

## Priority rules govern the organization of traffic on foraging trails under crowding conditions in the leaf-cutting ant *Atta colombica*

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### SUMMARY

Foraging in leaf-cutting ants is generally organized along well-defined recruitment trails supporting a bi-directional flow of outbound and nestbound individuals. This study attempts to reveal the priority rules governing the organization of traffic on these trails. Ants were forced to move on a narrow trail, allowing the passage of only two individuals at a time. In this condition, a desynchronization of inbound and outbound traffic was observed, involving the formation of alternating clusters of inbound and outbound ants. Most clusters of inbound ants were headed by laden ants followed by unladen ants. This occurred because inbound unladen ants did not attempt to overtake the laden ants in front of them. As unladen ants move on average faster than laden ants, these ants were thus forced to decrease their speed. By contrast, this decrease was counterbalanced by the fact that, by staying in a cluster instead of moving in isolation, inbound unladen ants limit the number of head-on encounters with outbound ants. Our analysis shows that the delay induced by these head-on encounters would actually be twice as high as the delay induced by the forced decrease in speed incurred by ants staying in a cluster. The cluster organization also promotes information transfer about the level of food availability by increasing the number of contacts between outbound and inbound laden ants, which could possibly stimulate these former to cut and retrieve leaf fragments when reaching the end of the trail.

Key words: leaf-cutting ant, traffic, priority rule, cooperation.

### INTRODUCTION

The traffic snarls of the world's big cities show how difficult it can be for smooth collective movement to occur, especially when the traffic comprises a mixture of vehicles of different sizes (Hossain and McDonald, 1998) (reviewed by Helbing et al., 2007). Traffic flows could be improved if all drivers adhered to the strict priority rules devised by traffic-engineers. Admittedly, however, this is not always the case, and the tireless effort of the traffic police to enforce these rules testifies to the immense difficulty of the task... When moving on trails, social insects such as ants or termites provide one of the best examples of a smooth and ordered traffic flow in the animal world. In many social insect species, collective motion is organized along well-defined recruitment trails. These trails are initially created by pheromone deposition, but, in case of sustained traffic over a long period of time, they can turn into long-lasting trunk-trails through the physical modification of the environment (Hölldobler and Wilson, 1990; Anderson and McShea, 2001). Because social insects are central-place foragers, the movements on these trails, unlike most collective movements that take place in a migration context, are bi-directional. This adds to the difficulty in the maintenance of a smooth traffic flow (John et al., 2004) and makes these insects an excellent model for the study of traffic dynamics and traffic-related problems – for biologists (reviewed by Burd, 2006) and traffic-engineers alike (reviewed by Chowdhury et al., 2004; Chowdhury et al., 2005).

As ants are social insects, the behavior of individual workers is subordinated to the interest of all the members of the colony. One

should thus expect natural selection to have selected for organizational rules that can maximize the traffic flow on the trails in order to ensure a high rate of food return to the nest. This is generally the case (Burd et al., 2002). However, the question of the robustness of these organizational rules arises. For example, bottlenecks can be created if some of the trail sections are too narrow, as occurs for example when ants are moving on liana or small branches. Overcrowding can occur, and this can slow down the progression along the trails (Burd et al., 2002; Burd and Aranwela, 2003; Dussutour et al., 2005). However, solutions exist to prevent overcrowding. In the black garden ant *Lasius niger*, for example, overcrowding is avoided by a temporal organization of the flow as a sequence of alternating clusters of inbound and outbound ants (Dussutour et al., 2005). This organization emerges through the implementation of priority rules between ants, and it allows the minimization of head-on encounters. It explains why a narrow trail can sustain the same flow intensity as a wide trail, thus ensuring the same rate of food return to the nest. In *Lasius niger*, however, ants carrying internal loads (i.e. within their bodies) coming from the food source do not behave differently than emptied ants coming from the nest. The priority rules generating the ant clusters are the same in both directions: the ant that gives way is always the one that has the possibility to do it, by moving aside and waiting before entering a narrow passageway. Moreover, nestbound loaded ants and outbound emptied ants do not have a significantly different locomotory rate (Mailleux et al., 2000). In species carrying external loads, by contrast, laden individuals

returning to the nest are always given way by those going to the food source [army ants: *Dorylus sp.* and *Eciton burchelli* (Gottwald, 1995; Couzin and Franks, 2003); termites: *Longipeditermes longipes* and *Hospitalotermes* (Miura and Matsumoto, 1998a; Miura and Matsumoto, 1998b)] and they progress more slowly than unloaded individuals [*Atta cephalotes* (Rudolph and Loudon, 1986); *A. colombica* (Lighton et al., 1987); *Eciton hamatum* (Bartholomew et al., 1988); *Eciton burchelli* (Gottwald, 1995; Couzin and Franks, 2003); *Pogonomyrmex rugosus* (Lighton et al., 1993); *P. maricopa* (Weier and Feener, 1995); *Dorymyrmex goetschi* (Torres-Contreras and Vasquez, 2004)]. This difference in speed could potentially have a great impact on the organization of traffic. For example, differences in speed between vehicles are known to generate a temporal organization of traffic whereby fast vehicles adjust their speed to that of slower ones. This phenomenon creates clusters of vehicles moving in the same direction and leads to a reduction in the overall flow of vehicles on a road (Helbing and Huberman, 1998; Nagatani, 2000) (reviewed by Chowdhury et al., 2000; Helbing, 2001; Helbing et al., 2007).

