

Research article

## Crowding increases foraging efficiency in the leaf-cutting ant *Atta colombica*

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**Abstract.** Many animals, including humans, organize their foraging activity along well-defined trails. Because trails are cleared of obstacles, they minimize energy expenditure and allow fast travel. In social insects such as ants, trails might also promote social contacts and allow the exchange of information between workers about the characteristics of the food. When the trail traffic is heavy, however, traffic congestion occurs and the benefits of increased social contacts for the colony can be offset by a decrease of the locomotory rate of individuals.

Using a small laboratory colony of the leaf-cutting ant *Atta colombica* cutting a mix of leaves and Parafilm, we compared how foraging changed when the width of the bridge between the nest and their foraging area changed. We found that the rate of ants crossing a 5 cm wide bridge was more than twice as great as the rate crossing a 0.5 cm bridge, but the rate of foragers returning with loads was less than half as great. Thus, with the wide bridge, the ants had about six times lower efficiency (loads returned per forager crossing the bridge). We conclude that crowding actually increased foraging efficiency, possibly because of increased communication between laden foragers returning to the nest and out-going ants.

**Keywords:** Leaf-cutting ants, foraging, social facilitation, trail traffic, recruitment.

### Introduction

In many species, including humans (Helbing et al., 1997) foraging activity is organized along physically well-defined lanes or trails, that present a relatively smooth surface and are cleared of obstacles. Individuals may

move more rapidly along these trails than on unmanipulated terrain (Soulé and Goldman, 1972; Brannan, 1992). In ants, for example, it has been shown that the use of trails can significantly increase worker locomotory rates (Shepherd, 1982; Rockwood and Hubbell, 1987; Fewell, 1988; Howard, 2001).

The use of trunk-trails is a widespread feature of ant species and its benefit in terms of foraging efficiency is well documented (see review by Shepherd, 1982; Hölldobler and Wilson, 1990; Franks, 2001; Anderson and Mcshea, 2001). In mass-recruiting ants however, the traffic on the trails can reach very high volume. Traffic congestion can occur and, as a consequence, the overall flow of workers on the trails can dwindle (Burd et al., 2002). To avoid overcrowding, some ants organize the traffic spatially, by forming distinct lanes of outbound and nestbound workers (army ants: Couzin and Franks, 2003), or temporally, by desynchronizing the flow of outbound and nestbound workers (*Lasius niger*: Dussutour et al., 2005). The leaf-cutting ant *Atta cephalotes* does not seem to possess any regulatory mechanisms to prevent overcrowding (Burd and Aranwela, 2003). In this species, the flows of outbound and nestbound foragers are intermingled (Burd et al., 2002). Overcrowding increases the rate of head-on encounters between workers moving in opposite directions and decreases the overall flow (Burd et al., 2002; Burd and Aranwela, 2003). Ants of the genus *Atta* build and maintain foraging trails which may extend 100 m or more in length (Shepherd, 1985; Wirth and al., 2003), and so the decrease of the flow over the whole length of the trail may considerably reduce the overall foraging efficiency of the colony. One hypothesis suggested by Burd and Aranwela (2003) is that an increase in the rate of information exchange and/or leaf fragment transfer could compensate for the reduction in

foraging efficiency. It has indeed been demonstrated in several species of ants that outbound and nestbound workers laden with food exchange information about the characteristics of the food when they meet on foraging trails (Roces, 1990; 1993; Gordon, 1991; Roces and Núñez, 1993; Van Breda and Stradling, 1994; Howard et al., 1996; Le Breton and Fourcassié, 2004). Moreover, there is indirect evidence that simple and brief encounters among workers, whether or not they are transporting food, can have an important role in regulating task allocation (Gordon, 1999; 2002; Gordon and Mehdiabadi, 1999). In leaf-cutting ants, one could therefore hypothesize that outbound workers encountering nestbound laden ants could be stimulated to engage in the cutting and transport of leaf fragments. The higher rate of contact experienced in crowded conditions would then result in a higher number of workers engaging in the cutting and transport of leaf fragments to the nest, which could compensate for the overall decrease in traffic flow due to the high rate of head-on encounters (Burd and Aranwela, 2003).

In this paper we examine the foraging efficiency in the leaf-cutting ant *Atta colombica* when traffic congestion occurs along a trail. We carried out a series of laboratory experiments with two bridges of different width placed between the ant nest and a food source. We counted the number of loaded workers returning to the nest and measured their load size, when tested with a narrow or a wide bridge. Based on the behaviours measured at the individual level (head-on encounters), we then proposed four hypotheses that could account for the results we obtained at the collective level.

