immunity. In this case, we would require evidence that beetles strategically modify their production of quinones to suit others, for example, by upregulating quinone production when surrounded by kin, before concluding that this is an instance of social immunity.

In Figure 1, we summarize some of the diverse forms of immune function discussed above and classify them in 2 dimensions: according to whether they are internal or external and according to the extent of cooperation. We have estimated the extent of cooperation by judging the magnitude of the benefits it brings to others, relative to personal gain. At one end of this continuum is personal immunity where most of the benefits accrued are experienced solely by the actor, but in group-living species, this could contribute toward herd immunity. At the other end is extreme social immunity, where

the social benefits of immunity are far greater than those experienced personally. When organized in this fashion, it is clear that examples of social immunity under the current definition do not differ conceptually from the broader examples we describe above. Each involves internal and external immune function, and each varies in a similar way in the extent to which immune function is cooperative.

SOCIAL IMMUNITY VERSUS PERSONAL IMMUNITY

An individual's fitness depends on its likelihood of survival and its ability to transmit its genes into the next generation. Whereas personal immune function brings survival benefits, social immune function serves to improve the likelihood that individuals will successfully propagate their genes, for example, by protecting offspring, or reproductive kin, or potentially even nonkin that can offer direct benefits to the focal individual (Figure 2). Personal immune function thus serves to protect the contribution of lifespan to fitness, while social immune function effectively defends inclusive fitness.

A major goal of ecological immunology is to understand why individuals vary in the investment they devote to immune defense. If mounting a social immune response is costly (Cotter et al. 2010), then investment in personal immunity and social immunity could well trade-off against each other. Understanding the nature of the costs involved in mounting a social immune response could therefore explain individual variation in personal immunocompetence (cf., Zuk and Stoehr 2002). For example, a genetic trade-off could influence relative investment in the 2 types of immunity. There is circumstantial evidence for exactly this sort of relationship in honeybees who now possess many fewer genes for personal immunity than nonsocial insects and who instead bear genes for colony level immune function (Evans et al. 2006; Wilson-Rich et al. 2009). We might expect to see a marked genetic trade-off like this between the 2 forms of immunity in any species where contributions to each sort of immunity will be relatively constant, such as social insects. For those species where the social environment varies through the year, such as seasonally reproducing species, any genetic trade-off between the 2 arms of immunity might be less pronounced, but we might instead see phenotypic plasticity in the way that the trade-off is balanced. For example, females investing in the social immune defense of their young might temporarily be unable to mount an effective personal immune defense. Similarly, the trade-off between social and personal immunity may vary with age, or the 2 forms of immune function may senesce at different rates (DeVeale et al. 2004). It is difficult to predict on theoretical grounds alone what form the relationship might take even if we set aside the complicating factors that each form of immunity can be adaptive (i.e., requires no further investment after an initial immune challenge; Zuk and Stoehr 2002; Walker and Hughes 2009) and that there can be trade-offs between different arms of the personal immune response (e.g., Gehad et al. 1999; Gill et al. 2000; Cotter et al. 2004; Freitak et al. 2007). A recent state-dependent life-history model, for example, predicts that older individuals should restrain their investment in transmitting genes to the next generation to limit the extent of damage experienced by their bodies (McNamara et al. 2009). Translated into immune function, the prediction is that investment in personal immunity should increase with age while investment in social immunity declines. Terminal investment theory, by contrast, makes exactly the opposite prediction when recast in immunological terms (Williams 1966). Empirical work is clearly now required to determine which of these 2 theoretical alternatives best describes the immune systems of real organisms.

Physiological costs could further influence investment in personal versus social immunity, if the underlying physiological mechanisms have mutually antagonistic effects on each form of immunity, for example, or if sex-specific physiological profiles determine investment in either form of immunity (e.g., Klein 2005; Pasche et al. 2005). Evidence from several insect species suggests that hormones may mediate the immune response (see Wilson and Cotter 2009 and references therein). For example, sex-specific hormone profiles in dung beetles (Emlen and Nijhout 1999) and burying beetles (Panaitof et al. 2004; Scott and Panaitof 2004) correlate with investment in personal (Cotter et al. 2008) and social immune responses, respectively (Cotter and Kilner 2010). This could explain why female burying beetles contribute more to social immunity than males (Cotter and Kilner 2010). Sex-specific physiological effects on investment in each form of immunity could, of course, simply reflect differences between the sexes in life-history strategy (Zuk and Stoehr 2002; Zuk 2009). Males that adopt a “live fast, die young” strategy would be expected to invest relatively little in either social or personal immunity, instead channeling their resources into mating effort (Zuk 2009). But where males do invest in some form of parental care, life-history theory is required to predict whether the sexes differ in their contribution to each form of immunity.

