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Temporal organization of bi-directional traffic in the ant *Lasius niger* (L.)

Audrey Dussutour[1,*], Jean-Louis Deneubourg[2] and Vincent Fourcassié[1,†]

[1]*Centre de Recherches sur la Cognition Animale, UMR CNRS 5169, Université Paul Sabatier, 118 route de Narbonne, F-31062, Toulouse Cedex 4, France* and [2]*Service d'Ecologie Sociale and Centre d'Etudes des Phénomènes Non-linéaires et des Systèmes Complexes, Université Libre de Bruxelles, CP231, Boulevard du Triomphe, B-1050 Bruxelles, Belgium*

*Present address: Biology Department, Concordia University, 7141 Sherbrooke St W., Montreal, Quebec, Canada H4B 1R6
†Author for correspondence (e-mail: fourcass@cict.fr)

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Summary

Foraging in ants is generally organized along well-defined trails supporting a bi-directional flow of outbound and nestbound individuals and one can hypothesize that this flow is maximized to ensure a high rate of food return to the nest. In this paper we examine the effect of bottlenecks on the temporal organization of ant flow. In our experiments ants had to cross a bridge to go from their nest to a food source. Two types of bridges were used: one with and one without bottlenecks. Traffic counts show that, in spite of the bottlenecks and the reduction of path width, the volume of traffic and the rate of food return were the same on both bridges. This was due to a change in the temporal organization of the flow: when path width decreases alternating clusters of inbound and outbound ants were observed crossing the bridge. This organization limits the number of head-on encounters and thus allows to maintain the same travel duration as on the wide bridge. A model is proposed to assess in various conditions the importance of the behavioural rules observed at the individual level for the regulation of traffic flow. It highlights how the interplay between the value of the flow and cooperative behaviours governs the formation and size of the clusters observed on the bridge.

Supplementary material available online at
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Key words: ants, traffic, cooperation, crowding, foraging, mass recruitment, trails.

Introduction

The collective displacement of assemblies of organisms is certainly one of the most spectacular phenomena one can observe in nature. A column of army ants, a swarm of locusts, a herd of migrating wildebeests, a flock of birds or a shoal of fish can sometimes comprise several million individuals. Collective displacements are characterized by a high degree of coordination among individuals. This coordination is allowed by short response latencies: the movement of an individual is almost immediately followed by a parallel movement of the neighbouring individuals located within perceptual range. Each individual in a formation is submitted to conflicting forces of interattraction and repulsion (Couzin et al., 2002), and a rupture in the balance between the two categories of forces can lead to the collapse of the group. A number of recent reviews attests to the growing interest in the study of collective motion (Parrish and Hamner, 1997; Boinski and Garber, 2000; Camazine et al., 2001; Krause and Ruxton, 2002; Couzin and Krause, 2003; Chowdhury et al., 2004; Ball, 2004).

Ants provide an excellent model for the study of collective movement because of their highly social organization that functions in a completely decentralized manner (Camazine et al., 2001). Collective motion in ants is mainly organized along well-defined trails that are initially created by the deposition of pheromone but can turn into more or less permanent trunk-trails through the physical modification of the environment in the case of sustained traffic over a long period of time (Hölldobler and Wilson, 1990). Because social insects are central-place foragers, these trails, unlike most collective movements that take place in a migration context, support a bi-directional flow of outbound and nestbound individuals (John et al., 2004). They are used for the exchange of food or individuals between nests in polydomous colonies (i.e. the same colony is distributed among several nests linked by more or less permanent trunk-trails; e.g. Pfeiffer and Linsenmair, 1998) or for the collective harvesting of abundant food sources (clusters of prey, aphid honeydew, seeds or leaves in leaf-cutting ants). In the latter case, it is essential that ants maximize the traffic flow on the trails to ensure a high rate of food return to the nest.

In this paper, we examine the effect of bottlenecks on traffic flow in the ant *Lasius niger* (L.). To go from their nest to a food source, ants were forced to cross a bridge whose central part is so narrow that it allows the passage of a maximum of two ants at a time across its width. Because of this constraint, we were interested in the temporal organization of the flow, and not in its spatial organization, as in previous studies of ant trail traffic (Burd et al., 2002; Couzin and Franks, 2002; Dussutour et al., 2004). This kind of situation may occur when ants or termites are moving between nest chambers through narrow section galleries. In bi-directional streams of pedestrians, narrow passages (e.g. doors or narrowing corridors) give rise to jamming phenomena and to oscillatory changes in the flow direction (Helbing et al., 2001, 2005). Here, we show that a similar phenomenon can be observed in ants at high levels of traffic intensity. This temporal organization, which emerges through a cooperative behaviour between ants, can minimize the amount of head-on encounters per ant and per unit distance and explains why a narrow bridge can sustain the same flow intensity as a large bridge, thus ensuring the same rate of food return to the nest.

Materials and methods

Species studied and rearing conditions

We used the black garden ant, *Lasius niger*, a species that uses mass recruitment through scent trails to exploit abundant food sources. We collected four colonies of 4000–5000 workers in Toulouse (south-west France) in September 2001. Each of these colonies was subdivided into two or three queenless experimental groups, each containing 1000 workers without brood, yielding a total of 12 experimental groups.