## Materials and methods

### *Species studied and rearing condition*

We worked with the leaf-cutting ant *Atta colombica*, a species that uses mass recruitment through scent trails to exploit abundant food sources (Wirth et al., 2003). In this species, small colonies less than one year old have  $10^3$ – $10^4$  workers whereas established colonies can contain up to  $10^5$ – $10^6$  workers (Hart and Ratnieks, 2001). We used an experimental colony which consisted of one queen, brood, about 20,000 workers, and approximately 18,000 cm<sup>3</sup> of fungus in four clear plastic nest boxes (W x L x H : 12 x 23 x 10 cm). The nest boxes were kept in a plastic tray (W x L x H : 40 x 60 x 15 cm) whose walls were coated with Fluon® to prevent ants from escaping. The nests were regularly moistened and the colony was kept at room temperature ( $30 \pm 1^\circ\text{C}$ ) with a 12:12 L/D photoperiod. We supplied the colony with leaves of *Malus coccinella* four times a day (8:00 a.m., 12:00 a.m., 4:00 p.m. and 8:00 p.m.). The leaves were placed in a plastic tray (W x L x H : 40 x 60 x 15 cm) which was used as a foraging area and was linked to the colony by a plastic bridge 300 cm long and 5 cm wide. The bridge length we used is consistent with the foraging distance measured for small colonies in the field (Kost et al., 2005).

In the experiments this bridge was removed and replaced by a new unmarked bridge of the same width (5.0 cm: wide bridge) or of a reduced width (0.5 cm: narrow bridge).

### *Experimental procedure*

Because the removal of the marked bridge and its replacement by a new unmarked bridge was generally followed by a sharp decrease in ant traffic, a period of 24 hours was allowed before starting an experiment and measuring the effect of bridge change on the characteristics of the traffic. One hour and a half before the start of an experiment, the colony was deprived of foraging material by removal of all leaves remaining in the foraging area. Foraging material was placed again in the foraging area at the start of the experiment. This material consisted of 32 pieces of 6 x 6 cm Parafilm® film and 32 leaves of *Malus coccinella* (generally 6 x 4 cm). The size of the fragments cut by leaf-cutting ants is known to be influenced by the physical and chemical properties of the leaves they collect (see e.g. Burd, 1995). Using Parafilm® thus allowed us to work with homogeneous material (Roces and Núñez, 1993; Van Breda and Stradling, 1994). The pieces of Parafilm® that were used had previously been soaked for 24 hours in a solution of apple juice (900cl) and 70° alcohol (100cl) in which 30 *Malus coccinella* leaves had been crushed. We offered *M. coccinella* leaves to the ants during the experiments because foraging activity was poorly stimulated by the pieces of Parafilm®. This also prevented too high an accumulation of Parafilm® fragments on the fungus.

To minimize crowding effects on the foraging material, the pieces of Parafilm® and the leaves, rather than being placed directly on the ground, were hung from the branches of 16 artificial trees (2 leaves and 2 pieces of Parafilm® on each tree).

Twelve replicates of the experiment were achieved with each type of bridge (wide bridge – and narrow bridge). In all replicates the traffic on the bridge was filmed from above and at the center of the bridge for 60 minutes with a SONY Digital Handycam DCR VX 2000E camera.

### *Data collection*

#### *Effects of bridge width on the flow of laden ants*

To measure foraging efficiency, we counted, for each interval of one minute of each replicate, the number of laden (with a leaf fragment or a piece of Parafilm®) and unladen ants traveling in both directions across a marked point in the middle of the bridge. This measure gives us the flow of ants per minute crossing the bridge. Counting began when the first laden ant reached the nest. We used a two-way ANOVA with repeated measures on time to test for the effect of bridge width and time interval on the total flow of workers (laden or unladen) and on the flow of laden workers only.

#### *Effects of bridge width on the size distribution of unladen and laden ants*

In leaf-cutting ants of the genus *Atta*, the tasks performed by the workers on the trails are strongly correlated with their size (Wilson, 1980; Stradling, 1978). In order to investigate whether in our experiments forager size distribution on the trails was affected by bridge width, we collected a sample of unladen ants on a single replicate for each bridge ( $N= 263$  and  $N= 366$  for the wide and narrow bridge, respectively). These ants were randomly collected within an interval of 5 min, starting 30 min after the beginning of the replicate.

During the whole duration of each replicate we also collected a sample of approximately 30 ants loaded with a fragment of Parafilm®, as soon as they had travelled 2 cm onto the bridge from the foraging area. Over all replicates, a total of 361 and 380 laden ants were collected for the wide and narrow bridge, respectively. Leaf-cutting ants often pick up leaf fragments that are either dropped on the ground by other ants (Anderson and Jadin, 2001; Hart and Ratnieks, 2001) or directly transferred from one individual to the other (Fowler and Robinson, 1979; Hubbell et al., 1980; Anderson and Jadin, 2001). Therefore, to ensure that the fragments had been cut by the workers we collected, the ants were followed from the moment they had completed their cut in the foraging area.

The maximal head width of unladen and laden ants was then measured to the nearest 0.05 mm under a dissecting microscope equipped with an ocular micrometer (Wilson, 1980; Feener et al., 1988). We used a Kolmogorov-Smirnov test to compare the ant size

distribution between the two types of bridges for each category of ants (laden and unladen).

#### Effects of bridge width on load size

The Parafilm® fragment carried by each laden ant collected was placed in an individual Eppendorf® and stored at 4°C. Its area was then measured from digitized images obtained by scanning it at 75dpi, allowing a resolution of approximately 0.1 mm<sup>2</sup>.

