SHORT COMMUNICATION

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Influence of interspecific competition on the recruitment behavior and liquid food transport in the tramp ant species *Pheidole megacephala*

Abstract This study was conducted on the reactions of *Pheidole megacephala* scouts when finding liquid food sources situated on territories marked by competing dominant ant species or on unmarked, control areas to see if the number of recruited nestmates is affected and if soldiers behave in ways adapted to the situation. We show that scouts recruit more nestmates, particularly soldiers, on marked rather than on unmarked areas. This recruitment allows *P. megacephala* to organize the defence and rapid depletion of these food sources prior to any contact with competitors. Soldiers can carry liquid foods both (1) in their crops like other Myrmicinae and (2), in a new finding concerning myrmicine ants, under their heads and thoraxes like certain poneromorph genera because the droplets adhere through surface tension strengths. Later, the liquids stored in the crop are distributed to nestmates through regurgitations during trophallaxis and the external droplets are distributed through "social buckets", or the mode of liquid food transfer common in poneromorphs. Their flexibility to use or not use the latter technique, based on the situation, corroborates other reports that *Pheidole* soldiers have a relatively large behavioral repertoire.

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Introduction

The division of labour, that gives colonies ecological and reproductive advantages, is accompanied in some 15% of all ant genera by a "worker polymorphism." This corresponds to a worker caste that is greatly variable in body size and shape with certain individuals morphologically specialised to perform a small subset of tasks. In contrast to the majority of ants with weak variations in worker size and shape, the largest workers of highly polymorphic species, called "majors," may be a dozen times the size of the smallest workers or "minors." Also, as opposed to isometry when the body parts grow at the same rate, in adult allometry certain body parts grow at a different rate than others (Hölldobler and Wilson 1990; Tschinkel et al. 2003). For instance, major workers of most allometric species have a disproportionately large head compared to smaller individuals. This is the case for the worker caste of most *Pheidole* species which is dimorphic with no intermediary body size between small minors and the big-headed majors (or soldiers) specialised in colony defence, food storage, seed milling and foraging for large food sources, but also able to perform tasks inside the nest (Sempo and Detrain 2004).

The ecological success of numerous ant species depends on the workers' morphological ability to retrieve large quantities of liquids and to adjust their foraging behavior to the quality and quantity of the resources available (Völk et al. 1999; Mailleux et al. 2000; Davidson et al. 2004). In this context, we hypothesised that the number of nestmates, particularly soldiers, recruited by foraging *Pheidole* scouts depends on (1) whether the food sources are likely to be exploited by competing species or not, and (2) their ability to transport relatively large loads, permitting them to quickly deplete these food sources.

Materials and methods

This study was conducted in Cameroon in the field on four *Pheidole megacephala* Fabricius colonies and in the

laboratory on one colony that we regularly provisioned after having found it naturally installed in the building as frequently occurs for several tramp ant species. This omnivorous species, whose minor workers are approximately 2 mm long and soldiers 3–4 mm long, nests in the ground or in the crevices of trees. Workers prey on invertebrates and small vertebrates, scavenge, harvest seeds, and attend honeydew-producing hemipterans (Campbell 1994; Taylor 2005). Considered to be of Afrotropical origin, *P. megacephala was* dispersed by human commerce throughout the tropical belt where it represents a serious threat to biodiversity (Holway et al. 2002).

During preliminary observations we noted that under natural conditions *P. megacephala* scout workers ventured onto areas abandoned at night by *Oecophylla longinoda* Latreille workers, long after the latter had left these areas, therefore avoiding any encounters. Indeed, both species are dominant and will compete for territory (Taylor 2005) and, although they defend absolute territories, *O. longinoda* colonies occupy peripheral parts of their territory only diurnally, while *P. megacephala* forage nocturnally (Dejean 1990; Hölldobler and Wilson 1990). Note that *O. longinoda* workers deposit clearly visible chemical territorial markers (plus transparent ones) that last for several months (Hölldobler and Wilson 1990; Beugnon and Dejean 1992). Also, under natural conditions *P. megacephala* workers must be able to exploit large quantities of liquid food when they attend certain hemipterans, mostly Auchenorrhyncha, or when they forage for the honeydew that accumulates on leaves situated under unattended hemipterans (Delabie 2001; A.D. personal observation).