Each experimental group was housed in a plastic box of 100 mm diameter, the bottom of which was covered by a layer of plaster moistened by a cotton plug soaking in a water reservoir underneath. The box was connected to an arena (diameter, 130 mm) whose walls were coated with Fluon® to prevent ants from escaping. The nests were regularly moistened and the colonies were kept at room temperature (25±1°C) with a 12 h:12 h L:D photoperiod. We supplied ants with water and a mixed diet of vitamin-enriched food (Bhatkhar and Withcombs, 1970), as well as maggots (*Calliphora erythrocephala*), three times a week.

Experimental set-up and protocol

In each experiment, an experimental group starved for 5 days was given access to a food source (2 ml of 1 mol l^{-1} sucrose solution) placed on a platform (70×70 mm) at the other end of a bridge. The food source was spread over a surface large enough to accommodate a large number of ants without crowding. We used two kinds of bridges whose central part was characterized by a different width: 10 mm (control bridge) or 3 mm (experimental bridge). The total length of the bridges was 210 mm. For the purpose of the analysis, the bridges were divided into six different sections (see Fig. 1): an access ramp (95 mm long), which began in the small arena connected to the experimental nests, one bottleneck (15 mm) and one entrance (15 mm) at both ends of the bridge (hitherto defined as the nest and source side of the bridge), and a central part (60 mm). For the 10 mm bridge, all sections had a width of 10 mm. Fifteen trials were achieved with each type of bridge. All trials were filmed for 1 h by a video camera placed over the bridge.

Data collection

Traffic dynamics

The traffic on the bridge was counted over a 1 min period every three minutes during 1 h. Counting began as soon as the first ant was observed climbing the bridge. We measured the flow of ants leaving the nest and that leaving the food source at the level of the entrances on each side of the bridge.

Traffic organization

In order to investigate the traffic organization in extreme crowding conditions, we focused our analysis for each bridge on the trial characterized by the highest flow of ants

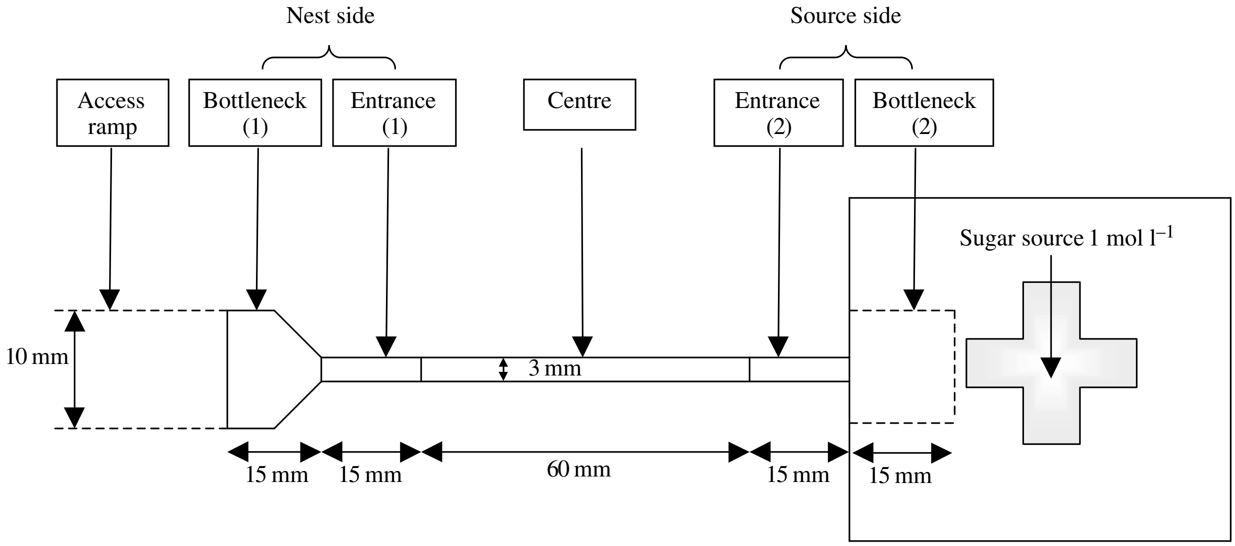

Fig. 1. Schematic illustration of the 3 mm-width bridge, with the different sectors defined for the analysis of the ants' individual behaviour.

(approximately 120 ants min^{-1}). The following data were collected.

Travel duration and interactions between ants. For both types of bridges, we first computed, for a sample of 50 outbound ants, the time required for an ant to travel the length of the bridge between the two bottlenecks in the absence of interactions with other ants. The times were measured from the time stamp of the video frames, allowing a precision of 1/25=0.04 s. Because 120 ants min^{-1} was too high to allow the passage of an ant without interactions, these data were obtained for each bridge from another trial, characterized by a smaller traffic volume (~60 ants min^{-1}).

We then counted for both types of bridge, on a sample of 150 outbound ants on the trial characterized by the highest flow of ants, the number of encounters occurring per ant when travelling between the two bottlenecks. An encounter was counted each time an ant passed another one in the same or in the opposite direction, with or without contact. A contact could be the result of either a collision (when the heads of two ants enter into contact) or a push (when the head of an ant enters into contact with the gaster of the ant preceding it). The net travel duration (i.e. including the time spent in interactions) for each ant was also measured. The measurements began 10 min after the beginning of the experiment, when the outbound and nestbound flow of ants was at equilibrium.

The time lost per interaction with contact was estimated by regressing the net travel duration on the number of encounters with contact. The probability to be contacted during an interaction was estimated by regressing the number of encounters with contact on the total number of encounters with or without contact.