We used a multiple regression analysis to study the effect of bridge width and head width on the size of the Parafilm® fragments collected. For the purpose of the analysis, head width was centered on its mean (i.e. the mean value was subtracted from each observation) and bridge widths were coded as scalar numbers centered on zero. This procedure is recommended because it reduces the covariation between linear variables and their interaction terms (Aiken and West, 1991). The equation of the model was the following:

Fragment area = Constant +  $b_1$  head width +  $b_2$  bridge width +  $b_3$  (interaction between head width and bridge width).

#### Effects of bridge width on interaction rate

For the two types of bridges we counted the number of encounters occurring per ant for a sample of 60 laden and 60 unladen ants traveling to the nest on a 20 cm section at the centre of the bridge. An encounter was considered each time an ant passes another one in the opposite direction, whether a physical contact occurred or not between the ants. Encounters with or without physical contact were distinguished. A contact was always the result of a head-on collision. The probability of being contacted during an interaction was estimated by regressing the number of encounters with physical contact on the total number of encounters with or without contact. Our objective was to assess specifically the probability for an outbound ant to contact a laden ant returning to the nest. However, because the traffic of laden ants on the bridge was relatively low, we found it more suitable to consider nestbound instead of outbound ants. As the traffic on the bridge had already reached a steady state when we began counting, the outbound and nestbound flows of workers were approximately equal. In this condition, the probability for an outbound (hence unladen) ant to contact a nestbound laden (or unladen) ant was the same as that of a nestbound laden (or unladen) ant to contact an outbound ant. We also noted at the midpoint of the experiment the duration of 100 contacts between two unladen ants and 100 contacts between a laden and an unladen ant for each type of bridge.

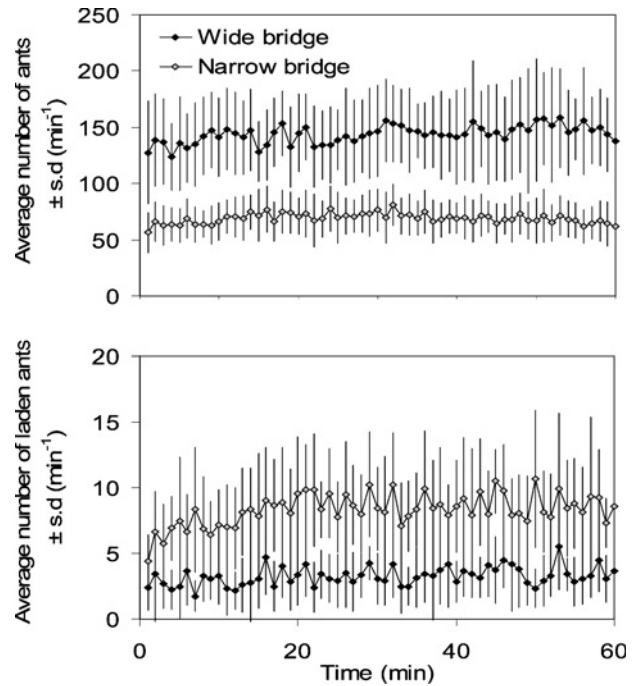
We used a multiple regression analysis to investigate the effect of bridge type and load carriage on the probability of being physically contacted during an encounter. For the purpose of the analysis the number of encounters was centered on its mean and bridge width and ant category were coded as scalar numbers centered on zero (Aiken and West, 1991).

## Results

#### Effects of bridge width on the flow of laden ants

As would be expected, the total flow of ants was significantly higher on the wide bridge than on the narrow bridge (Fig. 1a, two-way ANOVA with repeated measures on time interval: width effect,  $F_{(1, 22)} = 72.44$ ,  $P < 0.001$ ). On the other hand, the flow of laden ants was twice as high on the narrow bridge as on the wide bridge (Fig. 1b,  $F_{(1, 22)} = 95.99$ ,  $P < 0.001$ ). The rate of food return to the nest was thus notably higher on the narrow bridge than on the wide bridge. There was a fivefold increase in foraging efficiency between the wide bridge and the narrow bridge (the percentage of laden workers returning

to the nest per minute represented respectively  $4.3\% \pm \text{SD } 0.8$  and  $\sim 23.1\% \pm \text{SD } 2.9$  on the wide and narrow bridge).



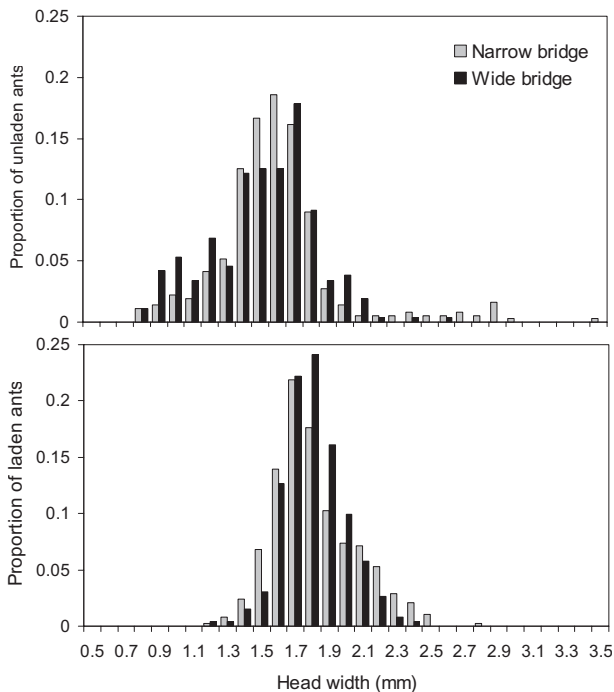
**Figure 1.** Average number of laden and unladen ants (a) and laden ants only (b) per minute crossing the wide or the narrow bridge in both directions every minute.  $N = 12$  replicates of the experiment for each bridge.