Here, we examine the effect of trail width on traffic organization in ants carrying external loads. We chose leaf-cutting ants for our study because, in these species, the relation between speed and load mass is well documented [*Atta cephalotes* (Rudolph and Loudon, 1986; Burd, 2000; Burd and Aranwela, 2003); *A. colombica* (Lighton et al., 1987; Shutler and Mullie, 1991; Burd, 1996); *Atta vollenweideri* (Röscher and Roces, 2002); *Acromyrmex lundii* (Roces and Nuñez, 1993)]. Moreover, although they have never been precisely quantified, the existence of priority rules has been reported (Burd et al., 2002). Our experiment involved forcing ants going from their nest to a food source to cross a narrow bridge whose width allowed the passage of a maximum of two ants at a time. We show that, in this condition, a temporal organization of traffic through a cooperative behavior between ants can emerge. This organization facilitates minimization of head-on encounters between unloaded ants traveling in opposite directions and promotes head-on encounters between outbound ants traveling away from the nest and those returning from the food source loaded with food. These contacts could potentially stimulate outbound ants to cut and retrieve leaf fragments to the nest and thus increase the colony foraging efficiency (Dussutour et al., 2007).

## MATERIALS AND METHODS

### Species studied and rearing conditions

We worked with the leaf-cutting ant *Atta colombica* Linnaeus, 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  $10^5$ – $10^6$  workers (Hart and Ratnieks, 2001). We used an experimental colony that consisted of one queen, brood, approximately 20,000 workers and  $\sim 11,000$  cm<sup>3</sup> of fungus distributed in four clear plastic nest boxes (W×L×H: 12×23×10 cm). The nest boxes were kept in a plastic tray (W×L×H: 40×60×15 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±1°C) with a 12h:12h light:dark photoperiod. We supplied the colony with leaves of *Malus coccinella* four times a day (08:00h, 12:00h, 16:00h and 20:00h). The leaves were placed in a plastic tray (W×L×H: 40×60×15 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, the bridge was removed and replaced by a new unmarked bridge of the same width (50 mm: 'wide bridge') or of a reduced width (5 mm: 'narrow bridge').

### Experimental procedure

Because the removal of the marked bridge and its replacement by a new unmarked one was generally followed by a sharp decrease in ant traffic, a period of 24 h 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 then placed again in the foraging area at the start of the experiment [see Dussutour and colleagues (Dussutour et al., 2007) for details on the experimental procedure].

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 at the center of the bridge for 60 min with a Sony Digital Handycam DCR VX 2000E camera.

### Data collection

#### Temporal organization of the flow of ants

We first analyzed the temporal organization of the flow as a function of bridge width. For five replicates chosen randomly for each bridge, we noted during one hour the travel direction of the sequence of successive ants (+1 for inbound ants, –1 for outbound ants) crossing a line in the middle of the bridge. The number of individuals in each sequence was:  $N=3836$ ,  $N=5627$ ,  $N=6317$ ,  $N=5622$ ,  $N=5692$  ants for the narrow bridge and  $N=8822$ ,  $N=8224$ ,  $N=9556$ ,  $N=7590$ ,  $N=9821$  ants for the wide bridge. In addition, we also noted whether each inbound ant was laden.

In order to investigate whether the sequences of inbound and outbound ants were random or consisted of an alternation of groups of ants traveling in opposite directions, we used a one-sample runs test of randomness (Siegel and Castellan, 1988). This test is based on the number of runs in a sequence of categorical data. A run is defined as a succession of data belonging to the same category (in our case +1 or –1) and is delimited at both ends by data belonging to the other category. The total number of runs in a sequence gives an indication of whether or not the sequence is random. The occurrence of very few runs suggests a time trend or some bunching owing to a lack of independence between data. Conversely, the occurrence of many runs indicates systematic cyclical fluctuations of a short time period. We tested with a Kolmogorov–Smirnov two-sample test whether the distribution of the size of the groups of ants traveling in the same direction was random by comparing it with that given by a theoretical sequence of same size generated on a basis of equal probability of occurrence of nestbound and outbound ants.