In the burying beetle, *Nicrophorus vespilloides*, for example, females value each breeding attempt more highly than males but gain less fitness than males from a long life (Ward et al. 2009). We therefore predict that in this species, females should put more effort into the social immune defense of offspring than males (which is the case, Cotter and Kilner 2010) but that males should exhibit a stronger personal immune response than females (which has yet to be determined).

Extrinsic factors could additionally determine the levels of investment in social immunity, thereby altering any trade-off with personal immunity. These could be socially determined, for example, if several individuals contribute the immune defense of a public resource, such as a nest or other breeding resource. Individuals might then flexibly adjust their contribution to social immunity in relation to investment levels shown by others, just as happens in the burying beetle *N. vespilloides* (Cotter and Kilner 2010). In addition, the nature and prevalence of pathogens could influence investment in each form of immunity. Some pathogens might pose a particular threat to adult survival, whereas others may compromise the survival of offspring or reproductive kin. A greater threat from the former might boost investment in personal immune defense (Restif and Amos 2010), whereas a greater risk of attack from the latter could increase levels of social immune defense (Cotter et al. 2010). Among birds, life-history strategies predict the magnitude of response to predators that threaten offspring and predators that take adults, with short-lived species responding more vigorously to former and less strongly to the latter (Ghalambor and Martin 2001). It would be interesting to determine whether the magnitude of immune investment similarly varies with life history for each type of immunity. Do short-lived species respond more vigorously to a social immune challenge than a personal immune challenge, for example?

SOCIAL IMMUNITY AS A TOOL FOR STUDYING MAJOR TRANSITIONS IN EVOLUTION

In the same way that broadening the definition of an organism provides novel and revealing insights into the evolution of cooperation (Queller and Strassmann 2009), our broader definition of social immunity makes it possible to study the evolution of social immune function in greater depth than would otherwise be possible. For example, there are remarkable parallels between the social immune responses shown by social

insects and personal immunity exhibited by multicellular organisms (Cremer and Sixt 2009). Social immunity in insect societies even resembles social immunity seen in human agricultural societies (Fernandez-Marin et al. 2009). In each of these contexts, social immunity is characterized by a high level of cooperation with actors paying fitness costs to bring fitness benefits to others and with little conflict between them over how these costs should be shared. In other words, these acts of social immunity bear the hallmark of a major transition in evolution (Maynard Smith and Szathmary 1997). The key question is how did such a major transition in evolution take place? With comparative studies of different forms of social immunity, featuring contrasting levels of cooperation and inclinations to conflict over the division of the costs, we can start to find out (c.f. Queller and Strassmann 2009). The social immune responses exhibited by bacteria, animal families, and subsocial insects are ideal in this regard because the fitness costs of mounting a social immune response are simpler to quantify when the individuals mounting the social immune response are also able to reproduce. This makes it possible to measure how individuals balance the costs of investment in social immunity versus personal immunity in different social settings and therefore to determine how cooperation and conflict influence individual contributions to social immunity. On a related note, it is intriguing that an increase in the strength of the antimicrobial compounds used to defend social insect colonies is associated with the evolution of sociality (Stow et al. 2007). This could be due to a direct trade-off between investment in social immune defense and fecundity. Could the necessity to mount costly social immune defenses of the colony have been directly responsible for the evolution of worker sterility? This is something that could be investigated by analysing social immunity in other species by testing whether increased investment in social immunity reduces adult fecundity.

In short, we have argued that social immune responses are more widespread than perhaps previously realized yet are a relatively neglected component of an organism's immune system. Nevertheless, social immune systems offer a fruitful avenue for future research. They may explain much of the variation we see in personal immune defenses, both within and among species. They also provide a novel context for investigating social evolution and the major transitions in evolution.

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