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2 **Title: Personal immunity versus social immunity**

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2 **Abstract**

3 It is well known that organisms defend their fitness against attack from parasites and
4 pathogens by mounting a personal immune response. However, there is increasing evidence
5 that organisms from diverse taxa also exhibit immune responses for the purpose of protecting
6 other individuals as well as themselves. We argue that any type of immunity that has fitness
7 consequences for both the challenged individual and one or more recipients should be
8 referred to as ‘social immunity’. We show that social immune systems are a widespread yet
9 relatively neglected component of immunity, ideal for the study of social evolution. Whereas
10 personal immune systems protect lifespan, social immune systems effectively defend the
11 fecundity component of fitness, commonly protecting offspring or reproductive kin. We
12 suggest that there are likely to be close links between life history and the extent of investment
13 in each form of immunity. Furthermore, trade-offs between social and personal immunity
14 may explain individual variation in personal immune responses, including sex-specific
15 immune defences.

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1 **Main text**

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3 Many organisms defend their fitness against attack from parasites and pathogens by mounting
4 an immune response. Most physiological immune responses are internal, and targeted at
5 organisms that have invaded the body. For example, invertebrates show innate responses to
6 parasites by producing antimicrobial peptides and lysozymes that either inhibit the growth of
7 microorganisms or kill them. Similarly, their blood cells phagocytose single-celled parasites,
8 whilst larger invaders are encapsulated in a layer of blood cells that are melanised, sealing off
9 the invader from the host's body (Rolff and Reynolds, 2009). Vertebrates additionally have
10 an adaptive immune response comprising lymphocytes that respond to antigens on the surface
11 of the parasite, and these provide a targeted response with immunological memory (Janeway
12 et al., 2001). In addition to this typical internal response, some defences are deployed
13 externally to overcome microorganisms in the environment. For example, the uropygial
14 secretion with which birds preen their feathers has been shown to have antimicrobial activity,
15 and is used to protect the feathers from feather-degrading bacteria (Martin-Vivaldi et al.,
16 2010; Shawkey et al., 2003).

17 These are examples of personal immunity, in which the challenged individual is the
18 main beneficiary of the immune response. However, there is increasing evidence that immune
19 systems can also provide fitness benefits to others, besides the individual mounting the
20 response. In the evolutionary literature, when behaviours have fitness consequences for both
21 the actor and a recipient they are described as 'social' (e.g. (West et al., 2006). Applying the
22 same logic to immune function, we suggest that any type of immune response that has been
23 selected to increase the fitness of the challenged individual and one or more recipients should

1 be classified as social immunity. According to our definition, therefore, social immunity
2 includes the immune services provided for others in animal families, sub-social insects and
3 social microbes as well as the social insects, some group-living primates and other kin-
4 structured populations.

5

6 *Social immunity is seen in diverse contexts*

7 Our definition of social immunity is significantly broader than the current use of the term
8 (e.g. (Cremer et al., 2007; Cremer and Sixt, 2009; Wilson-Rich et al., 2009). In a landmark
9 paper, ‘social immunity’ was first coined to describe the group level immune function
10 exhibited by social insects and group-living primates (Cremer et al., 2007). Specifically, it
11 describes immune defences that are mounted by a collective for the benefit of themselves and
12 others (e.g. (Cremer et al., 2007; Cremer and Sixt, 2009; Wilson-Rich et al., 2009). It
13 includes, for example, the antifungal faecal pellets that termites use to coat the inside of their
14 chambers (Rosengaus et al., 1998), antimicrobial sternal gland secretions in termites
15 (Rosengaus et al., 2004) and metapleural gland secretions in leaf-cutting ants, which are
16 deployed against fungi and bacteria that compete with their symbiotic fungus (Nascimento et
17 al., 1996), as well as against pathogenic microorganisms (see (Cremer et al., 2007) and
18 references therein). It also encompasses the behavioural social fevers, triggered when
19 individuals huddle to raise temperatures beyond those optimal for pathogens (Wilson-Rich et
20 al., 2009). The key idea is that by acting collectively, individuals are better able to mount a
21 defence than is possible were they to act independently. According to this definition, it is the
22 collective nature of the immune response that puts the ‘social’ into ‘social immunity’, rather
23 than the fact that it is being mounted for the benefit of others as well. We suggest using the
24 term ‘collective immunity’ to describe these immune services, so as to free up the use of

1 'social immunity' for the more broadly defined acts of social immune function that we
2 outline below. As we illustrate in Figure 1, acts of collective immunity are nested within our
3 broader definition of social immunity.