#### Travel duration

We investigated how travel duration was affected by the direction of travel, the load carried and the position occupied by an ant within a group. We measured on a single replicate of the experiment with a narrow bridge the travel duration of a sample of ants traveling on a 15 cm section at the centre of the bridge. We defined four categories of ants: outbound ants, inbound laden ants, inbound unladen ants following a laden ant and inbound unladen ants preceding a laden ant. We followed 110 ants of each category. We considered only the individuals that did not encounter other ants while traveling the bridge section. The durations were measured from the time stamp of the video frames, allowing a

precision of  $1/25=0.04$ s. The measures began 15 min after the beginning of the experiment, when the outbound and nestbound flow of ants were at equilibrium.

#### Interaction probability and time loss per contact

In order to assess the probability for an inbound unladen ant to contact an outbound unladen ant, we counted in a single replicate with the narrow bridge the number of encounters occurring per ant for a sample of 100 unladen ants preceding a laden ant and traveling to the nest on a 15 cm section at the center of the bridge. An encounter was considered each time an ant passes another one traveling 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 encounter was estimated by regressing the number of encounters with physical contact on the total number of encounters with or without contact.

The net travel duration (i.e. including the time spent in contact) for each ant was also measured. The time lost per encounter with contact was estimated by regressing the net travel duration on the number of encounters in which a contact occurred. The measurements began 15 min after the beginning of the experiment, when the outbound and nestbound flow of ants were at dynamic equilibrium.

#### Priority and cooperative rules between ants

To investigate the mechanisms allowing the formation of alternating groups of ants traveling in opposite directions on the narrow bridge, we analyzed on a single replicate the outcome of head-on collisions between outbound ants and inbound laden ants ( $N=300$ ), and that between outbound ants and inbound unladen ants ( $N=400$ ). Typically, after a collision occurred, one ant moves to the bridge side to allow the passage of the oncoming ant (Fig. 1). We noted for each collision which of the inbound or outbound ant moved to the side of the bridge in order to give way and how many ants benefited from this behavior by following the ant that was given way. This latter effect corresponds to a cooperative behavior between ants because the subsequent ants benefit from the passage of the leading ant (the ant that was given way) (Fig. 1).

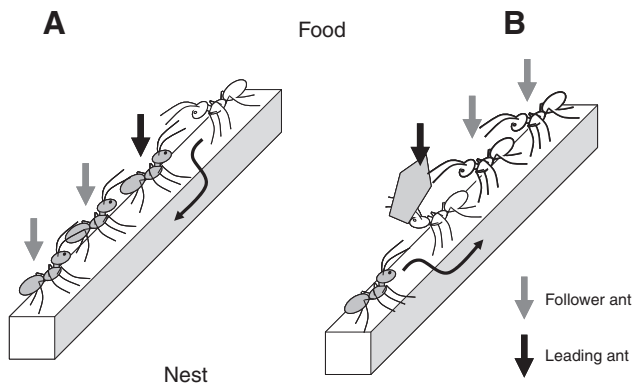


Fig. 1. Head-on collisions between (A) outbound and inbound unladen ants and (B) outbound and inbound laden ants. After a collision, either the inbound or the outbound ant moves to the bridge side to allow the passage of the oncoming ants. The follower ants might benefit from the passage of the leading ant (the ant that was given way) before the ant that gave way returns to the top of the bridge.

## RESULTS

### Temporal organization of the flow of ants

On the narrow bridge, the one-sample runs test of randomness allowed us to identify in the five replicates of the experiment the formation of groups of successive ants traveling in the same direction (run test:  $Z=-36.7$ ,  $Z=-44.58$ ,  $Z=-50.43$ ,  $Z=-43.44$  and  $Z=-49.10$ ;  $P<0.001$  for all replicates). The distribution frequency of the size of the groups did not differ between the inbound and outbound flow (Kolmogorov–Smirnov:  $Z=0.61$ ,  $Z=0.34$ ,  $Z=1.32$ ,  $Z=0.79$  and  $Z=1.14$ ;  $P>0.05$  for all replicates). The distribution of the size of the groups identified in the sequence on the narrow bridge was significantly different from that given by a random sequence of nestbound and outbound ants (Fig. 2) (Kolmogorov–Smirnov,  $Z=7.99$ ,  $Z=9.48$ ,  $Z=10.81$ ,  $Z=9.60$  and  $Z=9.66$ ;  $P<0.001$  for all replicates). The size of a group was 5.2 ants on average and reached a maximum of 73 ants. On the wide bridge, by contrast, the sequence of inbound and outbound ants was not different from random ( $Z=1.36$ ,  $Z=1.06$ ,  $Z=0.63$ ,  $Z=0.46$  and  $Z=0.19$ ;  $P>0.1$  for all replicates), and the distribution of group size observed on the wide bridge was not different from that computed from a random sequence (Fig. 2) (Kolmogorov–Smirnov,  $Z=0.67$ ,  $Z=0.48$ ,  $Z=0.59$ ,  $Z=0.61$ ,  $Z=0.63$ ;  $P>0.1$  for all replicates). The size of a group was 1.9 on average and reached a maximum of 14 ants.

