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Minor workers have a major role in the maintenance of leafcutter ant pheromone trails

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Ants, especially those species that use pheromone trails for communication and orientation, are dominant in many ecosystems. Trail-using ants form large networks of foraging trails, which require regular updating because of pheromone decay and physical interruptions to continuity. We tested the hypothesis that leafcutter ants, *Atta* spp., possess trail maintenance workers to maintain trail network connectivity. The smallest workers in leafcutter ant colonies (minims) are always present on trails but never engage in leaf transport. Using smoked glass we visualized trails and found that minims deposited pheromone trail with a much higher frequency (83.3%) than nonminims (20%). In the field, minims were observed to perform frequent U-turns on trails. Over the course of 10 min minims made a mean frequency of 18.0 U-turns while walking on the trail, whereas nonminims not engaged in leaf transport made a mean of only 2.02 U-turns. Ants carrying leaves never made U-turns. We investigated the effect of interruptions on trail traffic composition and the subsequent process of trail re-establishment. We simulated trail interruptions with two techniques: scraping away a section of trail and covering trail with soil. We found that the frequency of minims in the interrupted regions of trails increased by 21.0% following both types of interruption treatment. In contrast the frequency of nonminim workers in the interrupted regions declined by 44.8%. In the interrupted regions the proportion of workers represented by minims increased by 118%. Our results show a key role for *Atta* minims in the maintenance of pheromone trails.

Keywords: ant foraging; *Atta*; division of labour; leafcutter; pheromone trail; specialist

Social foraging is widespread and defined as an economic interdependency among individuals in a group (Maynard Smith 1984). The term 'social foraging' is now widely applied to the collective behaviour of even very simple aggregations (Giraldeau & Caraco 2000). Two major stimuli are generally considered to drive the evolution of social foraging: increased foraging efficiency (Murton 1971) and reduction of predation (or parasitism) risk (Hamilton 1971). Recent models suggest that predation avoidance is the main factor in the formation of social aggregations (Reluga & Viscido 2005; Wood & Ackland 2007). Predation avoidance demands vigilance, and individuals with high vigilance could shift the burden of predation to less vigilant group members (Beauchamp 2007). The relative location of individuals in foraging groups will also determine their likelihood of detecting and avoiding predators (Krause & Godin 1996).

In sophisticated insect societies, such as ants, some foraging individuals (or castes) may perform tasks that increase their risk of predation, while others may be specialized in defending groups from predatory attacks. The group, or colony, may benefit from the presence of these more vigilant specialists, especially if they aid in the defence of the less vigilant engaged in other tasks.

Ants are the most abundant social insects (Wilson 1987) and comprise over 20% of total animal biomass (Fittkau & Klinge 1973). They are ecologically dominant in many

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environments mainly because they outcompete their rivals for food. The most abundant ants use pheromone trails to organize their foraging activities when exploring and exploiting their environment (Hölldobler & Wilson 1990). A high reliance on pheromone trails for orientation and communication makes these trails crucial to the success of ant foraging.

Ant trails are often visualized as linear routes from nest to food whereas most ants produce networks of trails to explore their environment. Maintenance of these long-lived trail networks must be of great importance and trail maintenance specialists have recently been discovered in Pharaoh's ants, *Monomorium pharaonis*. These trail-laying specialists make frequent U-turns and mark intensively with trail pheromone as they repeatedly walk along trails (Hart & Jackson 2006). Maintaining trails ensures that disruptions to trail continuity are rapidly repaired, so ants can efficiently orient between the food and the nest.

Physical and temporal specialization of workers characterizes division of labour in ants. Temporal polyethism, where tasks vary with age, is commonplace, but only 15% of ant genera contain polymorphic species (Hölldobler & Wilson 1990). The Pharaoh's ant is a monomorphic species, but trail-laying specialization has also been reported in polymorphic species. Minor workers of the physically dimorphic *Pheidole embolopyx* specialize in laying trail pheromone, but both major and minor workers follow trails during foraging (Wilson & Hölldobler 1985). Major workers never lay trails and are specialized in transporting food. We anticipate that many more polymorphic trail-using species might possess an obvious division of labour between trail users and trail maintainers.