We noted that when *P. megacephala* scout workers discovered food sources situated in areas where *O. longinoda* colonies had deposited territorial markers, the proportion of *P. megacephala* soldiers recruited seemed high. Consequently, during this study we tested the influence of *O. longinoda*'s territorial marking on the recruitment behavior of *P. megacephala* when scouts discovered a large liquid food source placed in a "neutral area" (control lot) versus a "marked area" (experimental lot).

For each of the 30 experiments conducted in the field, we placed at the same time one neutral and one marked area on the territory of a *P. megacephala* colony. Each area corresponded to a sheet of A3-type paper with a large drop of honey (0.3 ml) deposited on a plastic disk 2 cm in diameter placed at its centre. Neutral areas consisted of blank sheets whereas marked areas were sheets previously left for 48h on the territory of an *O. longinoda* colony (three colonies were used). Using Student's *t*-test, we compared the total number of individuals (workers plus soldiers) and the percentage of soldiers recruited on neutral versus marked areas 12 min after the scouts discovered the drop of honey.

As we previously noted, *P. megacephala* soldiers sometimes gather honey through surface tension strengths and we compared the occurrences of this behavior on neutral versus marked areas using Fisher's exact-test. In order to determine the weight of the loads transported by minors and soldiers, we used a microbalance (capacity: 3.5 g; readability: 0.001 mg). During other series of experiments we firstly weighed individuals walking toward the drop of honey (10 minors and 10 soldiers weighed individually during five series of experiments), and the same number of individuals returning to their nest with swelled gasters. We compared the mean weight of their loads using Student's *t*-test.

In the laboratory we established a *P. megacephala* colony on the former foraging area of an *O. loginoda* colony, permitting us to observe in detail how the soldiers gather honey and how they transfer their loads to nestmates. We weighed 10 soldiers individually with droplets of honey adhering to the underside of their heads and thoraxes. We then placed each of them into a small plastic box containing approximately 100 workers and larvae starved for 3 days, to which they distributed their honey load (including most of the honey from their crop). As the plastic boxes were numbered, the amount of weight each individual soldier lost was deduced by weighing them again 36 h later. All statistical tests were performed using Statistica 5.0 software.

Note that we did not conduct experiments when *O. longinoda* workers were present on *P. megacephala* territory as they immediately monopolize the food sources and attack any intruder, including *P. megacephala* scouts that in turn do not recruit nestmates. Nevertheless, in the field *P. megacephala* is able to repel larger competitors such as *Crematogaster africana* Mayr (Taylor 2005).
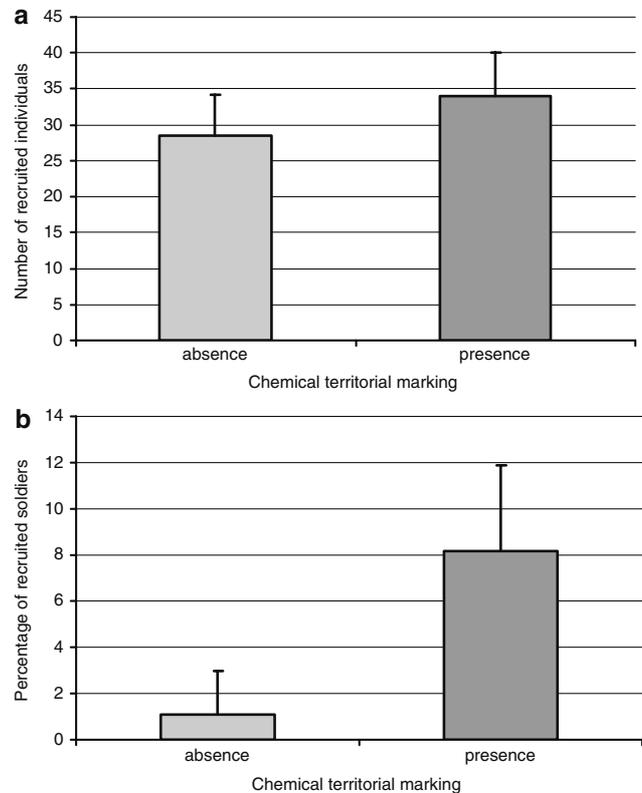

