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ORIGINAL ARTICLE

Collective decisions in ants when foraging under crowded conditions

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Abstract In this paper we examine the effect of crowding on the selection of a path in the mass-recruiting ant *Lasius niger*. In our experiment, ants had to go from their nest to a food source by crossing a diamond-shaped bridge, giving the choice between two paths. Two types of bridges were used: the first had two branches of equal length but different width while the second had two branches of different length and width. Experiments at high traffic volume always ended up with the selection of the wider branch, even if it was longer. This result shows that overcrowding on the narrow branch plays an essential role in the mechanism underlying the choice of route in ants. A mathematical model was developed to evaluate the importance of two mechanisms that could account for this result. The first is based on the difference in travel duration between the two paths. The second is based on the repulsive interactions between workers making head-on encounters. The model shows that travel duration *per se* is not sufficient to explain path choice. Rather, it is the interplay between trail following behaviour and repulsive interactions that allows ants to choose the path that minimizes their travel time. When choosing a path ants thus prefer to trade time against energy. Our results demonstrate that any environmental constraint that alters the dynamics of trail recruitment can lead to the emergence of adaptive foraging decisions without any explicit coding of information by the foragers at the individual level.

Keywords Formicidae · Ants · *Lasius niger* · Recruitment · Collective behaviour · Foraging

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Introduction

Central-place foraging animals sometimes exploit abundant food sources that require several trips to be retrieved in totality. In that case they have to decide at which location they will establish a path in their environment and, in doing so, they are faced with a trade-off between different factors, each associated with specific costs and benefits. In addition, complexity is added in central-place foragers that exploit food resources collectively. In ants, for example, path choice between the nest and a food source not only depends on factors acting at the individual level, but also on factors acting at the collective level (Dussutour et al. 2005a).

The formation of a recruitment trail is based on the amplification of random fluctuations of pheromone deposits of the first returning ants (Heredia and Detrain 2005). Therefore, the factors that act at the individual level are the most important in the initial stage of the trail development. The path chosen by a scout ant can be influenced by external factors, such as the physical structure of the environment (Dussutour et al. 2005a) and the risk associated with a particular path (Nonacs and Dill 1988; Nonacs 1990), or by internal factors, e.g., the ant's spatial knowledge of the environment (Collett and Collett 2004). The formation of a recruitment trail also depends on the nature of the substrate on which the pheromone was deposited by the scouts (Detrain et al. 2001) and on the propensity of the scouts to lay a trail. This latter is influenced by many factors, e.g., food characteristics (Beckers et al. 1992a; Portha et al. 2002; Le Breton and Fourcassié 2004), presence of brood (Portha et al. 2002, 2004), or colony size (Mailleux et al. 2003).

Once a trail has been initiated, traffic rapidly grows and its stabilization along a certain path depends essentially on factors that act at the collective level. The trail can become unstable if overcrowding occurs because some of its sections are too narrow to allow a high volume of traffic. Overcrowding can slow down the progression of the ants and thus lead to a decrease in traffic flow (Burd et al. 2002; Burd and Aranwela 2003; Dussutour et al. 2005b). Ants have developed particular strategies to prevent traffic congestion on recruitment trails. On a long-lasting recruitment trail ("trunk-trails") they can clear debris on the trail (Howard 2001) or enlarge it to support a high volume of traffic (Berghoff et al. 2002; see also Bruinsma 1979 for termites). On relatively ephemeral recruitment trails on the other hand, they can overcome congestion effects without lowering their flow by using several different strategies. When the trail is wide enough ants can be spatially organized with a distinct central lane of returning laden workers, flanked by two lanes of outbound foragers (army-ants: Couzin and Franks 2002; leaf-cutting ants: Dussutour 2004). When the trail is too narrow, either the flow can be temporally organized with alternating clusters of inbound and outbound ants (Dussutour et al. 2005b) or part of the traffic can be diverted onto another path (Dussutour et al. 2004). All these phenomena arise through self-organized processes without explicit measure of the density of ants at the individual level.