The proportion of laden ants in the inbound flow on the narrow bridge was not significantly different between replicates ( $\chi^2=6.06$ , d.f.=4,  $P=0.195$ , mean proportion  $\pm$ s.d.:  $0.24\pm 0.01$ ). The proportion of laden ants in each group varied according to group size (Fig. 3). For groups of less than five workers, the proportion of laden ants was significantly lower than the expected proportion – that is, the mean proportion of laden ants in the inbound flow (0.24). This means that laden ants were overrepresented in inbound groups whose size was greater than five individuals. Moreover, laden ants were not randomly distributed within the groups. They were significantly more likely to occupy the first and second position within the groups than any other positions (Fig. 4). Moreover, when the size of the group was higher than three individuals, the proportion of groups led by a laden ant was significantly higher than the expected value – that is, the proportion of laden ants in each group size (Fig. 5). Thus, the size of a group led by a laden ant was significantly higher than the size of a group led by an unladen ant (Mann–Whitney test,  $U=502$  228,  $P<0.001$ , mean  $\pm$ s.d.,  $6.58\pm 5.29$  and  $4.49\pm 4.08$ , respectively).

### Travel duration

Laden and unladen inbound ants that followed a laden ant spent more time crossing a 15 cm section of the bridge (mean travel duration  $\pm$ s.d.:  $7.85\pm 1.96$ s and  $8.17\pm 2.69$ s, respectively) than outbound ants or inbound unladen ants that preceded a laden ant ( $6.42\pm 1.07$ s and  $6.57\pm 1.47$ s, respectively) (one-way ANOVA:  $F_{3,439}=24.02$ ,  $P<0.001$  followed by a Bonferroni *post-hoc* test). Only eight ants out of the 110 inbound unladen ants observed walking behind a laden ant passed it when crossing the 15 cm bridge section, suggesting that inbound unladen ants adjust their speed to the laden ants in front of them instead of passing them. When they were not preceded by a laden ant, inbound unladen ants crossed the bridge section as fast as outbound ants.

### Interaction probability and time loss per contact

The regression model of the number of encounters with physical contacts on the number of encounters per ant yielded a significant linear relationship (ANOVA for the model:  $F_{1,99}=198.94$ ,  $P<0.001$ ) and accounted for 67% of the variance. As expected, the number of contacts increased significantly with the number of encounters

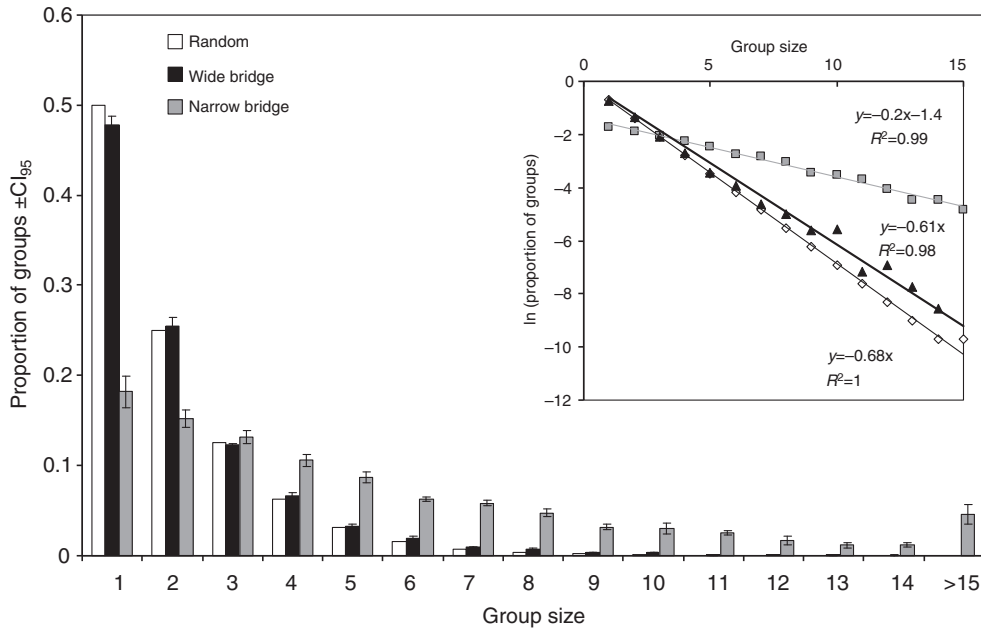


Fig. 2. Distribution frequency of the size of the groups of successive ants traveling in the same direction for the two types of bridges used in the experiment. The distributions for the two directions have been pooled on the graph. The distribution frequency of the group size obtained with a random sequence of ants generated on the basis of an equal probability of occurrence of nestbound and outbound ants is also represented.  $N=5$  replicates for each bridge. The inset shows the distribution frequency as a function of group size in natural log scale.

