Social Evolution: Sick Ants Face Death Alone

Social insects not only live altruistically, they die so: a new study reveals that moribund ants abandon their nests to die in seclusion, which reduces the risk of transmitting diseases to relatives.

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Workers of social insects are famous for being selfless. They build the nest, collect food, rear the young and defend the colony. Most of them do not reproduce, but help to rear non-descendant kin, who share copies of their genes [1]. The protection of kin can take spectacular forms: termites explode during fights, bees die after stinging, or ants condemn themselves by sealing the nest from the outside [2,3].

In this issue of *Current Biology*, Heinze and Walter [4] document a more discreet form of self-sacrifice: ant workers infected by a fungal pathogen abandon their nest to die in social isolation. The researchers transferred colonies of *Temnothorax unifasciatus* to their laboratory. Each colony is formed by a single queen and her offspring — hence, workers living in the same nest are highly related. The tiny ants (Figure 1) established their nests inside small artificial cavities placed in foraging arenas. The authors exposed a sample of workers to spores of the generalist entomopathogenic fungus *Metarhizium anisopliae*. They observed that most of the workers who died from the fungal infection permanently left the nest hours or days before death, and died in the foraging arena, away from nestmates. This behaviour minimizes the risk of infecting nestmates, and might thus have evolved for disease prevention.

Heinze and Walter [4] had to rule out the alternative explanation that workers were manipulated by the fungus. Indeed, many parasites are able to change the behaviour of their hosts in order to increase their own transmission. Flu viruses make us cough, parasitic hairworms cause their cricket host to jump into water [5], and flatworms or specialized fungi make ants bite vegetation to increase their transmission or growth [6].

To control for the effect of parasite manipulation, Heinze and Walter [4] had the clever idea to reduce the lifespan of workers by exposing them to CO_2. The vast majority of the workers who survived the treatment, but died prematurely after it, left the nest before death. This simple experiment demonstrates that nest leaving is not caused by parasite manipulation, but by the imminence of death.

The fact that workers dying from other causes than disease also left the nest does, however, raise some new questions about the ultimate causes of self-exclusion. Heinze and Walter [4] hypothesize that death in nature commonly results from infection, so that moribund workers should leave the nest to prevent the spread of disease. Unfortunately, we know little about mortality causes and disease prevalence in ants under natural conditions. If diseases are rare, or in species other than social insects, moribund individuals might also leave the group in order to spare scarce resources.

Additional observations and experiments helped to clarify the causes and process of self-exclusion. When observing unmanipulated colonies, Heinze and Walter [4] recorded that workers who died from natural but unknown causes left their nests too, which shows that this behaviour was not due to experimental manipulation. The behaviour of moribund workers, whatever the cause of death, was strikingly distinct from that of healthy nestmates: dying workers left the nest and did not return to it, whereas healthy workers spent most of their time within the nest and regularly returned to it after short foraging trips. Hence, the site where workers died did not reflect the normal day-to-day activity of healthy workers.

Moribund workers who left the nest paid a cost in terms of decreased survival, which demonstrates that self-exclusion is altruistic. Indeed, CO_2-exposed workers who abandoned their nests died before CO_2-exposed workers who were experimentally forced to stay inside their nests. This finding is important, because the reverse pattern has been documented in another social insect: bumblebee workers parasitized by conopid fly larvae prolonged their life-span by spending the night out of the nest and seeking cold temperatures that slowed down the development of the parasite [7].

Figure 1. A worker of the ant *Temnothorax unifasciatus*, marked with copper filaments (Photo: Elisabeth Brunner).

Another interesting finding was that *T. unifasciatus* workers left the nest voluntarily, and were not carried away by other workers. This contrasts sharply with other species of ants, such as leaf-cutting ants, in which specialized workers carry corpses to refuse piles located in precise locations [8]. Heinze and Walter [4] suggest that self-exclusion is more likely to evolve in species that have few workers per colony and occupy simple nests. Indeed, in small colonies moribund workers can stop all social contacts by walking out of the nest for a short distance. In contrast, when colonies are populous and occupy large and complex nests, moribund workers will need the help of other workers to leave the colony. These workers are generally specialized in waste and corpse removal, which further minimizes the spread of infection [8,9]. Waste removal is also altruistic. In leaf-cutting ants, workers exposed to waste have reduced longevity [10]. In gall-forming aphids, soldiers occasionally fall out of the gall when trying to throw sticky pellets of dejections, debris or dead aphids overboard [11].

Overall, the evolution of altruistic self-exclusion will depend on its net effect on the inclusive fitness of the potential altruist [1]. When an individual is old or sick, its future contribution to colony productivity is expected to be small, so that even small costs to related individuals may lead to kin-selected self-exclusion. The hypothesis that such self-sacrifice evolved in order to minimize the risk of disease transmission appears likely in ants, but remains to be proven. This is not an easy task, as it will require comparison of the colony-level costs caused by the spread of diseases when individuals die in and out of their nests, respectively.

It has long been considered that social animals are particularly sensitive to disease, and that parasites might be a selective pressure limiting social evolution [12]. This is because social animals have frequent contacts and generally live in groups of highly related individuals, so that parasites can spread among and adapt to genetically similar group members. In response to parasite pressure, however, social animals have evolved a variety of behavioural and social defences [9,13,14].

The self-exclusion of sick individuals constitutes one of the simplest forms of cooperative defence against diseases. Such altruistic suicide requires no major innovation and will be most effective in small societies composed of highly related individuals. In larger groups, division of labour and collective actions open the way to increasingly sophisticated types of hygienic behaviour. For example, social insect workers may collectively avoid contaminated nest sites, minimize contact with waste, groom infected individuals, exclude sick individuals, share antibiotic secretions, rear symbionts, or protect themselves with antimicrobial plant compounds (reviewed in [9,13,14]). There are even fascinating reports indicating that disease resistance can be transferred between group members [15,16] or across generations [17,18].

In view of these powerful ways to limit the impact of parasites and pathogens, I believe that the role of disease in social evolution has to be reconsidered. Diseases are likely to hinder the first stages of social evolution. But as group members develop efficient and diverse means to collectively combat infections, the impact of diseases will progressively decrease. Animals living in cooperative groups and using social defences may thus gain better control over diseases, as compared to solitary animals that only rely on individual defences. Over evolutionary time, diseases might therefore become a factor contributing to the maintenance of advanced social behaviour. The current data are insufficient to compare the load of parasites between animals living solitarily, in small annual societies or in large perennial societies. However, a pioneer comparative study already revealed that the life-history and ecology of major social insect groups covary with the number and types of their parasites [14].

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