The recruitment dynamics were not influenced by bridge width (ANOVA, interaction of bridge width x time:  $F_{(59, 22)} = 0.99$ ,  $P = 0.491$  and  $F_{(59, 22)} = 0.99$ ,  $P = 0.487$  for the total flow of ants and the flow of laden ants, respectively). The total flow of ants remained stable for both bridges during the whole duration of the experiments (ANOVA, time effect:  $F_{(59, 22)} = 1.41$ ,  $P = 0.201$ ), whereas the flow of laden ants on the narrow bridge slightly increased during the first 20 min of the experiments (ANOVA, time effect:  $F_{(59, 22)} = 2.14$ ,  $P = 0.014$ ).

#### Effects of bridge width on the size distributions of unladen and laden ants

There was a weak significant difference between the size distribution of unladen ants on the two bridges (Fig. 2a; median headwidth: 1.50 and 1.54 mm for the wide and narrow bridge, respectively;  $Z = 1.438$ ,  $P = 0.032$ ). The difference was mainly due to an excess of workers with a headwidth larger than 2.2 mm on the narrow bridge. On the other hand, the size distribution of laden ants did not differ significantly between the two bridges (Fig. 2b; median headwidth: 1.74 mm for both wide and narrow bridge;  $Z = 1.249$ ,  $P = 0.088$ ). Finally, on both bridges,

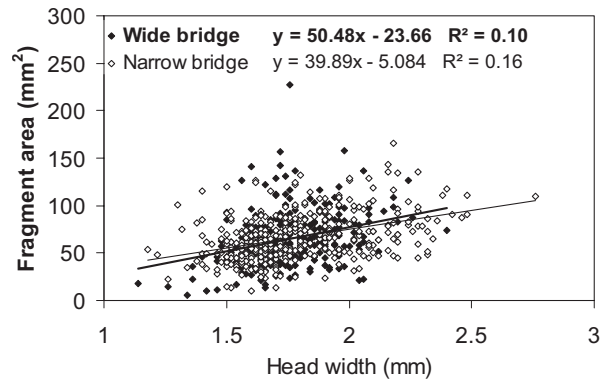
laden ants were on average bigger than unladen ones ( $Z = 5.298$ ,  $P < 0.001$  and  $Z = 5.628$ ,  $P < 0.001$ , for the wide and narrow bridge respectively). This latter result is consistent with the findings of previous studies on division of labour in ants of the genus *Atta* (Wilson, 1980).



**Figure 2.** Head width frequency distribution for a) unladen ( $N = 361$  and  $N = 380$  for the wide and narrow bridge, respectively) and b) laden ants ( $N = 263$  and  $N = 366$  for the wide and narrow bridge, respectively).

#### Effects of bridge width on load size

The interaction between headwidth and bridge width was not significant ( $b_3 = 5.29$ ,  $t_{(737)} = 1.07$ ,  $P = 0.284$ ). Therefore, following Engqvist's (2005) recommendation, we subsequently removed it from the multiple regression model. Head width and fragment area were positively correlated for the two types of bridges ( $b_1 = 42.74$ ,  $t_{(738)} = 9.75$ ,  $P < 0.001$ ), i.e. bigger ants tended to cut larger fragments. Moreover, bridge width did not have any effect on the size of the Parafilm® fragments cut and transported by foragers of the same size ( $b_2 = 0.07$ ,  $t_{(738)} = 0.07$ ,  $P = 0.941$ ). The relationship between Parafilm® fragment size and maximal headwidth in our study is comparable to that found with leaf fragments by other authors (Shutler and Mullie, 1991; Burd, 1996a). Therefore, one can assume that ants were not disturbed by the artificial texture of the Parafilm®.



**Figure 3.** Relationship between head width and fragment area. ( $N = 361$  and  $N = 380$  for the wide and narrow bridge, respectively).