( $t=14.10$ ,  $P<0.001$ ). The slope of the regression line describing the relationship between the number of encounters with contact and the number of encounters indicates that the probability to physically contact another ant during an encounter was 0.30. An inbound unladen ant contacted on average four ants per 15 cm (mean  $\pm$  s.d.:  $3.9 \pm 2.4$ ). The regression model of the net travel duration on the number of contacts was also significant (ANOVA:  $F_{1,99}=297.77$ ,  $P<0.001$ ) and accounted for 75.2% of the variance. Travel duration increased significantly with the number of contacts ( $t=16.38$ ,  $P<0.001$ ). The time lost per contact was on average 0.80 s.

**Priority and cooperative rules between ants**

Close observations of the head-on encounters occurring on the bridge between ants traveling in opposite directions show that the majority of outbound ants stopped and gave way to the laden ants (in 294 out of 300 head-on encounters) but were mostly given way by unladen

ants traveling away from the food source (in 301 out of 400 head-on encounters). When an ant gave way to another, it generally moved to the side of the bridge and allowed the passage of the oncoming ants before returning to the top of the bridge. The probability for an ant to benefit from the passage of the leading ant depended both on its position as a follower and on the category of the leading ant (Fig. 6). When an outbound ant gave way to an inbound ant, the number of individuals that benefited from its behaviour was significantly higher when the inbound ant was laden than when it was not (mean  $\pm$  s.d.:  $5.40 \pm 3.16$  and  $1.18 \pm 1.40$  ants, respectively) (one-way ANOVA  $F_{2,693}=62.53$ ,  $P<0.001$ , followed by a Bonferroni *post-hoc* test) (Fig. 6, inset). Moreover, the number of individuals that benefited from the passage of the leading ant was significantly lower when an outbound ant gave way to an inbound unladen one than when an inbound unladen ant gave way to an outbound one ( $1.18 \pm 1.40$  and  $3.68 \pm 3.90$  ants, respectively).

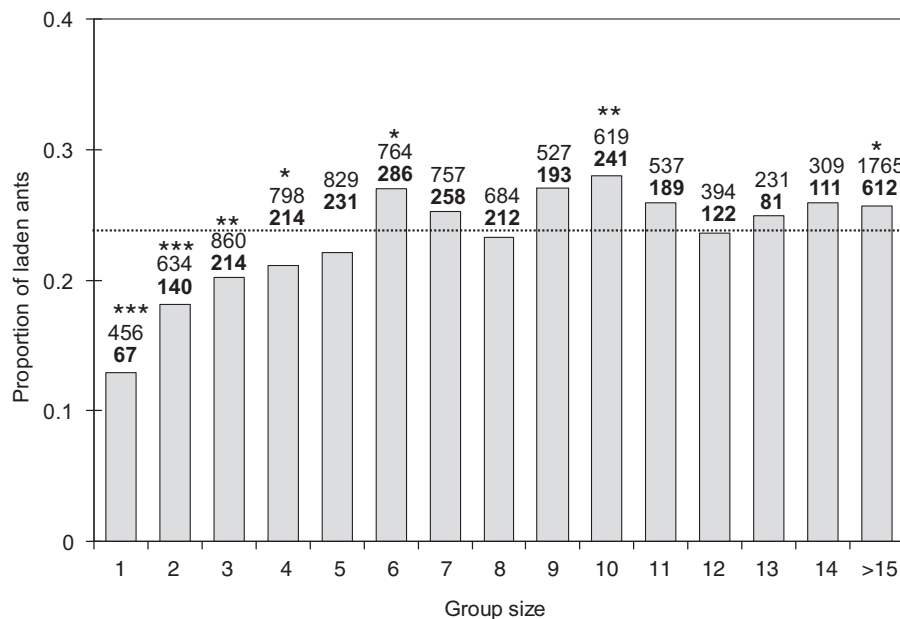


Fig. 3. Proportion of laden ants for each size of the groups of inbound ants. The number of laden and unladen ants are indicated in bold and regular font style, respectively. The results of five replicates have been pooled. The dashed line shows the expected proportion of laden ants for each group size, i.e. the mean proportion of laden ants in the inbound flow of the five replicates (0.24). We used a  $\chi^2$  goodness-of-fit test to test whether the proportion of laden ants for each group size differed from the expected value. A significant result means either that laden ants are underrepresented (for group size  $<5$ ) or overrepresented (for group size  $>5$ ) in the groups. \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

