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The distribution of parasite strains among hosts affects disease spread in a social insect

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ABSTRACT

Social insects present highly interesting and experimentally amenable systems for the study of disease transmission because they naturally live in dense groups of frequently interacting individuals. Using experimental inoculations of five trypanosomatid strains into groups of its natural host, the bumblebee *Bombus terrestris*, we investigate the effects of the initial parasite strain distribution across group members on the establishment and transmission success of the different strains to new hosts. For a given number of parasite strains circulating within a host group, transmission to new hosts was increased when the strains were initially inoculated as mixed infections (as opposed to separate single infections), presumably because mixed infections generally favored fast replicating strains. In contrast, separate single infections reduced transmission at least in part through a precedence effect, whereby weak strains appeared to persist by making their host unavailable to superinfection. These results suggest that host groups could benefit from 'compartmentalizing' infections by different parasite strains across different group members, which might be achieved in social insects, for example, by division of labor.

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1. Introduction

Most parasite populations are genetically diverse, and when several strains (genotypes) of a parasite circulate in a host population, individual hosts can become infected with more than one strain, i.e. carry a mixed genotype infection (Balmer and Tanner, 2011). A major current challenge is to understand if mixed genotype infections have different consequences for the host and the parasite, not only in the short-term (e.g. for the fitness of the infected individual and the relative success of the co-infecting strains) but also in the long-term (e.g., for the evolution of host defenses and parasite virulence). Transmission to the next host is one of the most essential components of parasite fitness, but few systems allow to experimentally study and quantify transmission and most laboratory studies have so far measured parasite success at the single-host scale (Balmer et al., 2009; Ben-Ami et al., 2008; Davies et al., 2002; de Roode et al., 2005a; de Roode et al., 2003; Gower and Webster, 2005; Hodgson et al., 2004; Hughes and Boomsma, 2004; Imhoof and Schmid-Hempel, 1998; Jäger and Schjørring, 2006; Johnson and Hoverman, 2012; Wargo et al., 2007), with notable exceptions, e.g. in a mouse-malaria model (de Roode et al., 2005b) and more recently, a plant-fungus system (Susi et al., 2015).

Social insect-parasite systems are particularly amenable to the experimental study of disease transmission because hosts naturally live in dense colonies, allowing – at least in principle – for rapid transmission between nestmates. Furthermore, colonies and worker groups can be experimentally modified and the consequences of such manipulations on transmission and the dynamics of an epidemic studied. Social insects colonies are also interesting entities for the study of host-parasite interactions in general, because they are highly integrated and function to a large extent as a single organism (Hölldobler and Wilson, 2008) when it comes to anti-parasitic defenses (Cremer et al., 2007; Cremer and Sixt, 2009; Fefferman and Traniello, 2008). Infection and its consequences can therefore be envisaged at two relevant levels in such systems: the individual and the colony (Wilson-Rich et al., 2009).

Here, we investigated how the distribution of parasite strains among individual hosts in a group affects the further transmission dynamics. In social insect colonies, differences in parasite strain distribution across colony members can in principle result from a variety of factors, such as division of labor (e.g. if behavioral specialization leads to differential exposure), genetic heterogeneity (e.g. if some host genotypes are more susceptible to infections by some parasite strains) or strategies of social immunity (e.g. contact

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networks reducing exposure to a colony's most valuable members) and are expected to affect disease dynamics to various degrees (Stroeymeyt et al., 2014). We exposed individual hosts within experimental groups to parasite inocula of various compositions before letting the infection spread to new group members in semi-natural conditions. The initial infections were designed so as to represent different degrees of individual-level and group-level infection multiplicity: infections were single or mixed at the group level (with a single, or multiple strains circulating within the group), as well as at the individual level (with individual hosts receiving a single or mixed inoculum). We asked if and how these different treatments affected parasite transmission to new hosts and the relative success of the different strains.

We used various strains (defined here as distinct multilocus microsatellite genotypes) of the gut trypanosome *Crithidia bombi* circulating in groups of its natural host, the bumblebee *Bombus terrestris*. *C. bombi* spreads within and between colonies *via* infective faces deposited on the nest material and on flowers (Durrer and Schmid-Hempel, 1994), respectively. In the field, host colonies are typically exposed to numerous, genetically distinct strains and frequently become multiply infected (Schmid-Hempel and Reber Funk, 2004). Similarly, nearly half of all wild-caught individuals are infected by more than one strain (Salathé and Schmid-Hempel, 2011) and queens can carry over 25 different strains (Tognazzo et al., 2012). Finally, an experiment showed a positive link between strain diversity in individual workers from a colony and the likelihood that this colony will produce infected offspring (Ulrich et al., 2011).