Fig. 1 Response of *Pheidole megacephala* to drops of honey on the basis of the presence versus absence of *Oecophylla* chemical territorial marking ($N=30$ in each case). (**a**) Mean number ($\pm$SD) of recruited individuals (both workers and soldiers). (**b**) Percentage of soldiers. The number of recruited nestmates was significantly higher on marked than on neutral areas. The same was true for the percentage of soldiers

Fig. 2 **a** Recruited *Pheidole megacephala* individuals, including a soldier, imbibing honey. **b** A soldier carrying a supernumerary droplet of honey that adheres under its head and thorax through surface tension strengths. **c** "Social bucket" between a soldier loaded with an external droplet of honey and soliciting minor workers that directly imbibe the honey. Note that the soldier extends its forelegs to give soliciting minor workers better access to the droplet of honey
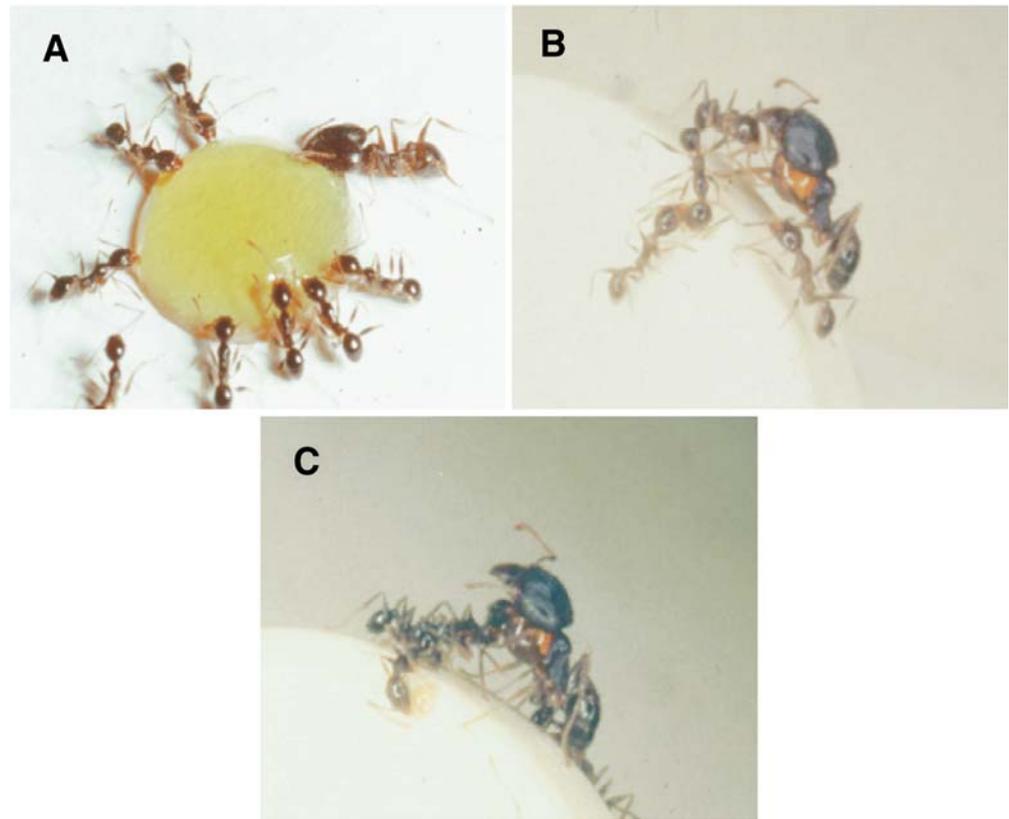
Results