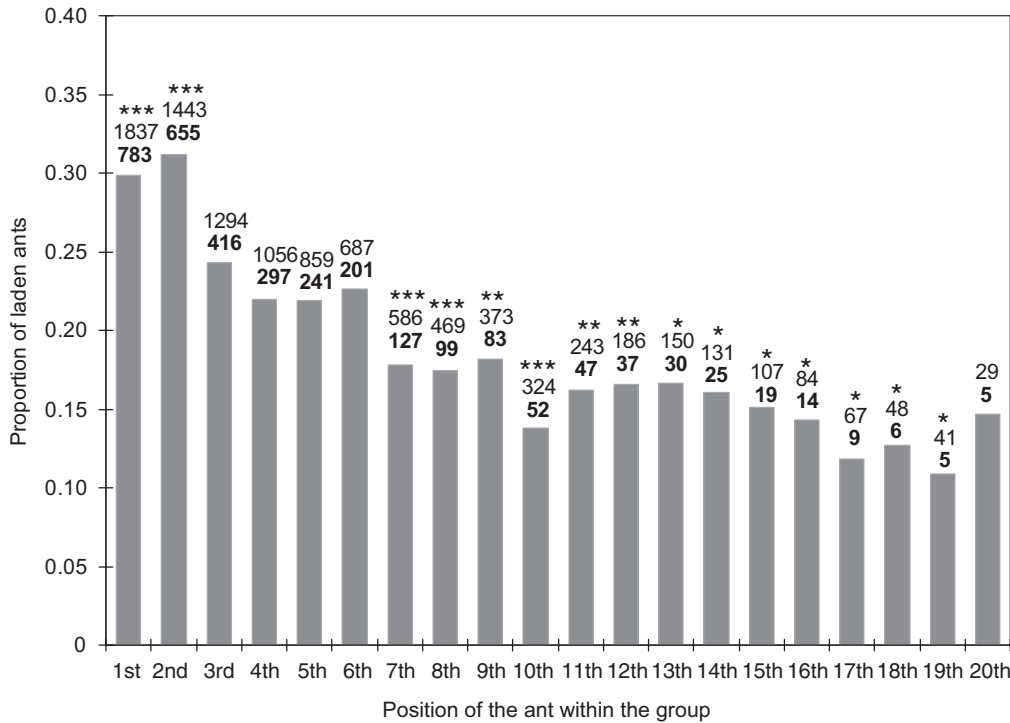


Fig. 4. Proportion of laden ants occupying each position within a group (>1 individual) of inbound ants – that is, the number of laden ants in the *i*th position divided by the total number of ants in the *i*th position. The numbers of laden and unladen ants for each position are indicated in bold and regular font style, respectively. The results of five replicates have been pooled. We used a  $\chi^2$  goodness-of-fit test to test whether the proportion of laden ants occupying each position differed from the expected value – that is, the proportion of laden ants in groups whose size is  $\geq(i+1)$ . Laden ants were significantly overrepresented in the first and second position and were significantly underrepresented in position >6th. \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

**DISCUSSION**

This study shows that leaf-cutting ants, in the same way as *Lasius niger* (Dussutour et al., 2005), avoid crowding on recruitment trails by changing the temporal organization of the flows of inbound and outbound individuals. On wide bridges, the sequence of outbound and inbound ants was not different from random, whereas alternating groups of inbound and outbound ants were observed on narrow bridges.

We found that laden workers moved more slowly on a recruitment trail than unladen workers. This confirms the results obtained by others authors (Lighton et al., 1987; Burd, 1996; Burd,

2000; Shutler and Mullie, 1991; Couzin and Franks, 2003). We observed in addition that inbound unladen ants generally never attempted to overtake the laden ants in front of them and instead preferred to slow down their pace and stay behind. This speed adjustment passively induces an accumulation of ants behind laden ants and generates inbound groups led by laden ants. Similar phenomena are also observed in vehicular traffic when a mixture of trucks and cars are present on a highway (Peeta et al., 2005) and in pedestrians when individuals prefer to follow a person ahead than move against an opposing stream (reviewed by Helbing et al., 2007).