Temporal organization of the flow of ants. For both types of bridges, we noted the travel direction for a sequence of 2700 successive ants (+1 for inbound ants, –1 for outbound ants) and the time at which each ant crossed the line between the bottleneck and the entrance on the nest side of the bridge. The sequence lasted approximately 20 min.

Data analysis

The relationship between variables across bridge widths (3 or 10 mm) or bridge sides (nest or source) was examined using multiple regression analysis. For this purpose, continuous predictor variables were centred on their means (i.e. the mean value was subtracted from each observation), and categorical variables (either bridge width or bridge side) were coded as scalar numbers. This procedure is recommended in multiple regression analysis because it reduces the covariation between linear variables and their interaction terms (Aiken and West, 1991).

In order to investigate whether the sequence of inbound and outbound ants was random or consisted of an alternation of groups of ants travelling 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 a value 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. The occurrence of many runs indicates systematic cyclical fluctuations of short period. In addition, we tested with a Kolgomorov–Smirnov two-sample test whether the distribution of the size of the groups of ants travelling in the same direction was random by comparing it with that given by a theoretical sequence generated on a basis of equal probability of occurrence of nestbound and outbound ants.

Results

Traffic dynamics

The recruitment dynamics and the traffic volumes were not influenced by bridge width (Fig. 2; two-way ANOVA with repeated measures on time interval; width effect, $F_{1,32}=0.62$, $P=0.439$; interaction width × time effect, $F_{19,32}=1.21$, $P=0.247$) and were typical of a trail-recruitment process (Pasteels et al., 1987). The flux reaches a peak after ~12 min (time effect; $F_{19,32}=17.20$, $P<0.001$).

Traffic organization

Travel duration and interactions between ants

There was no significant difference between the two bridge widths in the time required to cross the bridge without interaction [mean ± S.D., 2.96±0.61 s and 2.93±0.56 s (N=50) for 10 mm and 3 mm bridges, respectively; Student's t-test; $t=0.73$, $P=0.735$]. Therefore, the geometry of the system alone did not have any effect on the mean travel speed of the ants.

The regression model of the net travel duration on the number of contacts across bridge width was significant (Fig. 3; ANOVA for the whole model; $F_{3,255}=626.43$, $P<0.001$) and accounted for 88.1% of the variance. As a confirmation of the preceding analysis, the model indicates that, in the absence of contacts, there was no effect of bridge width on the time required for an ant to cross the bridge [intercept of the regression lines with the y-axis (±C.I.$_{0.95}$) indicated on Fig. 3:

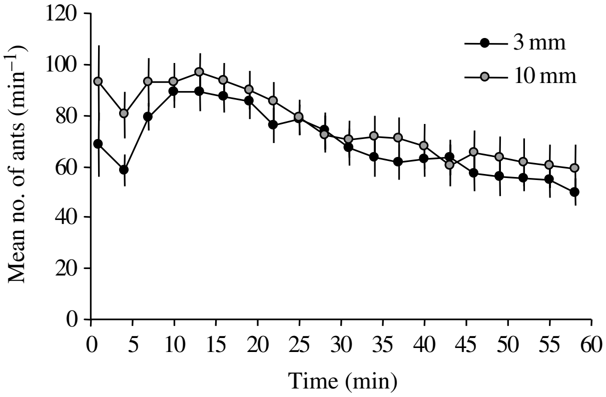

Fig. 2. Mean number of ants per minute crossing the bridge in both directions every 3 min. Values are means ± S.E.M. N=15 trials for both bridge widths.

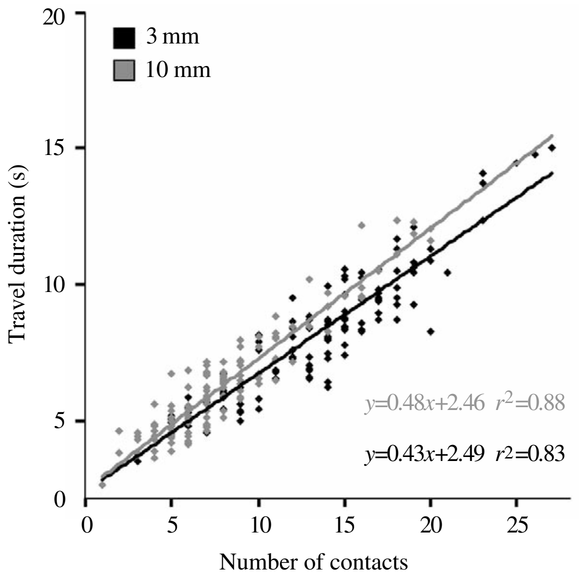

Fig. 3. Effect of the number of encounters with contact on the duration of travel between the two bottlenecks of the bridge for the two bridge widths studied. The slope of the linear regression lines corresponds to the time lost by each ant per interaction; its intercept gives the duration of travel without interaction. N=133 and N=126 for the 3 mm and 10 mm bridge, respectively.