4 Our broader definition of social immunity encompasses immune services performed
5 for others in at least three new contexts. The first of these is the animal family, which is
6 effectively a transient animal society in miniature. Parental investment in offspring (Trivers,
7 1972), a social behaviour at the heart of animal family life, is a kin-selected form of
8 cooperation (Dawkins, 1989; Komdeur, 2006) that is analogous to worker care of larvae seen
9 in the eusocial insects: it involves individuals sacrificing future fitness for the benefit of
10 others, to whom they are not genetically identical, for their mutual benefit. Parental care can
11 therefore be treated just like any other kin-selected social behaviour (Kilner and Hinde,
12 2008). Just like the social insects and group-living primates, parents mount immune defences
13 for their own benefit and the benefit of others. Many of these immune services are externally
14 produced. For example, two species of blenny produce antimicrobial mucus in their anal
15 glands which they rub over the nest surface and directly on to eggs during egg guarding
16 (Giacomello et al., 2006). The sperm-duct gland secretions of the grass goby show similar
17 antimicrobial activity (Giacomello et al., 2008) as does the epidermal mucus of the fringed
18 darter, which is applied to protect eggs from microbial contamination (Knouft et al., 2003).
19 The three-spined stickleback uses antimicrobial mucus to glue together his nest, protecting
20 the eggs inside from microbes (Little et al., 2008) and the foam with which tungara frogs
21 cover their eggs contains a cocktail of chemicals that protect the eggs from microbes
22 (Fleming et al., 2009).

23 Insects with parental care exhibit similar external immune defences. Bark beetles tunnel
24 chambers into living wood in which to lay their eggs and they coat the inside of these

1 chambers with oral secretions that contain a fungus-inhibiting bacterium (Adams et al., 2008;
2 Cardoza et al., 2006). Without the protection of this secretion, eggs would be killed by
3 invasive fungi (Cardoza et al., 2006). Similarly, houseflies that lay their eggs in manure cover
4 the surface of their eggs with bacteria that inhibit the growth of fungi which can affect larval
5 development (Lam et al., 2009). Burying beetles exhibit elaborate pre- and post hatching
6 parental care, one aspect of which involves preparing a vertebrate carcass for their offspring
7 by covering it with anal exudates that have potent antibacterial activity (Cotter and Kilner,
8 2010). This defends the resource from microbial attack, and thus improves the survival of the
9 offspring (Rozen et al., 2008).

10 Parents can also endow immune defences for their offspring internally. For example,
11 invertebrates, fish, reptiles, mammals and birds provide their young with maternally-derived
12 antibodies (vertebrates) or other immune factors (invertebrates), either directly in the egg or
13 in milk (see (Grindstaff et al., 2003) and references therein). Another option is to collect
14 material from the environment to aid in immune defence, for example, some bird species line
15 their nests with aromatic plants as a prophylactic immune defence (e.g.(Gwinner and Berger,
16 2005; Lafuma et al., 2001).

17 Each of these examples qualifies as an instance of social immunity, according to our
18 definition, although the nature of the resulting benefit varies from case to case. In the
19 simplest scenario, such as the fish examples, a single parent provides an immune service for
20 its offspring, and the other parent benefits as well, simply through the offspring's improved
21 fitness. Where there is biparental care, such as in the burying beetle, and both parents
22 contribute to social immunity (Cotter and Kilner, 2010), then each potentially gains
23 additional benefits, in some cases this may be because there is increased genetic diversity in
24 the immune service, which may well make it more effective (e.g. (Sherman et al., 1988) and

1 partly because the cost of investing in social immunity is shared. These benefits increase in
2 magnitude if several adults breed together on a resource, as in the bark beetles and burying
3 beetles, and if all the breeding adults contribute to social immunity.