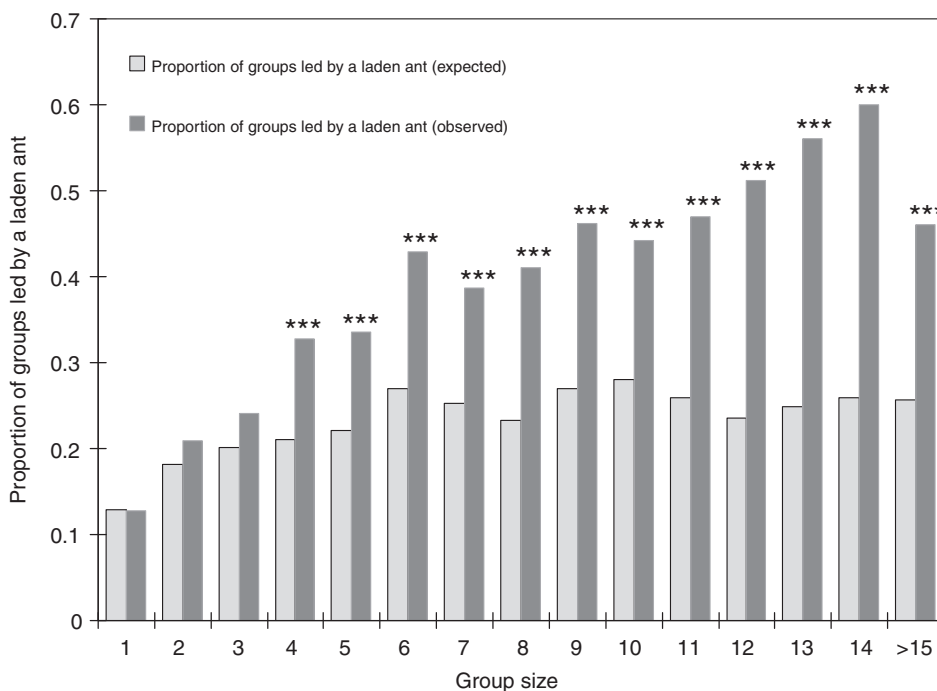


Fig. 5. Expected and observed proportions of inbound groups led by a laden ant as a function of group size. The expected proportion corresponds to the proportion of laden ants observed for each group size (see Fig. 3). If the laden ants were equally distributed within the group, we would expect a 0.24 chance to observe them in the first position. We used a  $\chi^2$  goodness-of-fit test to test whether the proportion of laden ants for each group size differed from the expected value. The significant result for group size >3 means that laden ants are significantly more likely to occupy the first position than any other position within the groups. The results of five replicates have been pooled. \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

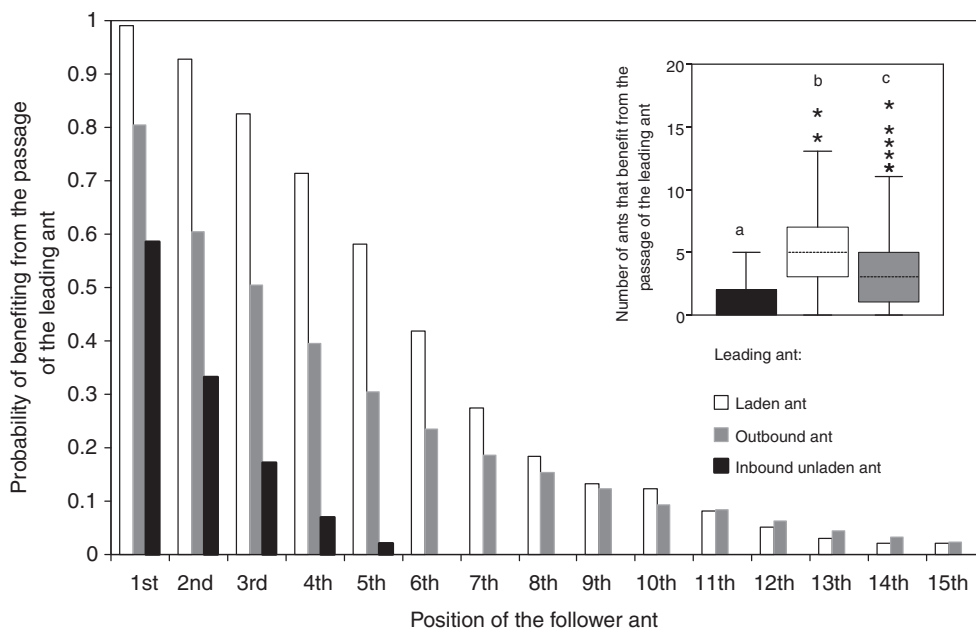


Fig. 6. Probability of a follower ant of benefiting from the passage of the leading ant according to its position in a group of inbound or outbound ants. The leading ants are the ants that are given way to after a head-on encounter ( $N=99$ ,  $N=301$  and  $N=294$  for inbound unladen ants, outbound ants and laden ants, respectively). The ant occupying the first position is the one immediately behind the leading ant. The probability for each  $i$ th position is computed by dividing the number of ants in the  $i$ th position that benefited from the passage of the leading ant by the total number of groups whose size is  $\geq(i+1)$ . For example, an ant immediately behind (1st position) a laden ant has a 0.99 probability of benefiting from the passage of the leading ant. The probability value becomes 0.59 if the leading ant is unladen. The inset shows the distribution of the number of ants that benefited from the passage of a leading ant. The dotted line within the boxplots represents the median, and the lower and upper boundaries of the boxes represent, respectively, the 25th and 75th percentiles, while the whiskers extend to the smallest and largest values within 1.5 box lengths. The asterisks represent the outliers. The bars bearing different letters are significantly different at the 1% level of significance (one-way ANOVA followed by a Bonferroni *post-hoc* test).

When an outbound ant encounters a group led by a laden ant, it first stops and gives way to the laden ant. This phenomenon has also been reported in army ants [*Dorylus sp.* (Gottwald, 1995); *Eciton burchelli* (Couzin and Franks, 2003)] and in the termites *Longipeditermes longipes* and *Hospitalotermes* (Miura and Matsumoto, 1998a; Miura and Matsumoto, 1998b). The outbound ant generally moves to the side of the bridge, allows the passage of the incoming ants and returns to the top of the bridge. This behavior prevents the fission of the incoming group of ants. In addition, as the outbound ant moving to the side is frequently followed by other ants, this produces an accumulation of outbound ants on the side of the bridge. As soon as the path is free, these ants return to the top of the bridge to move as a cluster. The priority rules followed by outbound ants might therefore help to maintain the inbound groups led by laden ants along the recruitment trail. At the same time, it also generates groups of outbound ants. The temporal organization of the flow can therefore be described as a self-organized process emerging from the simple rules of priority between individuals moving in opposite directions.