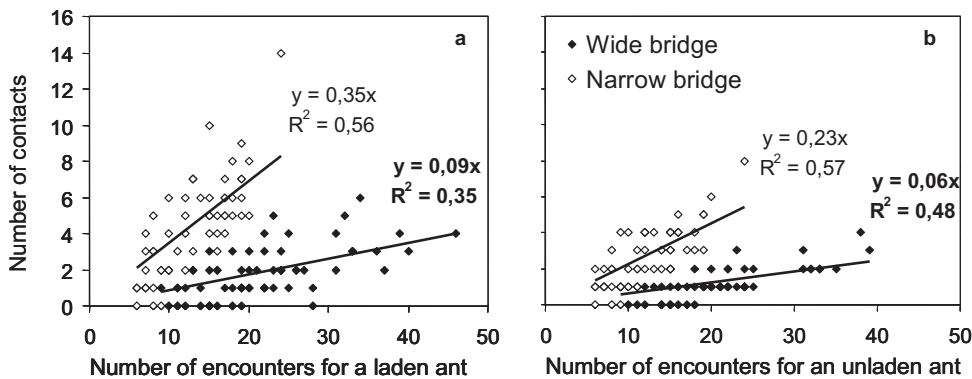
#### Effects of bridge width on interaction rate

The model investigating the effect of bridge width and load carriage on the probability of being physically contacted during an encounter was significant (Table 1 and Fig. 4; ANOVA for the whole model:  $F_{7,239} = 73.915$ ,  $P < 0.001$ ) and accounted for 69% of the variance. The model indicates a significant effect of the number of encounters, of bridge width and ant category (laden or unladen), as well as of all interaction terms between the variables considered (Table 1). Examination of the standardized regression coefficients shows that the main effect on the number of contacts was due to bridge width, followed by number of encounters and by ant category (Table 1).

The slopes of the four regression lines represented in Fig. 4 give the probability of contacting another ant during an encounter. This probability was significantly higher for the narrow bridge than for the wide bridge, whatever the ant category (Table 1: interaction between bridge width and number of encounters). Moreover, the probability of contacting another ant was significantly higher for laden than for unladen ants, whatever the bridge width (Table 1: interaction between ant category and number of encounters). Finally, for the same number of encounters and whatever the bridge width, laden ants had a higher probability of being contacted than unladen ants (Table 1: interaction between ant category and bridge width). Consequently, an ant coming from the nest and going to the food source had a probability about four times higher of contacting one or more laden ants on a narrow bridge than on a wide bridge (mean  $\pm$  CI<sub>0.95</sub>:  $0.35 \pm 0.03$  vs.  $0.09 \pm 0.01$ , respectively) and a laden ant contacted a significantly higher number of ants on the narrow bridge than on the wide bridge. Our results show in addition that the duration of contact between an outbound and a nestbound laden ant was significantly higher on a narrow bridge than on a wide bridge (mean  $\pm$  SD:  $0.62 \pm 0.24$  and  $0.41 \pm 0.25$  s, respectively, Student  $t$  test:  $t = 6.05$ ,  $df = 198$ ,  $P < 0.001$ ) whereas it was the same between an outbound and a nestbound unladen ant (mean  $\pm$  SD:  $0.16 \pm 0.08$  and  $0.15 \pm 0.07$  s, for the narrow

**Table 1.** Multiple regression analysis testing the relationship between the number of encounters with physical contact and the number of encounters with or without physical contact across bridge width and ant category (laden or unladen).

| Independent variables                              | Unstandardised regression coefficients <i>b</i> | Standard regression coefficients $\beta$ | <i>t</i> | Signification |
|--|---|--|----------|---------------|
| Constant   | 3.10  |  | 30.38    | $P < 0.001$   |
| Bridge width                                       | -2.02   | -0.96                                    | -19.82   | $P < 0.001$   |
| Ant category                                       | 0.63  | 0.30                                     | 6.19     | $P < 0.001$   |
| Number of encounters                               | 0.24  | 0.87                                     | 16.48    | $P < 0.001$   |
| Bridge width * Number of encounters                | -0.14   | -0.41                                    | -9.68    | $P < 0.001$   |
| Ant category * Number of encounters                | 0.04  | 0.16                                     | 3.06     | $P = 0.002$   |
| Ant category * Bridge width                        | -0.40   | -0.19                                    | -3.95    | $P < 0.001$   |
| Ant category * Bridge width * Number of encounters | -0.04   | -0.13                                    | -2.48    | $P < 0.014$   |

**Figure 4.** Relationship between the number of encounters with physical contact and the total number of encounters per ant for a) laden b) unladen ants. The slope of the lines corresponds to the probability for an ant traveling on the bridge to be contacted by another ant during an encounter. ( $N = 60$  for each category of ants and each bridge).

and the wide bridge, respectively, Student *t* test :  $t = 0.951$ ,  $df = 198$ ,  $P = 0.343$ ). This difference might be explained by a greater difficulty of outbound ants in avoiding nest-bound laden ants on the narrow bridge.

## Discussion

A striking result from this study was that the foraging efficiency of the colony increased when the bridge was narrow. The number of fragments brought back to the nest per unit time was twice as large on a narrow bridge as on a wide bridge. This was true even though, as expected, bridge width strongly affected the traffic of workers: ant flow was higher on a wide bridge than on a narrow bridge.

What are the factors that could stimulate workers to cut more fragments, thus leading to an increase of the foraging efficiency under crowded condition?