In the field experiments, the *P. megacephala* scouts that discovered the drops of honey first filled their crops before returning to their nests. The number of nestmates that they then recruited was significantly higher on marked territories than on neutral areas (Fig.1a; mean ± SD; 28.53±5.67 vs. 33.97±6.14; $t=3.56$; 58 df; $P<0.001$). The same was true for the percentage of soldiers recruited (Fig.1b; 1.07±1.89 vs. 8.16±3.70; $t=9.34$; 58 df; $P<0.001$). Minor workers imbibed the honey, filling their crops, or patrolled around the drop of honey, as did certain soldiers (probably to defend the food source against potential intruders). Many soldiers also filled their crops and then collected a supernumerary, external droplet by repeatedly (up to four times) dipping their heads and thoraxes in the honey, until a droplet formed and adhered through surface tension strengths (Fig. 2). On 21 out of 30 marked areas at least one soldier gathered honey in this way, something that was noted only twice on neutral areas (Fisher's exact test: $P<0.01$). During the experiments conducted in the laboratory on a large *O. longinoda* territory, this behavior was noted in 27% of the recruited soldiers ($N=74$): 4% gathered honey only under their heads, while the other 23% gathered honey under both their heads and thoraxes. Sometimes the soldiers retreated a short distance (approximately 5 mm) while their heads dipped in the drop of honey, leaving a trail of honey on the substrate that permitted more individuals access to this food source.

The weight of the honey transported by minor workers was significantly lower than that transported by soldiers in their crops (mean ± SE: 0.08±0.01 mg vs. 0.26±0.02 mg; $t=8.61$; 8 df; $P<0.001$). Soldiers bearing external droplets of honey carried a total load of up to 1.88 mg, often more than their own body weight (average 1.65 mg). This load (1.12±0.01 mg as a mean) corresponds to the weight of the honey imbibed and stocked in the crop plus that of the external droplet. Although the load carried in the crop can vary with different factors (however we conducted the experiments during the same time period, using the same liquid food source), we can estimate that the weight of the external droplets varies between approximately 0.8 and 0.9 mg (1.12 − 0.26 mg = 0.86 mg). After returning to their nests, these soldiers were solicited by starved workers that first licked the external droplet (see "social bucket' in Hölldobler and Wilson 1990), and then triggered a typical trophallactic exchange.

Discussion

We noted in this study that *Oecophylla* territorial marking, that is also recognized by and deter herbivores (Offenberg et al. 2004), can modify the recruitment behavior of *P. megacephala*. The ability of the recruited *P. megacephala* soldiers to use surface tension strengths to retrieve large quantities of sugary liquids is advantageous because high sugar concentration limits the quantity of liquid food transported in the crop (Josens et al. 1998) and

honeydew that accumulates under unattended hemipterans becomes viscous. As a result, *P. megacephala* scouts can respond quickly to the territorial marking of competing species by recruiting more individuals, including more soldiers, which are able to retrieve larger liquid quantities despite the high sugar concentration.

The transportation of liquid food through surface tension strengths is known in several poneromorph genera for which, with a few exceptions, the musculature and the morphology of the proventiculus that regulates food flow from the crop to the midgut (where digestion occurs) does not permit the regurgitations necessary for trophallactic exchanges (Eisner 1957; Hölldobler 1985; Hölldobler and Wilson 1990). As a consequence, many arboreal poneromorphs use their mandibles to gather liquids to which they adhere through surface tension strengths, while *Platythyrea conradti* workers carry nectar under their heads and thoraxes (Dejean and Suzzoni 1997). To compensate for their inability to perform true trophallaxis, arboreal poneromorph ants employ an elementary technique used for liquid food transmission known as the "social bucket" where soliciting individuals directly imbibe the externally transported liquids (Hölldobler 1985; Hölldobler and Wilson 1990).

Like *Platythyrea* (Dejean and Suzzoni 1997), neither the underside of the head nor the thorax of *P. megacephala* soldiers bear structures particularly adapted to liquid transport, so that the transportation of liquids though surface tension strengths corresponds to a behavioral adaptation.

In conclusion, *P. megacephala* soldiers have the ability to employ the modes of liquid transport of both phylogenetically advanced subfamilies of ants (filling their crops and performing trophallaxis) and by less closely related poneromorph genera (Bolton 2003) (using surface tension strengths and the "social bucket"). Their flexibility to use or not use the latter technique, based on the situation, corroborates other reports that *Pheidole* soldiers have a relatively large behavioral repertoire (Sempo and Detrain 2004) and their ability to rapidly gather and transport large loads of liquid food gives them a certain edge in interspecific competition among arboreal ants (see Davidson et al. 2004).

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