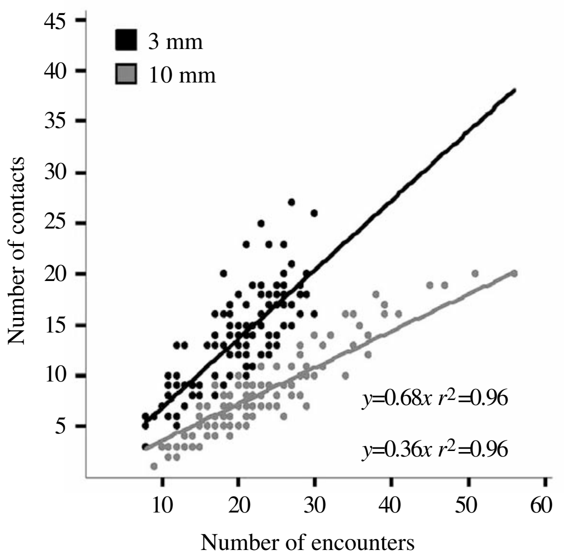

Fig. 4. Relationship between the number of encounters with contact and the total number of encounters per ant for each bridge width studied. The slope of the lines corresponds to the probability of an ant travelling on the bridge to be contacted by another ant during an encounter. N=133 and N=126 for the 3 mm and 10 mm bridge, respectively.

2.46±0.27 s and 2.49±0.47 s for 10 mm and 3 mm bridges, respectively]. Travel duration increased significantly with the number of contacts (t=38.87, P<0.001) and was significantly affected by bridge width (t=4.87, P<0.001): for the same number of contacts, the duration of travel was higher for 10 mm bridges than for 3 mm bridges. Moreover, there was a significant interaction effect between bridge width and the number of contacts (t=2.43, P=0.016). Travel duration increased slightly more rapidly for 10 mm than for 3 mm bridges: the time lost per contact (which corresponds to the slope of the regression lines indicated in Fig. 3) amounted to 0.430±0.017 s (mean ± S.E.M.) on the 3 mm bridge and to 0.480±0.015 s (mean ± S.E.M.) on the 10 mm bridge. Examination of the standardised regression coefficients (which are in units of S.D. and therefore can be compared directly) of the multiple regression model shows, however, that travel duration was almost entirely determined by the number of contacts with other ants (β=1.00, 0.12 and 0.05 for the effect of the number of contacts, bridge width and the interaction term between the two variables, respectively).

The regression model of the number of encounters with contacts on the number of encounters per ant across bridge width yielded a significant linear relationship (Fig. 4; ANOVA for the whole model; $F_{3,258}$=323.52, P<0.001) and accounted for 79% of the variance. The model indicates a significant effect of the number of encounters (t=24.30, P<0.001), of bridge width (t=–24.05, P<0.001) and of the interaction term between these two variables (t=–4.80, P<0.001). Examination of the standardised regression coefficients shows that the main effect on the number of contacts was due to the number of encounters (β=0.780), followed by bridge width (β=–0.710) and the interaction between these two variables (β=–0.149). A separate regression analysis on the data for each bridge width explains 95.7% and 96.4% of the variance for 3 mm and 10 mm bridges, respectively (Fig. 4). The slope of the regression lines on Fig. 4 gives the probability of contacting another ant during an encounter. It is significantly higher for the 3 mm (0.681±0.013, mean ± S.E.M.) than for the 10 mm (0.360±0.06, mean ± S.E.M.) width. The fact that we obtained a good fit with a linear regression shows that the probability of contact does not increase with the volume of traffic and depends only on the width of the bridge.

Since the volume of traffic was not significantly different on the two bridge widths (see Fig. 2), one would have expected the number of encounters (with and without contacts) per ant on the 3 mm bridge to be at least equal to that on the 10 mm bridge. However, this is not what we actually observed. In fact, the number of encounters per ant was lower on the 3 mm bridge than on the 10 mm bridge [mean ± S.D., 19.86±5.53 (N=126) and 23.09±8.29 (N=133) for 3 mm and 10 mm bridges, respectively; Student's t-test; t=3.67, P<0.001]. This discrepancy suggests that there is some temporal organization in the flow of ants, decreasing the number of interactions on the 3 mm bridge. This is indeed what is shown in the following section.

Temporal organization of the flow of ants

The one-sample runs test of randomness allowed us to identify the formation of groups of successive ants travelling in the same direction in the sequence of ants observed on the 3 mm bridge (Z=–26.15, P<0.001; see Movie 2 in

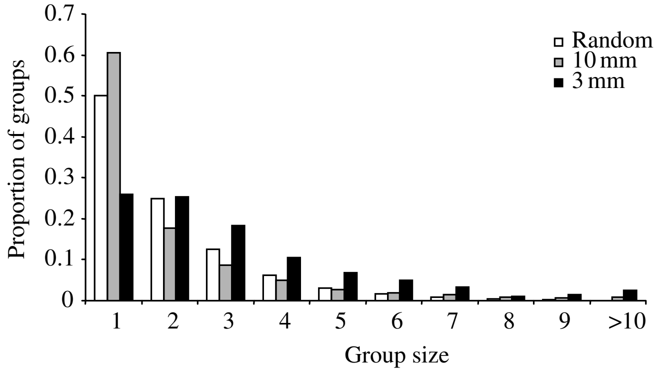

Fig. 5. Experimental results. Distribution frequency of the size of the groups of successive ants travelling in the same direction identified at the level of the line between the bottleneck and the entrance on the nest side of the bridge for each bridge width. The distribution frequency of group size 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. $N=1203$ and $N=905$ for the 10 mm and 3 mm bridge, respectively.

supplementary material). The distribution of the size of the groups identified in the sequence was significantly different from that given by a random sequence of nestbound and outbound ants (Fig. 5; Kolmogorov–Smirnov; $Z=1.58$, $P=0.013$). The mean size of a group on a 3 mm bridge was 3.3. By contrast, the sequence of ants on a 10 mm bridge was not different from random ($Z=0.58$, $P=0.560$) and the distribution of group size observed on a 10 mm bridge was not different from that computed from a random sequence (Fig. 5; Kolmogorov–Smirnov; $Z=0.67$, $P=0.759$; see Movie 1 in supplementary material). A Fourier analysis conducted to test the periodicity between groups of opposite direction for 3 mm bridges did not give any conclusive results.