In this paper, we investigate the choice of a path by an ant colony when traffic congestion occurs along a trail. We carried out a series of laboratory experiments with a simple experimental set-up consisting of a diamond-shaped bridge placed between the ant nest and a food source, offering the choice between one short narrow branch and one long wide branch. In the absence of overcrowding the ants should choose the shortest path to the resource (Goss et al. 1989; Beckers et al. 1992b), whereas congestion may alter their preference so that a longer, less congested path is preferred over a shorter more congested one. We investigate the colony choice according to traffic volume and measure the individual behaviors that could be responsible for the selection of a particular path. Then a theoretical model helps us to determine the mechanisms that account for the collective choice observed in the experiments.

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 five colonies of 4,000–5,000 workers in Toulouse (Southwest France) in September 2001. Each of these colonies was subdivided into two to three queenless colony fragments, each containing 1,000 workers without brood, yielding a total of 12 colony fragments. A few hundred workers were kept in the stock colonies to maintain a stable number of ants in the colony fragments throughout the duration of the experiment.

Each colony fragment was housed in a plastic box of 100 mm in 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 (∅ 130 mm) with walls 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 12:12 light/dark photoperiod. We supplied ants with water and a mixed diet of vitamin-enriched food (Bhaktar and Whitcomb 1970) and maggots of *Calliphora erythrocephala* three times a week.

Experimental set-up and protocol

The experiment consisted of two treatments, each performed with one particular type of bridge (Fig. 1). The first treatment manipulated crowding only using a bridge that had two branches of equal length (L=80 mm) but different width, i.e., a narrow branch (w=3 mm) and a wide branch (w=10 mm). For the second treatment we manipulated both crowding and travel time using a bridge that had two branches of different length and width, i.e., a long and wide branch (L=120 mm and w=10 mm) and a narrow and short branch (L=80 mm and w=3 mm).

We replicated each treatment 15 times using the 12 colony fragments originating from our five different colonies. To obtain 15 replicates, three colony fragments were tested twice in each treatment. Because the two replicates on the same colony fragment were run at a 10-day interval, we assumed that they could be considered as independent. All replicates were thus treated as independent statistical units. Throughout the experiments the traffic on the bridge was filmed from above for 60 min.

Before each replicate, the colony fragment was starved for 5 days and the replicate started when the ants were given access to a food source placed on a platform (70×70 mm) at the other end of the bridge. The food consisted of 5 ml 1 M sucrose solution contained in a small cavity carved in a block

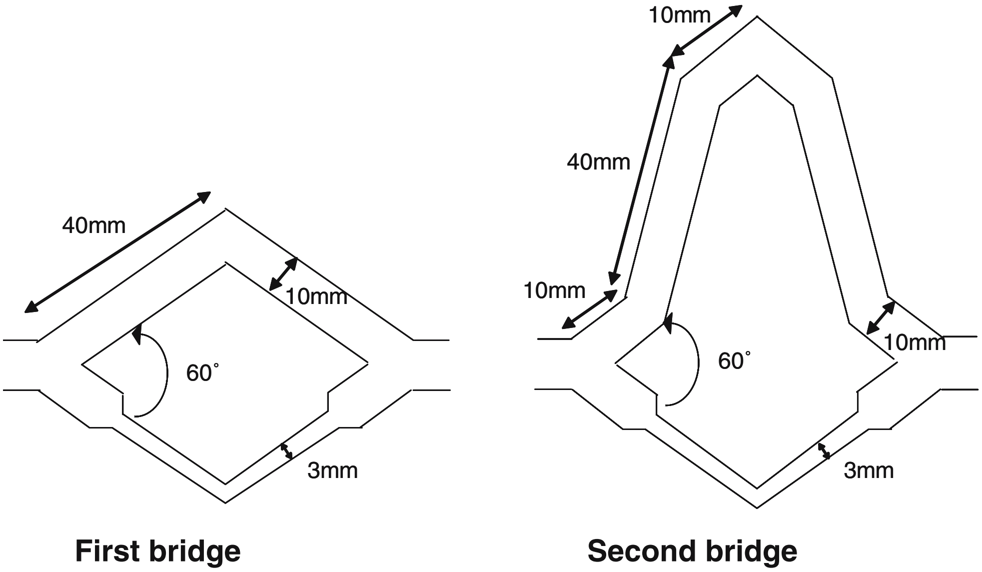

Fig. 1 Bridges used in the two treatments of the experiment

of paraffin wax. To prevent crowding effects at the food source, the cavity had a star-shaped form with dented edges so that a very large number of ants could access the food. The whole experimental set-up was isolated from any sources of disturbance by surrounding it with white paper walls.