4 Immune defences mounted on behalf of other individuals can also be found among the
5 social microbes. It might seem peculiar to suggest that microbes have immune systems, but
6 perhaps this appears less odd if we consider that immune systems function to provide
7 resistance to external agents that damage the body, and that they have co-evolved with those
8 agents for precisely this purpose. Mechanisms of antibiotic resistance might justifiably then
9 be regarded as microbial immune systems because there is good evidence that antibiotic
10 resistance has co-evolved with the organisms that produce the antibiotics themselves (Davies,
11 1994). Furthermore, the organisms that thrive as a consequence of producing antibiotics
12 presumably then go on to attack more susceptible bacteria, in much the same way as
13 pathogens thriving within a host go on to attack another susceptible host. The dynamics of
14 this interaction could therefore be very similar to those involving more conventional
15 examples of immunity. Work on *Staphylococcus aureus* has demonstrated that these bacteria
16 exhibit antibiotic resistance that is socially acquired. In other words, they show social
17 immunity. When *S. aureus* cells are grown in the presence of an antibiotic, some members of
18 the population switch to an antibiotic resistant phenotype that also confers protection to the
19 non-resistant wild type cells (Massey et al., 2001). The resistant cells lower the pH of the
20 medium thus rendering the antibiotic ineffective for the entire population, whether the cells
21 themselves are resistant or not (Massey and Peacock, 2002). Growth of wild type cells starts
22 to increase after the proportion of resistant cells reaches 10% of the population (Massey et al.,
23 2001). This type of social immunity is therefore analogous to the social fever exhibited by
24 bees in that several individuals must participate for the defence to be successful. It is unclear

1 why only some individuals switch to becoming antibiotic resistant but there is some
2 indication that they benefit through selection acting at the group level. By promoting the
3 survival of non-resistant wild-type individuals, the antibiotic resistant microbes maintain
4 genetic diversity in the population and effectively store up a genetic reserve for countering
5 new environmental conditions or antibiotic treatments, which they (or their descendants) may
6 benefit from in the future (Dugatkin et al., 2005). This is not the only mechanism by which
7 microbes share immune defences. In other species, for example, defences are shared through
8 the transfer of plasmids containing antibiotic resistance genes, thereby providing susceptible
9 neighbours (commonly kin) with the means to defend themselves against an attack (Davies,
10 1994).

11 The third form of social immunity that falls within our broader definition is a form of herd
12 immunity (Frank, 1998) that arises from investment in personal immunity (see Figure 2),
13 through the consequent reduction in the force of infection felt by neighbouring susceptible
14 individuals. Just as with any investment in a public good, herd immunity is vulnerable to
15 cheats who seek the benefits it confers without contributing to the costs involved (Frank,
16 1998). Nevertheless, theoretical analyses suggest that contributions to herd immunity are
17 favoured when individuals live in kin-structured populations (Frank, 1998). Consistent with
18 this idea is the evidence that cooperatively breeding adult African birds mount a stronger
19 immune response than equivalently immune-challenged pair-breeding birds (Spottiswoode,
20 2008), perhaps because this reduces the levels of infection that their nestling kin then
21 experience. Herd immunity in populations with limited dispersal might even be considered a
22 form of niche construction, if it persists through overlapping generations, and this too could
23 be kin-selected (Lehmann, 2007). In future work it would be interesting to determine the
24 extent to which herd immunity influences levels of investment in personal immunity. In

1 species with sex-biased dispersal, for example, we might expect the dispersing sex to exhibit
2 lower investment in personal immunity when it joins a new group, because it stands to gain
3 fewer herd immunity benefits than the philopatric sex that remains near kin. Sex-biased
4 dispersal could thus offer a novel explanation for the sexual dimorphism in immune
5 investment that is commonly observed and that is more usually attributed to resource-based
6 life history trade-offs (Stoehr and Kokko, 2006; Zuk and Stoehr, 2002).

7 Herd immunity could also be attributed to external immune responses. Flour beetles
8 produce a quinone-rich secretion that reduces microbial growth in the flour in which they live
9 (Prendeville and Stevens, 2002), to their personal advantage, and potentially to the advantage
10 of other beetles living in their proximity. Whether or not this constitutes a form of social
11 immunity is yet to be determined. If beetles modified their production of quinones when
12 surrounded by kin rather than unrelated beetles, this would provide evidence that this form of
13 immunity had been selected specifically to benefit others. In general, when individuals gain
14 immune benefits simply as a by-product of someone else's personal immunity rather than as a
15 consequence of selection, this is not an instance of social immunity.

16 In Figure 1, we summarize some of the diverse forms of immune function discussed above
17 and classify them in two dimensions: according to whether they are internal or external, and
18 according to the extent of cooperation. We have estimated the extent of cooperation by
19 judging the magnitude of the benefits it brings to others, relative to personal gain. At one end
20 of this continuum is personal immunity where most of the benefits accrued are experienced
21 solely by the actor, but in group living species this could contribute towards herd immunity.
22 At the other end is extreme social immunity, where the social benefits of immunity are far
23 greater than those experienced personally. When organized in this fashion, it is clear that
24 examples of social immunity under the current definition do not differ conceptually from the

1 broader examples we describe above. Each involves internal and external immune function,
2 and each varies in a similar way in the extent to which immune function is cooperative.