To investigate the mechanisms allowing the formation of alternating groups of ants travelling in opposite direction on a 3 mm bridge, we noted, for both travel directions and for both sides of the bridge, the time at which 500 successive ants travelling in the same direction crossed (Fig. 1) (1) the line between the access ramp (or the platform) and the bottleneck, (2) the line between the bottleneck and the entrance and (3) the line between the entrance and the centre of the bridge. The sequence of inbound and outbound ants crossing each line was then reconstructed from the time tag of each ant. A total of 2000 ants was followed: 500 ants for each direction and each side of the bridge.

The run test applied to the sequences of ants travelling between the different sections of the 3 mm bridge yielded a non-significant result for the sequence of ants crossing the line between the access ramp and the bottleneck for the nest side of the bridge ($Z=0.59$, $P=0.555$), and for that between the platform and the bottleneck for the source side of the bridge ($Z=0.74$, $P=0.458$). By contrast, the formation of groups of successive ants travelling in opposite direction was detected on the line between the bottleneck and the entrance ($Z=-8.81$, $P<0.001$ and $Z=-9.43$, $P<0.001$, for the nest and source side of the bridge, respectively), as well as on the line between the entrance and the centre of the bridge ($Z=-9.777$, $P<0.001$ and $Z=10.247$, $P<0.001$, for the nest and source side of the bridge, respectively). This result suggests that the formation of groups was generated at the level of the two bottlenecks, and not at the moment the ants left the nest or the food source.

In order to investigate the priority rules between ants at the level of the two bottlenecks, the following variables were measured. (1) The time spent crossing the two bottlenecks and the two entrances ($N=500$ for each bridge side). (2) The number of encounters at the level of the two bridge constrictions, on the line between the bottleneck and the entrance (Fig. 1); the delay between the time each ant was stopped by an encounter and the time it started again was also noted). (3) The number of contacts in the two bottlenecks ($N=250$ for each bridge side).

A three-way ANOVA was used to test for the effect of sector (bottleneck *vs* entrance), travel direction (ants travelling towards the centre of the bridge *vs* those travelling out of the centre) and bridge side (nest *vs* source) on the time spent by ants to cross the bottlenecks and the entrances. Since the ants were individually followed when travelling across the bottlenecks and the entrances on both sides of the bridge, the sector effect was treated as a repeated measure factor. The data were log-transformed to allow for normality.

Examination of the estimates of effect size of the ANOVA (partial correlation effect size; Kline, 2004) shows that the main effect on the total variance of the scores was due to the interaction between sector and travel direction (Fig. 6; Table 1;

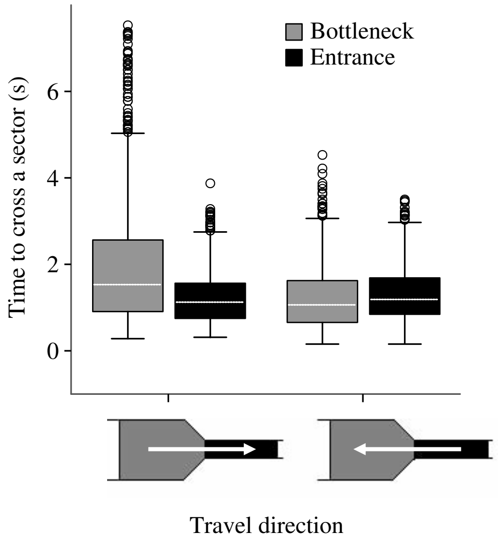

Fig. 6. Distribution of the time spent crossing the bottlenecks and the entrances for ants travelling to and from the centre of a 3 mm bridge (for each sector, the results for the nest and source sides of the bridge have been pooled). The dotted lines within the boxplots represent the median, the lower 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 open circles represent the outliers. $N=500$ for each box plot.

Table 1. *Results of a three-way ANOVA to test for the effect of the travel direction (ants travelling from the bridge ends towards the centre of the bridge* vs *those travelling from the centre towards the bridge ends), the bridge side (nest* vs *source) and the sector (bottleneck* vs *entrance) on the time required to cross a sector by an ant*

Source of variation	Mean squares	d.f.	*F*	*P*
Between ants				
Travel direction	5.469	1	74.04	<0.001
Bridge side	0.082	1	1.07	0.301
Travel direction × bridge side	2.520	1	33.03	<0.001
Within ants				
Sector	2.657	1	44.80	<0.001
Sector × travel direction	9.448	1	158.14	<0.001
Sector × bridge side	0.004	1	0.07	0.792
Sector × travel direction × bridge side	0.321	1	5.37	0.021

As ants were individually followed across the two sectors, the sector effect was treated as a repeated measure factor. The data were log-transformed to allow for normality.