First, crowding at the foraging area caused by the higher volume of traffic could explain the apparent decrease in efficiency when the wide bridge was present. In fact, in our experiment twice as many ants reached the foraging area per unit of time when the wide bridge was present. Crowding could prevent some of the ants from approaching and cutting leaf and Parafilm® fragments

(Burd, 1996b). Also, at high density ants engaged in cutting may hinder one another. To check this, we carried out an additional replicate with the wide bridge in which just one piece of Parafilm® or one leaf, instead of four as in the standard condition, was hung on each of the 16 artificial trees. If this "impoverished" condition induced crowding, then fewer fragments should have been brought back to the nest. However, there was no difference in the return rate of fragments (one-sample *t* test,  $t = 0.81$ ,  $df = 11$ ,  $P = 0.434$ ,  $181.00$  vs.  $195.00 \pm SD 17.63$  fragments, in the impoverished and standard conditions, respectively).

Second, a greater rate of leaf transport, without necessarily an increase in the rate of leaf cutting, could be achieved by a process of task partitioning through direct or indirect leaf transfer (Anderson and Jadin, 2001; Hart and Ratnieks, 2001). However, we never observed the formation of caches or the transfer of fragments between ants in our experiments.

Third, the higher number of workers cutting and transporting leaves on the narrow bridge might be due to the selective recruitment of individual workers predisposed to leaf cutting. This hypothesis therefore predicts that with the narrow bridge, the worker size classes that participate in leaf cutting would be over-represented.

However, the size distribution of laden ants was not affected by bridge width, and the difference in the size distribution of unladen ants was due mainly to an excess of large-sized ants, which rarely cut or transport leaves (Wilson, 1980), on the narrow bridge.

Fourth, one factor that may vary with the density of ants on the bridge is the concentration of the trail pheromone. Although the width of the narrow bridge we used was the tenth of that of the large bridge, it supported half its volume of traffic. Therefore one could expect the concentration of trail pheromone per unit width to be five times higher. A positive relationship between the concentration of the trail pheromone and the number of recruited ants has been shown in several species of mass-recruiting ants (see e.g. : *Linepithema humile* Van Vorhis Key and Baker, 1981; *Monomorium minimum* Adams and Traniello, 1981; *Atta sexdens* Billen et al., 1992). If the concentration of the trail pheromone had been higher on the narrow bridge however, we should have observed a higher number of recruited ants on that bridge. Yet, in our experiment the number of recruited ants was lower on the narrow bridge than on the large bridge. This is probably explained by the fact that the flow we observed might correspond to the maximum capacity of the narrow bridge (mean density ants.cm<sup>-2</sup> ±SD : 1.7±0.79 and 0.25±0.06 for the narrow bridge and the wide bridge, respectively, N=120 for each bridge). A higher concentration of pheromone trail may also stimulate recruited ants to collect and retrieve food back to the nest, which would explain our results on the narrow bridge. This reasoning holds only if the trail-laying behaviour of the workers is not affected by their density. As suggested by Jaffé and Howse (1979), ants may well be able to regulate their recruiting activity along a trail according to the density of workers on that trail. In that case, a narrower trail would not necessarily mean a more concentrated pheromone. As can be seen, this question requires further investigation.

The scenario we proposed to explain our result is that information could be transferred through head on encounters between outbound and nestbound workers on the narrow bridge. Following such an encounter outbound ants would become more likely to cut and transport leaves once they reached the foraging area. What matters here is most likely the rate of contact with nestbound laden workers rather than that with nestbound unladen workers. In fact, whereas the rate of contact with nestbound unladen workers was approximately the same between the two bridge conditions (the outbound flow and the probability of contacting unladen returning foragers were in inverse proportion and thus compensated each other between the two conditions), the rate of contacts with laden nestbound workers was four times higher on the narrow bridge than on the wide bridge. Moreover, the duration of these contacts was also significantly prolonged. This means that the narrow bridge induced a greater number of contacts with laden workers, and we suggest that outbound workers could be

more stimulated to cut and transport leaf fragments due to this higher rate of contact. Contacts with laden workers could be a cue that guides the decisions of outbound foragers with respect to leaf cutting and transport. Moreover contacts among workers on foraging trails in our experiments were not simply accidents and were not completely random. Indeed, unladen returning ants avoided outbound foragers whereas laden ants never attempted to do so (Dussutour, 2004), possibly because their loads hindered their capacity to maneuver (Zollikofer, 1994). Thus, the responses of ants to oncoming traffic may facilitate information transfer among the foragers.

Encounters between outbound and nestbound laden workers are known to play an important role in the transfer of information about the type and quality of the food being exploited by leaf-cutting ants (Roces, 1990, 1993; Howard et al., 1996). These encounters almost always involve multiple antennal contacts by outbound workers of the leaf fragments carried by nestbound workers. Our hypothesis is that this information may affect individual decisions to cut leaves as well. Ants may have different response thresholds to leaf material and respond to the rate of contacts according to this level. On a wide trail, at low density, only ants characterized by a low response threshold may cut and transport leaf fragments. At high density, however, the rate of contacts with laden nestmates increases and ants with a high response threshold may also start cutting when they enter in contact with the leaves at the end of the trail. Multiple contacts with the food could influence positively the level of central excitation of the ants and, consequently, their behavioral response when reaching the foraging area (see e.g. in locusts and flies: Simpson and Bernays, 1983). Such a system could be used by a colony to modulate its rate of leaf retrieval. Modulation of individual decisions to cut leaves could also be part of a system of task allocation that operates on the foraging trails, far from the nest. This mechanism could be used to balance leaf cutting against other tasks, e.g. exploring for other food patches. Making such adjustments out on the trail, near to the actual sites of leaf cutting, would be far more efficient than waiting for workers to travel to and from the nest. If a higher rate of encounters leads to a higher probability of leaf cutting, a lower rate of encounters with laden nestmates could equally well lead to a lower probability of leaf cutting. These responses could allow colonies to rapidly track the availability of leaves and to efficiently exploit leaf sources, for example different branches of the same tree as it is gradually defoliated. This mechanism could operate together with trail pheromone, but could conceivably allow more rapid and flexible decisions.