3

4 *Social immunity versus personal immunity*

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

12 A major goal of ecological immunology is to understand why individuals vary in the
13 investment they devote to immune defence. If mounting a social immune response is costly
14 (Cotter *et al* submitted), then investment in personal immunity and social immunity could
15 well trade-off against each other. Understanding the nature of the costs involved in mounting
16 a social immune response could therefore explain individual variation in personal
17 immunocompetence (cf (Zuk and Stoehr, 2002). For example, a genetic trade-off could
18 influence relative investment in the two types of immunity. There is circumstantial evidence
19 for exactly this sort of relationship in honeybees, who now possess many fewer genes for
20 personal immunity than non-social insects, and who instead bear genes for colony level
21 immune function (Evans et al., 2006; Wilson-Rich et al., 2009). We might expect to see a
22 marked genetic trade-off like this between the two forms of immunity in any species where
23 contributions to each sort of immunity will be relatively constant, such as social insects. For
24 those species where the social environment varies through the year, such as seasonally

1 reproducing species, any genetic trade-off between the two arms of immunity might be less
2 pronounced, but we might instead see phenotypic plasticity in the way that the trade-off is
3 balanced. For example, females investing in the social immune defence of their young might
4 temporarily be unable to mount an effective personal immune defence. Similarly, the trade-
5 off between social and personal immunity may vary with age, or the two forms of immune
6 function may senesce at different rates (DeVeale et al., 2004). It is difficult to predict on
7 theoretical grounds alone what form the relationship might take, even if we set aside the
8 complicating factors that each form of immunity can be adaptive (i.e. requires no further
9 investment after an initial immune challenge; (Walker and Hughes, 2009; Zuk and Stoehr,
10 2002), and that there can be trade-offs between different arms of the personal immune
11 response (e.g. (Cotter et al., 2004; Freitak et al., 2007; Gehad et al., 1999; Gill et al., 2000). A
12 recent state-dependent life history model, for example, predicts that older individuals should
13 restrain their investment in transmitting genes to the next generation to limit the extent of
14 damage experienced by their bodies (McNamara et al., 2009). Translated into immune
15 function, the prediction is that investment in personal immunity should increase with age
16 while investment in social immunity declines. Terminal investment theory, by contrast,
17 makes exactly the opposite prediction when recast in immunological terms (Williams, 1966).
18 Empirical work is clearly now required to determine which of these two theoretical
19 alternatives best describes the immune systems of real organisms.

20 Physiological costs could further influence investment in personal versus social immunity,
21 if the underlying physiological mechanisms have mutually antagonistic effects on each form
22 of immunity, for example, or if sex-specific physiological profiles determine investment in
23 either form of immunity (e.g. (Klein, 2005; Pasche et al., 2005). Evidence from several insect
24 species suggest that hormones may mediate the immune response (Rolff and Siva-Jothy,

1 2002; Wilson and Cotter, 2009) and there is evidence that sex-specific hormone profiles in
2 dung beetles (Emlen and Nijhout, 1999) and burying beetles (Panaitof et al., 2004; Scott and
3 Panaitof, 2004) correlate with investment in personal (Cotter et al., 2008) and social immune
4 responses respectively (Cotter and Kilner, 2010). This could explain why female burying
5 beetles contribute more to social immunity than males (Cotter and Kilner, 2010). Sex-specific
6 physiological effects on investment in each form of immunity could, of course, simply reflect
7 differences between the sexes in life history strategy (Zuk, 2009; Zuk and Stoehr, 2002).
8 Males that adopt a ‘live fast, die young’ strategy would be expected to invest relatively little
9 in either social or personal immunity, instead channelling their resources into mating effort
10 (Zuk, 2009). But where males do invest in some form of parental care, life history theory is
11 required to predict whether the sexes differ in their contribution to each form of immunity.
12 In the burying beetle, *Nicrophorus vespilloides*, for example, females value each breeding
13 attempt more highly than males, but gain less fitness than males from a long life (Ward et al.,
14 2009). We therefore predict that in this species, females should put more effort into the social
15 immune defence of offspring than males (which is the case, (Cotter and Kilner, 2010), but
16 that males should exhibit a stronger personal immune response than females (which has yet to
17 be determined).