What is the advantage for an inbound unladen ant to move slower by staying behind a laden ant instead of progressing more rapidly by moving at its desired speed? The most likely explanation is that the ants that follow a laden ant gain benefit of the right of way it is given by other ants. These ants avoid head-on collisions with outbound ants and thus spare the time they would waste by moving to the side of the bridge as they do most of the times when they face an outbound ant. On a 15 cm section of the bridge, an inbound unladen ant contacts on average four outbound ants and wastes on average 0.8 s per contact. Therefore, compared with an inbound unladen ant that does not make any contacts and moves at its desired

speed (travel duration: 6.57 s), an unladen ant preceding a laden ant wastes on average 3.2 s in frontal contacts, whereas an unladen ant following a laden ant wastes 1.6 s by adjusting its speed to that of the laden ant it is following. An unladen ant traveling on a 300 cm bridge would thus waste 32 s by staying behind a laden ant and not overtaking it while an unladen ant overtaking a laden ant would waste 64 s. In leaf-cutting ants, unladen ants, in the same way as laden ants, take part in the recruitment process by laying a chemical trail (Evison et al., 2008). Therefore, returning earlier to the colony allows acceleration of the build-up of the recruitment trail, which in turn allows a faster recruitment to the food source (Roces and Hölldobler, 1994).

Another advantage generated by the temporal organization of the flow is that head-on encounters between laden ants traveling away from the food and outbound ants traveling to the food are facilitated. Contacts between workers in our experiments were not simple accidents occurring at random. Unladen returning ants avoided outbound foragers by moving to the side, whereas laden returning ants never attempted to do so, possibly because their loads hindered their capacity to maneuver (Zollikofer, 1994). An outbound ant encountering an inbound group led by a laden ant generally moves to the side of the bridge, allows the passage of incoming ants, returns to the top of the bridge and there encounters again another group led by a laden ant. As a result of these priority rules, an outbound ant on its way to the food source contacts mostly laden ants. These contacts might increase information transfer on the availability of food at the end of the trail and stimulate outbound workers to cut and transport leaf fragments, leading to an increase in foraging efficiency (Dussutour et al., 2007). This phenomenon might be particularly important when leaf-cutting ants are traveling on narrow

branches to reach leaves because it could be a cue as to continue or not on a particular branch.

It remains to be seen whether, in the natural environment, trail widths are adjusted to optimize the net benefit of the trail, given the traffic demand, the cost of clearing (Howard, 2001) and the effect of traffic density on contact rates and information exchange. Indeed, according to our results, building wider foraging trails not only could be more costly but could also result in a lower foraging efficiency. This might also explain why leaf-cutting ants in their natural environment often prefer to settle their trails along small fallen logs or branches instead of building a wider trail by clearing the leaf litter.

Leaf-cutting ants present an interesting comparison with vehicles moving on highways or with pedestrians crossing a corridor (Helbing et al., 2007). Like a mixture of cars, trucks and other vehicles with a range of desired speeds, leaf-cutting ant foragers are highly polymorphic and vary widely in the locomotion speed they can attain (Burd, 2000). The mechanisms leading to the formation of clusters of ants on a foraging trail are analogous to those leading to clusters of cars on a highway. The temporal organization of the flow of ants we observed is also reminiscent of that observed in bidirectional pedestrian traffic through a narrow passageway (Helbing et al., 2005). If opposing flows of pedestrians interrupt at a narrow passageway, oscillations in passing direction are observed – that is, a temporal organization of the flow (Helbing et al., 2005). Typically, groups of individuals rather than single individuals go through the passage before individuals located on the other side have a chance to do the same. This occurs because it is easier to follow someone than to move against an opposing stream. The resulting stream of individuals going through the passage releases the pressure in the pedestrian crowd on one side, while the pressure on the other side increases. When the pressure difference reaches a certain threshold, the stream of people is stopped and individuals on the other side in turn are allowed through the passage (Helbing et al. 2005). In other ways, however, ant traffic is distinct from either pedestrian or vehicular traffic. Human pedestrians anticipate potential interactions, such as collisions, and act to avoid them in order to maintain high velocities and flows in the face of rising concentrations (Helbing et al., 2007). This is not the case of ants that, with their small mass, are not damaged by collisions and do not seem to employ particular means to avoid incoming workers in traffic streams. Ants have much lower inertia than humans: they can rapidly come to a halt and then accelerate to regain their former speed. Moreover, ants from the same colony presumably act with a unity of purpose very different to the multiplicity of individual interests pursued by pedestrians or drivers moving in a traffic stream.

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