A question remains: why are there so many unladen ants and what could be their function? A lot of hypotheses have been put forward but most of them remain speculative and have not been directly tested. In *A. colombica* Howard (2001) has clearly demonstrated that 5% of these ants are engaged in trail clearing. This

leaves however 95 % of ants whose exact function remain to be determined.

We found a significant response of the leaf-cutting ant colony to a small change in foraging conditions. The collective response of the ants on the narrow bridge went well beyond the compensation of the overall flow reduction. This suggests that leaf-cutting ants have the ability to regulate several components of foraging based on simple, local cues, without reference to any central integration of information or control mechanism. Our result suggests that the trail widths observed under field condition could be adjusted to optimize the net benefit of the trail, given the traffic demand, cost of clearing, and effect of traffic density on contact rates and information exchange. Making foraging trails that are wider than optimal not only could be more costly for an *Atta* colony, but also could result in lower foraging efficiency.

The significance of contacts between outgoing and incoming workers in leaf-cutting ants is not yet clear, but the high frequency of such contacts on trails clearly represents a mechanism by which information may potentially be exchanged and foragers allocated among the different food sources that are being exploited. Our work shows that increased knowledge of the relationship between the nature and frequency of worker interactions along the trails and the short term decisions they made, as well as of the impact of these decisions on colony foraging efficiency, will certainly repay further studies on social facilitation systems in ants.

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## References

- Adams E.S. and Traniello J.F.A. 1981. Chemical interference competition by *Monomorium minimum* (Hymenoptera: Formicidae). *Oecologia* **51**: 265 – 270
- Aiken L.S. and West S.G. 1991. *Multiple Regression: Testing and Interpreting Interactions*. Newbury Park, London, New Delhi: Sage Publications. 211 pp
- Anderson C. and Jadin J.L.V. 2001. The adaptive benefit of leaf transfer in *Atta colombica*. *Insect. Soc.* **48**: 404 – 405
- Anderson C. and McShea D.W. 2001. Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest. *Insect. Soc.* **48**: 291 – 301
- Billen J., Beeckman W. and Morgan E.D. 1992. Active trail pheromone compounds and trail following in the ant *Atta sexdens sexdens* (Hymenoptera: Formicidae). *Ethol. Ecol. Evol.* **4**: 197 – 202
- Brannan J.A. 1992. On modeling resource transport costs: suggested refinements. *Curr. Anthropol.* **33**: 56 – 60
- Burd M. 1995. Variable load size-ant size matching in leaf-cutting ants, *Atta colombica* (Hymenoptera: Formicidae). *J. Insect Behav.* **8**: 715 – 722
- Burd M. 1996a. Foraging performance by *Atta colombica*, a leaf-cutting ant. *Am. Nat.* **148**: 596 – 612
- Burd M. 1996b. Server system and queuing models of leaf harvesting by leaf-cutting ants. *Am. Nat.* **148**: 613 – 629
- Burd M., Archer D., Aranwela N. and Stradling D.J. 2002. Traffic dynamics of the leaf-cutting ant, *Atta cephalotes*. *Am. Nat.* **159**: 283 – 293
- Burd M. and Aranwela N. 2003. Head-on encounter rates and walking speed of foragers in leaf-cutting ant traffic. *Insect. Soc.* **50**: 3 – 8
- Couzin I.D. and Franks N.R. 2003. Self-organized lane formation and optimized traffic flow in army ants. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 139 – 146
- Dussutour A. 2004. Organisation spatio-temporelle des déplacements collectifs chez les fourmis. Doctorate thesis, Université Toulouse III
- Dussutour A., Deneubourg J.-L. and Fourcassié V. 2005. Temporal organization of bi-directional traffic in the ant *Lasius niger* (L.). *J. Exp. Biol.* **208**: 2903 – 2912
- Engqvist L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* **70**: 967 – 971
- Feener D.H. Jr., Lighton J.R.B. and Bartholomew G.A. 1988. Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. *Funct. Ecol.* **2**: 509 – 520
- Fewell J.H. 1988. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. *Behav. Ecol. Sociobiol.* **22**: 401 – 408
- Fowler H.G. and Robinson S.W. 1979. Foraging by *Atta sexdens* (Formicidae: Attini): seasonal patterns, caste and efficiency. *Ecol. Entomol.* **4**: 239 – 247
- Franks N.R. 2001. Evolution of mass transit systems in ants: a tale of two societies. In: *Insect Movement: Mechanisms and Consequences*, Proc. 20th Symp. R. Entomol. Soc. pp 281 – 298
- Gordon D.M. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. *Am. Nat.* **138**: 379 – 411
- Gordon D.M. 1999. *Ants at Work: How an Insect Society is Organized*. New York: Free Press. 192 pp
- Gordon D.M. 2002. The regulation of foraging activity in red harvester ant colonies. *Am. Nat.* **159**: 509 – 518
- Gordon D.M. and Mehdiabadi N.J. 1999. Encounter rate and task allocation in harvester ants. *Behav. Ecol. Sociobiol.* **45**: 370 – 377
- Hart A.G. and Ratnieks F.L.W. 2001. Leaf caching in the leafcutting ant *Atta colombica*: organizational shift, task partitioning and making the best of a bad job. *Anim. Behav.* **62**: 227 – 234
- Helbing D., Keltsch J. and Molnar P. 1997. Modelling the evolution of human trail systems. *Nature* **388**: 47 – 50
- Hölldobler B. and Wilson E.O. 1990. *The Ants*. Cambridge, Massachusetts: Harvard University Press. 732 pp
- Howard J.J. 2001. Costs of trail construction and maintenance in the leaf-cutting ant *Atta colombica*. *Behav. Ecol. Sociobiol.* **49**: 348 – 356
- Howard J.J., Henneman M.L., Cronin G., Fox J.A. and Hormiga G. 1996. Conditioning of scouts and recruits during foraging by a leaf-cutting ant, *Atta colombica*. *Anim. Behav.* **52**: 299 – 306
- Hubbell S.P., Johnson L.K. and Stanislav E., Wilson B. and Fowler H. 1980. Foraging by bucket-brigade in leaf-cutter ants. *Biotropica* **12**: 210 – 213
- Jaffé K. and Howse P.E. 1979. The mass recruitment system of the leaf cutting ant, *Atta cephalotes* (L.). *Anim. Behav.* **27**: 930 – 939
- Kost C., de Oliveira E.G., Knoch T.A. and Wirth R. 2005. Spatio-temporal permanence and plasticity of foraging trails in young and mature leaf-cutting ant colonies (*Atta* spp.). *J. Trop. Ecol.* **21**: 677 – 688
- Le Breton J. and Fourcassié V. 2004. Information transfer during recruitment in the ant *Lasius niger* L. (Hymenoptera, Formicidae). *Behav. Ecol. Sociobiol.* **55**: 242 – 250
- Roces F. 1990. Olfactory conditioning during the recruitment process in a leaf-cutting ant. *Oecologia* **83**: 261 – 262
- Roces F. 1993. Both evaluation of resource quality and speed of recruited leaf-cutting ants (*Acromyrmex lundii*) depend on their motivational state. *Behav. Ecol. Sociobiol.* **33**: 183 – 189

