



Wood ants protect their brood with tree resin



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Social insects use multiple lines of collective defences to combat pathogens. One example of a behavioural group defence is the use of antimicrobial plant compounds to disinfect the nest. Indeed, wood ants collect coniferous tree resin, and the presence of resin in their nest protects them against fungal and bacterial pathogens. Many questions remain on the mechanisms of resin use, including which factors elicit resin collection and placement within nests. Here, we investigated whether the presence of brood induces *Formica paralugubris* workers to collect more resin, and whether the workers preferentially place resin near the brood. We also tested whether the collection and placement of resin depends on the presence of the fungal entomopathogen *Beauveria bassiana*. Workers brought more resin to their nest when brood was present, and preferentially placed the resin near the brood. In contrast, workers did not increase resin collection in response to exposure to *B. bassiana*, nor did they place resin closer to contaminated brood or contaminated areas of the nest. This lack of response may be explained by a limited effect of resin against the germination and growth of *B. bassiana* in vitro. Overall, our main result is that wood ants actively position resin near the brood, which probably confers prophylactic protection against other detrimental microorganisms.

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The use of plant compounds to combat parasites has been documented in various animal taxa, including insects, birds and mammals (Chapuisat, Oppliger, Magliano, & Christe, 2007; Clayton & Wolfe, 1993; Lefèvre, Oliver, Hunter, & de Roode, 2010; Simone, Evans, & Spivak, 2009). The mechanisms are also varied, from direct ingestion and topical application to nest fumigation (Gwinner & Berger, 2006; Huffman, 2003; Villalba, Provenza, & Shaw, 2006). Plant use may be prophylactic or curative, and may benefit the individual or its offspring (de Roode, Lefèvre, & Hunter, 2013). For example, monarch butterflies preferentially lay eggs on toxic plants when they are infected by protozoan parasites, which reduces the growth of the parasite in their offspring (Lefèvre et al., 2010, 2012). However, in many cases the mechanisms governing the use of medicinal substances by animals are still poorly known, and it is notably difficult to demonstrate that the contact with the substance is deliberate and primarily aimed at fighting parasites (Clayton & Wolfe, 1993; Gwinner & Berger, 2005; Manson, Otterstatter, & Thomson, 2010; Suárez-Rodríguez, López-Rull, & Garcia, 2013).

In social insects, many defences are collective and contribute to diminish the parasite pressure at the colony level (Cremer,

Armitage, & Schmid-Hempel, 2007; de Roode & Lefèvre, 2012; Wilson-Rich, Spivak, Fefferman, & Starks, 2009). The use of medicinal plant substances has been primarily documented in wood ants and bees (Chapuisat et al., 2007; Christe, Oppliger, Bancala, Castella, & Chapuisat, 2003; Simone-Finstrom & Spivak, 2010). Indeed, wood ants, honeybees and stingless bees collect and incorporate plant resin into their nests (Christe et al., 2003; Duangphakdee, Koeniger, Deowanish, Hepburn, & Wongsiri, 2009; Simone et al., 2009). Owing to its antifungal and antibacterial properties, this resin may protect the colony against multiple pathogens (Banskota, Tezuka, & Kadota, 2001; Chapuisat et al., 2007; Christe et al., 2003; Simone-Finstrom & Spivak, 2010). For example, in the wood ant *Formica paralugubris*, the presence of resin increased the survival of adult workers and larvae exposed to the bacteria *Pseudomonas fluorescens*, as well as the survival of larvae exposed to the fungal pathogen *Metarhizium anisopliae* (Chapuisat et al., 2007). Moreover, in wood ants and honeybees, the presence of resin reduced the microbial load and allowed individuals to downregulate some components of their immune system (Castella, Chapuisat, Moret, & Christe, 2008; Christe et al., 2003; Simone et al., 2009).

The mechanisms governing the use of resin by wood ants remain little known. Field experiments revealed that workers foraging on trails prefer to collect resin over other kinds of nest material, such as twigs and small stones (Castella, Christe, &

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Chapuisat, 2008). The preference for resin was higher in spring and summer than in autumn, raising the hypothesis that resin collection might primarily serve to protect the brood, which is produced at this time of the year (Castella, Christie, et al., 2008).

Laboratory experiments also suggested that the use of resin was prophylactic and constitutive rather than curative and infection-dependent, as the workers did not increase resin collection when their colonies were exposed to *M. anisopliae* (Castella, Christie, et al., 2008). However, the behavioural response may depend on the parasite. For example, honeybee colonies tended to increase resin collection after being challenged with the fungal pathogen *Ascosphaera apis* (Simone-Finstrom & Spivak, 2012). Hence, more fungal pathogens should be tested in wood ants. Moreover, the hypothesis that workers preferentially place the resin close to contaminated brood or contaminated nest areas, compared with uncontaminated ones, has not been tested so far.

Here, we investigated whether the presence of brood and/or of the virulent fungal entomopathogen *Beauveria bassiana* influences the rate of resin collection by wood ant workers, as well as the spatial distribution of resin in the nests. If *F. paralogubris* workers use resin to protect brood, we expected that they would collect more resin when brood was present in their nest, and that they would place the resin close to the brood. If the ants use resin in response to the fungal contamination rather than as a constitutive prophylaxis, we expected workers to increase resin collection after exposure to *B. bassiana*, and to preferentially place resin near contaminated brood or contaminated nest areas.