18 Extrinsic factors could additionally determine the levels of investment in social
19 immunity, thereby altering any trade-off with personal immunity. These could be socially
20 determined, for example, if several individuals contribute the immune defence of a public
21 resource, such as a nest or other breeding resource. Individuals might then flexibly adjust
22 their contribution to social immunity in relation to investment levels shown by others, just as
23 happens in the burying beetle *N. vespilloides* (Cotter and Kilner, 2010). In addition, the
24 nature and prevalence of pathogens could influence investment in each form of immunity.

1 Some pathogens might pose a particular threat to adult survival, while others may
2 compromise the survival of offspring or reproductive kin. A greater threat from the former
3 might boost investment in personal immune defence (Restif and Amos, 2010) while a greater
4 risk of attack from the latter could increase levels of social immune defence (Cotter *et al*
5 submitted). Among birds, life history strategies predict the magnitude of response to
6 predators that threaten offspring and predators that take adults, with short-lived species
7 responding more vigorously to former and less strongly to the latter (Ghalambor and Martin,
8 2001). It would be interesting to determine whether the magnitude of immune investment
9 similarly varies with life history for each type of immunity. Do short-lived species respond
10 more vigorously to a social immune challenge than a personal immune challenge, for
11 example?

12

13 *Social immunity as a tool for studying major transitions in evolution*

14 In the same way that broadening the definition of an organism provides novel and revealing
15 insights into the evolution of cooperation (Queller and Strassmann, 2009), our broader
16 definition of social immunity makes it possible to study the evolution of social immune
17 function in greater depth than would otherwise be possible. For example, there are
18 remarkable parallels between the social immune responses shown by social insects and
19 personal immunity exhibited by multicellular organisms (Cremer and Sixt, 2009). Social
20 immunity in insect societies even resembles social immunity seen in human agricultural
21 societies (Fernandez-Marin *et al.*, 2009). In each of these contexts, social immunity is
22 characterized by a high level of cooperation, with actors paying fitness costs to bring fitness
23 benefits to others, and with little conflict between them over how these costs should be
24 shared. In other words, these acts of social immunity bear the hallmark of a major transition

1 in evolution (Maynard Smith and Szathmary, 1997). The key question is how did such a
2 major transition in evolution take place? With comparative studies of different forms of
3 social immunity, featuring contrasting levels of cooperation and inclinations to conflict over
4 the division of the costs, we can start to find out (Queller and Strassmann, 2009). The social
5 immune responses exhibited by bacteria, animal families and sub-social insects, are ideal in
6 this regard because the fitness costs of mounting a social immune response are simpler to
7 quantify when the individuals mounting the social immune response are also able to
8 reproduce. This makes it possible to measure how individuals balance the costs of investment
9 in social immunity versus personal immunity in different social settings, and therefore to
10 determine how cooperation and conflict influence individual contributions to social
11 immunity. On a related note, it is intriguing that an increase in the strength of the
12 antimicrobial compounds used to defend social insect colonies is associated with the
13 evolution of sociality (Stow et al., 2007). This could be due to a direct trade-off between
14 investment in social immune defence and fecundity. Could the necessity to mount costly
15 social immune defences of the colony have been directly responsible for the evolution of
16 worker sterility? This is something that could be investigated by analysing social immunity in
17 other species, by testing whether increased investment in social immunity reduces adult
18 fecundity.

19

20 In short, we have argued that social immune responses are more widespread than perhaps
21 previously realised, yet are a relatively neglected component of an organism's immune
22 system. Nevertheless, social immune systems offer a fruitful avenue for future research. They
23 may explain much of the variation we see in personal immune defences, both within and

1 among species. They also provide a novel context for investigating social evolution and the
2 major transitions in evolution.

3

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9

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8 **Figure legends**

9

10 **Figure 1** – examples of immune function are classified in two dimensions: according to
11 whether they are internal or external, and according to the extent of cooperation by judging
12 the magnitude of the benefits they bring to others, relative to personal gain.