- Roces F. and Núñez J.A. 1993. Information about food quality influences load-size selection in recruited leaf-cutting ants. *Anim. Behav.* **45**: 135 – 143
- Rockwood L.L. and Hubbell S.P. 1987. Host-plant selection, diet diversity, and optimal foraging in a tropical leafcutting ant. *Oecologia* **74**: 55 – 61
- Shepherd J.D. 1982. Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. *Behav. Ecol. Sociobiol.* **11**: 77 – 84
- Shepherd J.D. 1985. Adjusting foraging effort to resources in adjacent colonies of the leaf-cutter ant, *Atta colombica*. *Biotropica* **17**: 245 – 252
- Shutler D. and Mullie A. 1991. Size-related foraging behaviour of the leaf-cutting ant *Atta colombica*. *Can. J. Zool.* **69**: 1530 – 1533
- Simpson S.J. and Bernays E.A. 1983. The regulation of feeding: locusts and blowflies are not so different from mammals. *Appetite: J. Intake Res.* **4**: 313 – 346
- Soulé R.G. and Goldman R.F. 1972. Terrain coefficients of energy cost prediction. *J. Appl. Physiol.* **32**: 706 – 708
- Stradling D.J. 1978. The influence of size on foraging in the ant, *Atta cephalotes*, and the effect of some plant defence mechanisms. *J. Anim. Ecol.* **47**: 173 – 188
- Van Breda J.M. and Stradling D.J. 1994. Mechanisms affecting load size determination in *Atta cephalotes* L. (Hymenoptera, Formicidae). *Insect. Soc.* **41**: 423 – 434
- Van Vorhis Key S.E. and Baker T.C. 1981. Effects of gaster extract trail concentration on the trail following behaviour of the Argentine ant, *Iridomyrmex humilis* (Mayr). *J. Insect Physiol.* **27**: 363 – 370
- Wilson E.O. 1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: Atta). I. The overall pattern in *Atta sexdens*. *Behav. Ecol. Sociobiol.* **7**: 143 – 156
- Wirth R., Beyschlag W., Herz H., Ryel R.J. and Hölldobler B. 2003. *The Herbivory of Leaf-Cutting Ants. A Case Study on Atta colombica in the Tropical Rainforest of Panama*. Ecological Studies 164. Heidelberg, Springer Verlag, 230 pp
- Zollikofer C.P.E. 1994. Stepping patterns in ants. 3. Influence of load. *J. Exp. Biol.* **192**: 119 – 127

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