METHODS

In our experiment, workers collected resin from foraging arenas and placed it in experimental nests (Fig. 1). We sampled

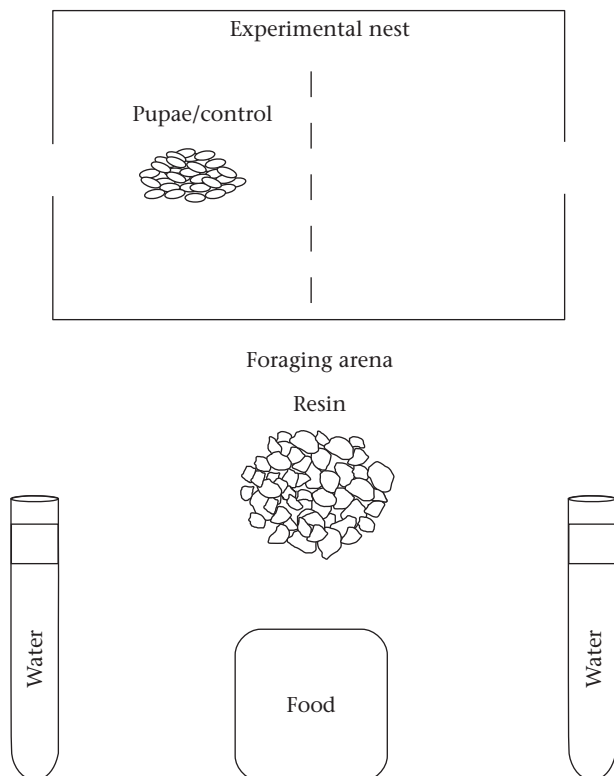


Figure 1. Outline of the experimental set-up. The dashed line indicates the internal separation of the nest material into two compartments. See [Methods](#) for details.

F. paralogubris workers, brood and nest material from 20 field nests in the 'Chalet à Roch' population. The study population is located in sparse spruce forest (*Asplenio – Piceetum*) at an altitude between 1320 and 1420 m in the Swiss Jura mountains (Cherix, 1980). It consists of hundreds of large and highly polygynous nests interconnected by trails and forming a supercolony (Chapuisat, Goudet, & Keller, 1997; Holzer, Chapuisat, Kremer, Finet, & Keller, 2006). The sampled brood consisted of pupae, which are abundant and easy to sample in the upper parts of mounds. Because of their soft cuticles, ant pupae tend to be highly susceptible to fungal entomopathogens (Tragust, Ugelvig, Chapuisat, Heinze, & Cremer, 2013).

In the laboratory, we removed the resin already present in the nest material. We split the samples from each field nest into four experimental nests, assigned to four treatments, in full factorial design: presence or absence of pupae and presence or absence of *B. bassiana*, a virulent generalist fungal entomopathogen (Uma Devi, Padmavathi, Uma Maheswara Rao, Khan, & Mohan, 2008). *Beauveria bassiana* has been reported to successfully infect and kill adult ant workers (Purcell, Brüttsch, & Chapuisat, 2012; Reber & Chapuisat, 2012a) and brood (Broome, Sikorowski, & Norment, 1976; Patterson, Briano, Wildey, & Robinson, 1993).

To monitor the spatial distribution of resin, each experimental nest had two internal compartments, one that received nest material with pupae and/or parasite contamination, while the other received only nest material (Fig. 1). The nest consisted of a dark plastic box (13.8 × 18.3 cm and 6.2 cm high) filled with resin-free nest material up to a height of 1.5–2 cm. The two equal-sized internal compartments were separated by a thin wall of plastic 3.5 cm high that divided nest material but did not reach the top of the box, so that the ants could easily move between compartments inside the nest. Each compartment had a small entrance hole giving way to a foraging arena consisting of a plastic tray (22 × 35 cm and 15 cm high) lined with Fluon to prevent ants from escaping. Each experimental nest received 200 workers.

In the foraging arena, the workers had access to 2.5 g of coniferous tree resin, in the form of approximately 300 grains of resin of various sizes that were previously removed from the nest material. Workers also had ad libitum access to water and standard jelly food (Reber & Chapuisat, 2012b).

For each of the 20 field nests, one of the four experimental nests received one of the four following experimental treatments.

(1) Presence of uncontaminated brood (Brood +, Pathogen –). We placed 100 pupae originating from the same field nest as the workers in one randomly chosen compartment of the nest. The group of pupae had been sprayed with approximately 220 µl of control solution (0.05% sterile Tween 20).

(2) Presence of uncontaminated control items (Brood –, Pathogen –). One of the nest compartments received 100 small plastic pieces similar to pupae in size and shape (approximately 4 mm long and 3 mm wide). These pieces had been sprayed with control solution.

(3) Presence of brood contaminated by the fungal pathogen (Brood +, Pathogen +). One of the nest compartments received 100 pupae that had been sprayed with approximately 220 µl of *B. bassiana* spore solution (4.6×10^7 conidia/ml).

(4) Presence of control items contaminated by the fungal pathogen (Brood –, Pathogen +). One of the nest compartments received 100 small plastic pieces that had been sprayed with *B. bassiana* spore solution.

We checked the content of the experimental nests on a daily basis, recording the position of brood or control plastic pieces. In three cases, the workers transferred all the brood to the opposite compartment towards the end of the experiment. We conservatively kept these nests and their original brood compartment in the analyses. However, we checked that excluding these three nests or

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