$P<0.001$, $\eta_p^2=0.074$): ants spent more time crossing the bottleneck than the entrance when they were travelling towards the centre than when they were travelling out of the centre. Overall, the effect of travel direction was significant for both sectors (Table 1; $P<0.001$, $\eta_p^2=0.036$), and the time spent crossing the two sectors did not depend on whether ants came from or went to the food source or the nest (Table 1; $P=0.301$). The other significant effects accounted for a minor part of the total variance (Table 1). We conclude from this analysis that the ants going to the centre of the bridge were slowed down in their progression at the level of the two bridge constrictions. This was not the case for the ants moving away from the centre. This asymmetry suggests that ants coming away from the centre are given way by the ants coming from the opposite direction.

Close observations of the encounters occurring at the level of the two bridge constrictions between ants travelling in opposite directions indeed show that the majority of ants travelling towards the centre stopped and gave way to those coming from the opposite direction, whether a contact occurred or not during the encounter (in 99 out of 105 and in 103 out of 106 encounters with contact, for the nest and source side of the bridge, respectively, and in 86 out of 87 and in 166 out of 168 encounters without contact, for the nest and source side of the bridge, respectively; see Movie 2 in supplementary material). The proportion of ants that encountered another ant at the level of the bridge constriction was the same for the nest and source side of the bridge (0.47 and 0.51 respectively, $\chi^2=0.84$, $P=0.358$).

To check whether the delay we observed in ants crossing the bottlenecks towards the centre (Fig. 6) was due to the time lost during an encounter at the level of the bridge constrictions, and not to an increased time lost in interactions while crossing the bottleneck, we selected a sample of ants that did not encounter another ant at the level of the bridge constrictions. We then compared the time that these ants spent crossing successively the bottleneck and the entrance of the bridge. These times were not significantly different (mean ± S.D., 1.09±0.10 s *vs* 1.23±0.04 s; Student's *t*-test for matched samples; $t=-1.74$, $P=0.084$), showing that indeed the delay in crossing the bottlenecks was essentially due to the ants stopping and giving way to those coming from the opposite direction, and not to the interactions occurring inside the bottlenecks.

Model

To better understand the interaction rules governing the organization of traffic on the bridge, we devised a model that we implemented in a 'Monte-Carlo' simulation. The model, based on the interactions measured in the experiments, describes the traffic on the bridge in both directions (inbound and nestbound). The simulation output gives the distribution of the size of the groups travelling in both directions.

The bridge in the model is divided into five different sectors, as in the experiments: one bottleneck followed by one entrance at both ends of the bridge, and a single central sector. The model is not spatially explicit, i.e. the lengths of each sector are not encoded in the model. Interactions between ants are considered only at the level of the bottlenecks and the entrances. Interactions occurring on the central part of the bridge are ignored. Since no significant effect of bridge side on the behaviour of the ants was found in the experiments, the behavioural rules followed by ants at either side of the bridge were the same in the model. A time step in the simulation lasts 0.5 s, and the simulations were run for 7200 time steps, corresponding to 1 h of experiment.

The first decision concerns the arrival of an ant in the bottleneck. At each time-step there is a probability, p, that one ant leaves the nest and enters the bottleneck on the nest side of the bridge. As the inbound and nestbound flows of workers were equal in the experiments, the probability to leave the food source and to enter the bottleneck on the source side of the bridge is also set to p. The value of the probability p corresponds to the value of the flow parameter. In the simulations, a random number is sampled from a uniform distribution between 0 and 1. If its value is less than or equal to p an ant enters the bottleneck.

The second decision corresponds to the crossing of the line between the bottleneck and the entrance on both sides of the bridge. If the entrance is empty, i.e. if there is no ant coming from the opposite direction, the ant in the bottleneck always enters the entrance. On the other hand, when the ant in the bottleneck is facing another ant in the entrance, coming from the opposite direction, the latter always has priority. The ant in the bottleneck gives way and does not move until the ant in the entrance has completely entered the bottleneck. This priority rule is always followed except if the ant in the bottleneck follows a previous ant that has just entered the entrance, in which case it has priority over the ants in the entrance. This

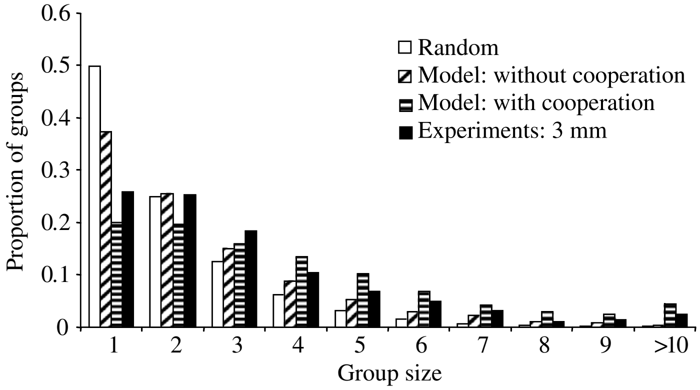

Fig. 7. Simulation results. Distribution frequency of the size of the groups of successive ants travelling in the same direction at the level of the line between the bottleneck and the entrance on the nest side of the bridge when the simulations were run with a flow of ants entering the bottlenecks of the bridge equal to 0.5 ants per time step, corresponding to the flow measured in the experiments on a 3 mm bridge. The simulations were run with and without implementing a cooperative rule between following ants. For explanations on the random distribution, see Fig. 5.

effect corresponds to a cooperative behaviour between ants because the second ant benefits from the passage of the first ant. When this rule is not introduced, we consider that there is a non-cooperative behaviour.