Leafcutter ants have evolved a remarkably sophisticated division of labour that optimizes colony efficiency in bringing leaves back to the nest (Wilson 1980). The most extreme and complex example of polymorphism is found in the castes of *Atta*, where workers (Fig. 1) are physically specialized for tasks in an agricultural production line (Wilson 1980). The largest workers (majors) are soldiers with powerful mandibles suited to defence. Medium-sized workers (media) are the prime foraging caste, bringing back plant material to the nest for processing. The smallest workers (minors or minims) work mainly within the nest where they process leaves, tend fungus gardens, and care for the brood (Oster & Wilson 1978; Wilson 1980). Leafcutter ants organize their foraging activities using pheromone trails (Cherrett 1968). Trails can extend as far as 250 m from the nest (Lugo et al. 1973).

Leafcutter ants live in tropical rain forests, which are highly dynamic environments. Regular interruptions to the continuity of trails are to be expected from deadfall, leaves and the activities of large vertebrates. However, the most frequent trail interruptions will be from heavy rainfall, especially during the rainy season. Lugo et al. (1973) suggested that the *Atta* workers found outside the nest, which never engage in leaf transport, may be involved in trail maintenance. By trail maintenance Lugo et al. (1973) explicitly referred to the physical clearing of debris from trails rather than pheromone deposition. Given the likely frequency of interruptions and the foraging demands of large colonies, trail maintenance should be an important task. Furthermore, we suggest that the task of trail maintenance might be best suited to the smallest workers, minims, because their small size means that they present no impediment to the progress of media and majors walking on trails. In support of this hypothesis we note that minims frequent pheromone trails but never transport leaves (Stradling 1978).

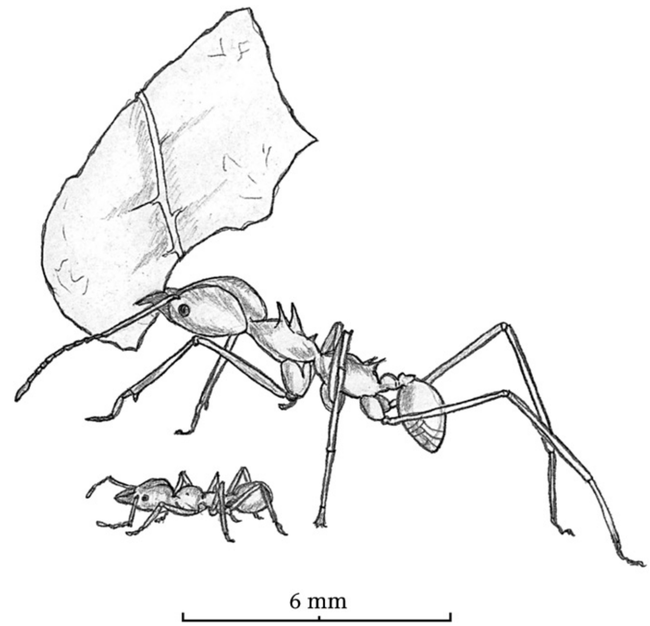

Figure 1. Small minim and large media worker castes of *Atta cephalotes*. The bar measures 6 mm.

The role of minims on pheromone trails is still unresolved. Minims on trails might protect leaf-carrying workers from parasitic phorid flies (Diptera: Phoridae) (Feener & Brown 1993). Orr (1992) showed that phorids prefer to attack larger *Atta cephalotes* foragers (media and majors) on trails, whereas minims frequently repel phorid attacks (Feener & Moss 1990). Minims are known to hitchhike on leaf fragments carried by larger workers, where they might be more exposed to phorid attacks. Feener & Moss (1990) proposed that hitchhiking minims are more vigilant and protect larger workers from phorid attacks and that this is their primary role on trails. One flaw in this hypothesis is that hitchhiking is not widespread. For example, a recent study showed that only 2.1% of ants transporting leaves carried hitchhiking minims, despite minims constituting approximately 10% of the workers on trails (Hughes & Goulson 2001).

We tested the possibility that minims have a specialized role in maintaining pheromone trails. We tested the hypothesis that minims behave like trail-laying specialists found in Pharaoh's ants and make frequent U-turns while marking pheromone trails intensively (Hart & Jackson 2006). *Atta* minims are known to make frequent U-turns on foraging trails (Hughes & Goulson 2001). We further hypothesized that, if the role of minims is that of trail maintenance workers, they should respond to interruptions in trail continuity and ensure that pheromone trails are rapidly re-established. It is too difficult to establish