The annual life-cycle of *B. terrestris* is central to its interactions with *C. bombi*. Colonies are initiated in spring by mated queens emerging from hibernation. Each queen initially lays eggs that develop into workers, which perform the tasks of colony maintenance and brood care. Queens are singly mated and all workers within a colony are thus highly related (because of haplodiploidy, relatedness between full sisters is 75%). Towards the end of summer, the queen produces sexual offspring by laying eggs that develop into males and new queens. All workers and males perish at the end of summer, and only the daughter queens enter hibernation after mating, to emerge and to found their own colony in the next year. *C. bombi* strongly reduces the colony founding success of infected queens (Brown et al., 2003), and shortens worker life span under adverse conditions (Brown et al., 2000), which together acts to reduce colony fitness. Hence, reducing the likelihood of transmission to queens is of prime interest to the colony. At the same time, *C. bombi* cannot survive outside its host for prolonged periods of time (Schmid-Hempel et al., 1999). Thus, parasite fitness is tightly linked to its ability to infect daughter queens at the end of the colony cycle (so as to survive into the next year) and, therefore, to how likely transmission from workers to queens occurs within the colony, as tested here.

2. Methods

2.1. Hosts and parasites

Nine 'stock' colonies of *B. terrestris* were started from uninfected bumblebee queens collected in spring 2010 in northeastern Switzerland. All bees used in the experiment were kept at 26 ± 2 °C under constant red light, with pollen and sugar water provided *ad libitum*. The five *C. bombi* strains (internal codes 08.021, 08.068, 08.075, 08.091 and 08.161, here labeled A–E) used for the experimental infections were obtained from feces of naturally infected queens collected in spring 2008 in the same population as the hosts. Single infective cells were isolated using a fluorescence-activated cell-sorter; the strains were then maintained and grown clonally in liquid medium (Salathe et al., 2012). The strains had distinct multi-locus genotypes at four polymorphic microsatellite loci, and could thus readily be differentiated by genetic markers in a mixture.

2.2. Experimental procedure

A total of 42 workers from each stock colony were randomly assigned to one of the following treatment groups: (1) mixed infections, (2) separate infections, or (3) single infections. Hence, there were 14 workers per group, and each group was housed in a box for the duration of the experiment (see Fig. 1). This setup was replicated across the nine stock colonies. In each group, four of the 14 workers were left uninfected as the targets of further transmission. The ten remaining workers of each group were starved for 4–5 h before being individually presented with 10 µl of sugar water containing an inoculum of 15,000 live *C. bombi* cells that they imbibed *per os*. In the mixed infections group (1), all ten workers received the same mix of five strains (3000 cells of each strain). In the separate infections group (2), each of the five strains was inoculated alone into two of the ten workers, so that all five strains were present in the group as single infections. In the single infections group (3), all ten workers received strain A. This single, arbitrarily selected strain was used for this last treatment group because the number of workers available in each colony was not sufficient to repeat the single infection treatment for all five strains. Exposed workers were paint-marked on the thorax according to the type of inoculum they received. In all cases, the total infective dose per individual host and group of hosts were identical at 15,0000 cells/-worker and 150,000 cells/group, respectively. The total number of cells of each strain inoculated in a group of workers was thus identical for the multiple exposure and the separate exposure treatments (30,000 cells/strain), but their initial distribution among hosts differed.

On day 7 post-exposure, the infection status of all workers in each group was assessed by microscopic inspection of feces. A random half of the exposed and non-exposed target hosts (in the separate exposures group, one of the two exposed hosts for each strain), that is, 7 workers per treatment, were then returned to the box, while the remaining 7 workers were frozen. On the same day, all daughter queens that had been produced in a stock colony between day 1 and day 7 were distributed among the three experimental boxes already containing workers from that same colony and the infection was left to spread without further intervention for 10 additional days. Because daughter queen production is highly variable among colonies, the number of queens that could be added to the experimental boxes was the same for all exposure treatments within a colony, but varied across colonies. On day 17 post-exposure, all daughter queens and remaining workers were frozen. The choice of the first time point (day 7) was based on previous work showing that infected hosts can reliably be detected by microscopic inspection of feces at seven days post-exposure (Schmid-Hempel et al., 1999). At the same time, transmission to the next workers is still limited; hence, target workers were unlikely to have contracted the parasite in this time window (see Section 3). The second time point (day 17) was chosen to ensure that the target workers would have become infected as the rate of transmission built up and that at least part of the daughter queens would had been thoroughly exposed to the circulating parasites and carry detectable infections as well. All hosts that died before sampling were discarded.

2.3. Infection composition and infection intensity

All individuals were dissected and their gut homogenized in 100 µl (workers) or 200 µl (queens) Ringer solution. DNA was

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