To take into account the fact that ants can follow each other very closely when the number of ants in the bottleneck or in the entrance is greater than one, there is a probability, q=0.33, that, during the same time step (0.5 s), one ant crosses the line between the bottleneck and the entrance, and a probability $(1-q)$ that two ants cross the line within the same time step. The probability that three or more ants cross the line during one time-step is equal to zero. This value is based on measurement of the time delay between two ants following each other and crossing the line between the bottleneck and the entrance. This delay was less than 0.4 s (0.5 s) for 31% (51%) of the total number of pairs of successive ants (N=242 pairs). The fraction of groups of three or more ants crossing the line during the same time step is negligible. Seven percent of the groups of three ants (N=135) took less than 0.5 s to cross the line; for larger groups (4, 5 and 6 ants; N=183), this time was always greater than 0.5 s. The time required for an ant to cross the central part of the bridge is set to a constant value of τ=12 time steps (6 s), corresponding to the mean time required for an ant to cross the centre of the bridge.

First, we ran the simulations with a value of p equal to 0.5, corresponding to the average flow of ants we observed in our experiments (~60 ants min^{-1}). The distribution of group size we obtained when the cooperative effect was implemented in the model is close to the experimental one (Fig. 7), although a little bit skewed towards high-size groups. In the absence of a cooperative effect, however, the distribution is closer to the theoretical distribution, corresponding to a random sequence of workers, than to the distribution observed in the experiments.

When we explored the model for different values of p, we found that for small values of p ($p \approx 0.1$) the distribution of group size was different from a random distribution (Fig. 8). The mean group size was close to 2 (Fig. 8, inset). Up to a value of p=0.35, the distribution was weakly modified: the most frequent size was 1, and the greater the size of the group, the lower its frequency. When p took values higher than 0.35, the mean size of the group increased abruptly. For p=0.6, large-size group became predominant.

Discussion

This study shows that crowding induced by a reduction of path width is avoided in ants by a change in the temporal organization of the flow of individuals going to and coming back from a food source. When path width decreases, the rate of contacts between workers coming from opposite direction is regulated by a desynchronisation of inbound and outbound traffic. This desynchronisation limits the number of head-on encounters and thus allows the decrease in travel duration. The

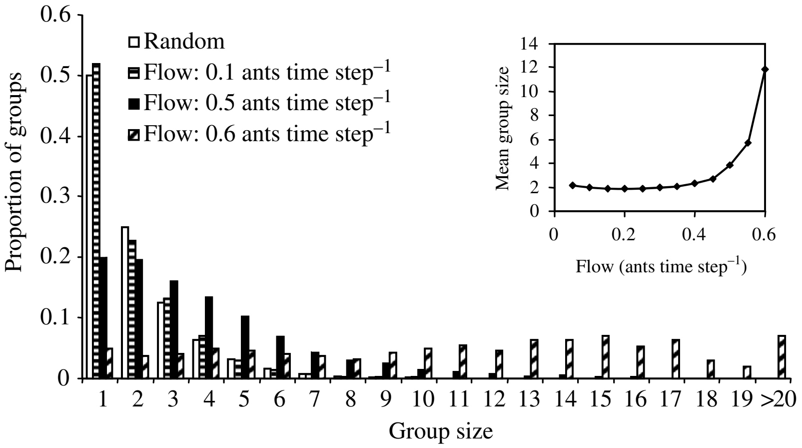

Fig. 8. Simulation results. Distribution frequency of the size of groups of successive ants travelling in the same direction at the level of the line between the bottleneck and the entrance on the nest side of the bridge, when the simulations were run with increasing values of the flow of ants entering the bridge. For explanations on the random distribution, see Fig. 5. The inset shows the mean group size obtained for different values of entrance flow.

same rate of food return to the nest is maintained, whatever the path width.

We found that the duration of travel of *L. niger* workers moving on a recruitment trail was significantly affected by the number of contacts with other ants. This result concords with that found by Burd and Aranwela (2003) in *Atta cephalotes*. In the latter species, however, the effect of encounter rate on the speed of the ants is small compared with the effect of their size and the mass of the load they carry. In *L. niger*, crop load does not have an influence on forager speed, since the speed of outbound emptied ants and nestbound loaded ants is not significantly different (Mailleux et al., 2000). Therefore, in the absence of polymorphism in *L. niger*, the overall increase in travel duration observed on a narrow bridge compared with a wider bridge is essentially explained by a higher rate of contact.

Independent of contact rate, we found that the duration of travel was slightly higher on a wide bridge than on a narrow bridge (multiple regression of Fig. 3; bridge effect). This result is related to the fact that the time lost per contact was slightly higher on a wide bridge than on a narrow bridge (Fig. 3; differences in the slope of the two regression lines). This could be due to the fact that the value of the angular deviation induced by a head-on encounter on a wide bridge could be larger than on a narrow bridge since ants have more lateral space available to stray from their initial trajectory. Finally, the duration of travel in the absence of contacts was slightly longer when traffic volume was low (60 ants min^{-1}; 2.96 and 2.93 s, for 10 mm and 3 mm bridge, respectively) than when it was high (120 ants min^{-1}; 2.46 and 2.49 s, for 10 mm and 3 mm bridge, respectively). This result suggests an effect of the concentration of the trail pheromone on the speed of the ants. Indeed, the concentration of the trail pheromone is directly related to the volume of traffic on the bridge and it is known that the speed of the ants increases with the concentration of the pheromone on the trail they follow (Beckers et al., 1992; see also Franks et al., 1991 in *Eciton burchelli*; Roces and Nuñez, 1993 in *Acromyrmex lundi*).