13

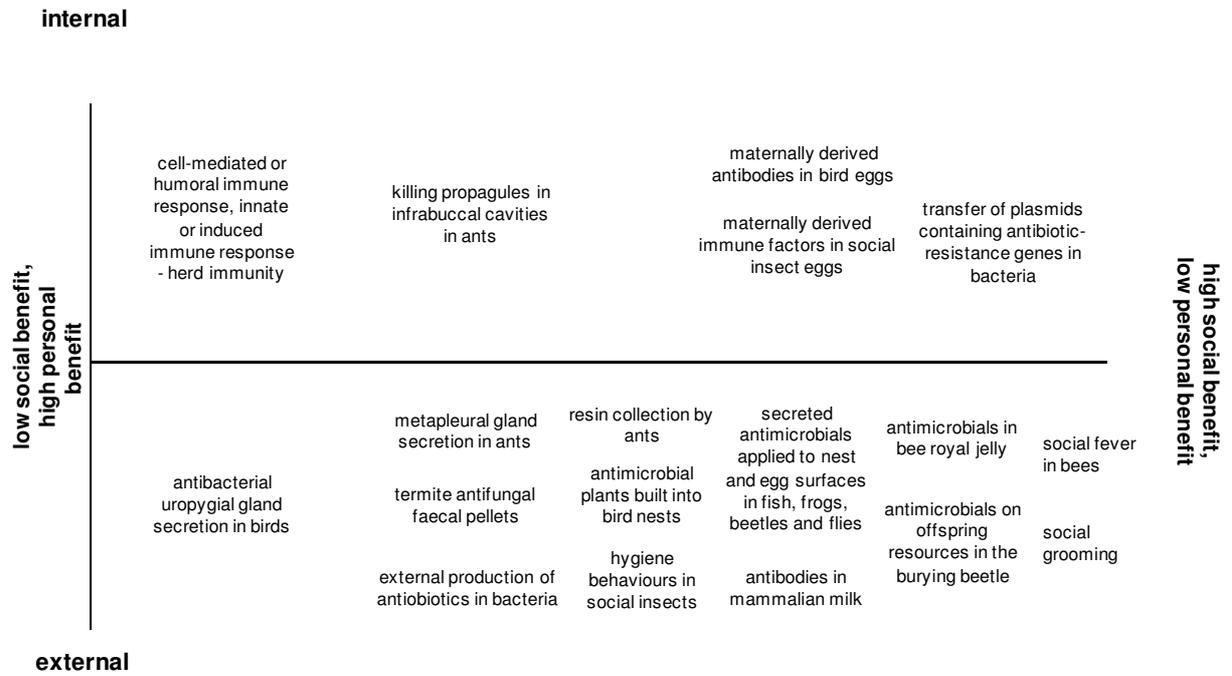
14 **Figure 2** – resource allocation to personal immunity and social immunity, illustrating their
15 respective roles in defending lifespan and the transmission of genes to the next generation
16 (after Figure 1a in Stoehr & Kokko 2006).

17

1 **Figures**

2 **Figure 1**

3



4

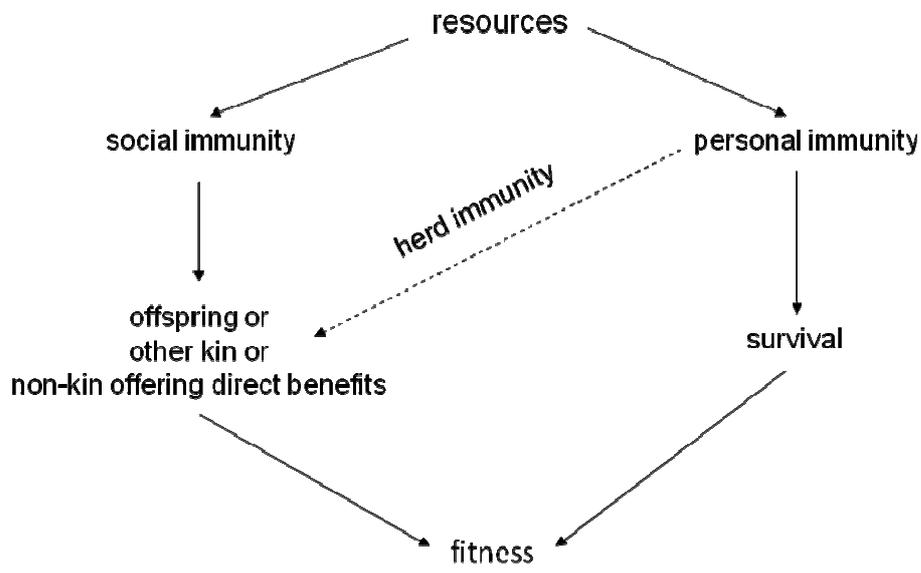
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1 **Figure 2**

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