Surprisingly, in spite of the fact that the volume of traffic did not vary with bridge width (Fig. 2), the mean rate of encounters per ant on a narrow bridge was lower than that on a wide bridge. This means that ants regulate their density on a narrow bridge in order to avoid the delay incurred by too high a rate of contact. The analysis of the sequence of out- and nestbound ants reveals that this regulation is allowed by a change in the temporal organization of the traffic on the bridge. Whereas on wide bridges this sequence is not different from random, on narrow bridges alternating groups of inbound and outbound ants were observed. This organization limits the number of head-on encounters because ants progress on the bridge as clusters of individuals moving in the same direction.

Examination of the sequence of out- and nestbound ants at different levels of the bridge shows that clusters arise at the bridge bottleneck. Ants arriving in the bottleneck give way to ants coming from the narrow part of the bridge and therefore accumulate at the level of the constrictions. When the path is free, the waiting ants cross the narrow part of the bridge, where they are given way by ants in the bottleneck at the other side. The mere presence of a bottleneck did not induce an additional delay in the ant progression, as shown by the fact that the ants that did not encounter another ant at the level of the bridge constriction spent the same amount of time crossing the bottleneck and the entrance. Examination of the sequence of inbound and outbound ants at different levels of the bridge shows that the clusters did not exist before the bottlenecks and thus that they were not formed at the departure from the nest or the food source.

The system is completely symmetrical and the mechanisms generating the ant clusters are the same at both ends of the bridge. This means that loaded ants coming from the food source do not behave differently from emptied ants coming from the nest. The rules are different in species carrying external loads. In the leaf-cutting ant *Atta colombica*, for example, workers carrying a leaf fragment and coming back to the nest are always given way by the workers going to the food source (Dussutour, 2004). This behaviour has also been observed in the workers of army ants loaded with prey items (*Dorylus* sp., Gottwald, 1995; *Eciton burchelli*, Couzin and Franks, 2002) or in the termites *Longipeditermes longipes* and *Hospitalotermes* loaded with food pellets (Miura and Matsumoto, 1998a,b). The priority towards loaded ants generally results in the emergence of lane formation, with loaded workers progressing in the centre of the recruitment column and outbound unloaded ones moving on both of its margins. Although workers of *L. niger* transporting a full crop load of sugar solution are bigger than emptied ones because of their distended abdomen, they are not as bulky and may not be as ill-at-ease as the workers of the species transporting external loads. This probably explains the differences in priority rules observed between species of ants carrying internal and external food load.

The priority rules we identified in our experiments are similar to those observed when branching occurs on a path at high traffic density; when an ant that has just engaged on one branch encounters another ant coming from the opposite direction it is immediately redirected to the other branch (Dussutour et al., 2004). The ant that gives way is thus always the one that has the possibility to do it, whether by veering towards the other branch at a bifurcation or by moving aside and waiting before entering the narrow passageway, as in our experiment.

We were unable to detect a periodicity in the alternating groups of inbound and outbound ants, either regarding the size of the clusters or on a temporal scale. We hypothesize that there was too much fluctuation in the interval of time between ants coming from the nest or the food source to generate clusters of ants of equal size alternating regularly over time: as soon as there was a gap in the group of ants coming from the narrow part of the bridge, ants waiting in the bottlenecks went ahead. Our theoretical model shows that a periodicity could have been generated with a stronger cooperative effect between ants, i.e. by extending beyond the second following ant the cooperative effect due to the passage of a first ant in the entrance from the bottleneck.

The model shows how the interplay between the value of the flow and the priority rules governs the formation and the size of the clusters. For low flow of ants, the distribution of the size of the clusters obtained through the simulations is similar to a random distribution, whereas for a flow corresponding to the experiments, the distribution is close to the experimental one. Most importantly, the model underlines the importance of cooperation between ants: without cooperative effect, no desynchronisation emerges for the values of the flow corresponding to those observed in the experiments. Moreover, the model predicts a collective phenomenon similar to a phase transition: the mean size of the cluster remains constant (close to a value corresponding to randomness) for $P<0.4$ and increases abruptly afterwards.

The temporal organization of the flow of ants we observed is reminiscent of that observed in bidirectional pedestrian flows moving through a narrow passageway in a corridor (Helbing et al., 2005). The speed of individuals is reduced at the level of the bottleneck, and oscillations in the passing direction are observed. When an individual enters the bottleneck, it is immediately followed by other individuals. This releases the pressure in the pedestrian crowd on one side of the passageway while it increases the pressure on the other side. When the pressure difference becomes too large, the people from the other side enter and pass the bottleneck. For long, narrow passageways, the frequency of the oscillations decreases and there is a high tendency for the passageways to be passed by clusters of individuals moving in the same direction rather than by single individuals, which is exactly what we observed in ants. In ants, as in pedestrians, 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 (Helbing et al., 2001).

The temporal organization of flow that we observed in our experiments should be particularly adapted to the movement of ants through the tunnels of their hypogaeic nest. In *L. niger*, the subterranean galleries have a small diameter (down to 2 mm, allowing the passage of a maximum of two individuals) and their length ranges from 4 to 12 cm (Rasse, 1999), which includes the length of the bridge we used in our experiments. One can thus imagine that, up to a critical flow volume for which clogging may occur, the temporal organization we observed will allow maintenance of the same flow of individuals through a gallery without engaging in the costly work of enlarging it (Berghoff et al., 2002).

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