Collective level

To assess traffic flow we measured the traffic on the bridge at 1-min intervals every 3 min for 1 h. Counting began as soon as the first ant discovered the bridge and climbed onto it. For both treatments we measured the flow of outbound and inbound ants at a point 1 cm from each choice point into each branch. We repeated this procedure for the 15 replicates and used a two-way ANOVA with repeated measures on time to test for the effects of treatment and time interval on the flow of workers.

To test whether ants preferred one branch over the other (asymmetric distribution) or whether they showed no preference (symmetric distribution), we used a binomial test on the number of ants traveling on each branch in each replicate. The null hypothesis was that ants choose both branches with equal probability (Siegel and Castellan 1988). We arbitrarily assumed that a branch was selected when the binomial test showed a significantly higher number of foragers on one branch.

Individual level

There are two mechanisms that could systematically lead to the collective selection of the wider branch, whatever its length. These mechanisms are based on (1) the difference in travel duration between the two branches of the bridges, owing to a higher initial level of congestion on the narrow branch, or (2) the differential occurrence of intrinsic U-turns at the entrance of the two branches of the bridges. The first mechanism is responsible for the choice of the shorter of the two paths with otherwise equal characteristics in the Argentine ant *Linepithema humile* (Goss et al. 1989), while the second is responsible for the selection of the shorter of the two paths in the ant *L. niger* (Beckers et al. 1992b). To test each of these mechanisms we analyzed several parameters at the individual level.

Travel duration and interaction between ants

The gross travel duration (i.e., including the time spent in interactions) was measured on the three branch types (short narrow, short wide, and long wide) that ants could encounter in the experiment. For the short narrow branch and the short wide branch, the gross travel duration was estimated from two different replicates of the first treatment (first bridge type). One replicate was characterized by the selection of the short narrow branch (see above for the statistical procedure used to decide whether a branch was selected or not) and the other was characterized by the selection of the short wide branch. For the long wide branch, we chose one replicate of the second treatment (second bridge type) characterized by the selection of the long wide branch. All replicates chosen were characterized by the same volume of traffic, which allows us to isolate the effects of branch width and branch length on travel duration. 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 replicate when the outbound and nestbound flow of ants were at equilibrium. We followed the first 100 outbound and 100 inbound ants traveling on the branch and measured the gross travel duration of those ants that crossed the branch completely.

To assess the impact of the encounter rate on travel duration, we also counted for each ant followed, the number of times it passed another ant traveling in the same or opposite direction. Encounters with and without physical contacts were distinguished. A contact could be the result of either a head-on collision or a rear-end collision (when the head of an ant enters in contact with the gaster of the ant preceding it). The probability to be contacted during an interaction was estimated by the slope of the regression line describing the relationship between the number of encounters with contact and the total number of encounters with or without physical contact. The time lost per contact was estimated by the slope of the regression line describing the relationship between the gross travel duration and the number of encounters in which a physical contact occurred.

U-turns

Three categories of U-turns can be distinguished in our experiment. The first category of U-turns (intrinsic U-turns) is due to the deviation of the branch from the direction of the nest or the food source. They are generally observed at some distance from the choice point. When ants are confronted with two branches of unequal length these U-turns play an important role in the initial selection of the shorter branch because they appear with a higher frequency on the longer branch (Beckers et al. 1992b). This initial selection is then amplified by the autocatalytic properties of the trail and eventually leads to the choice of the shorter branch.

The second category of U-turns (trail-based U-turns) is due to the difference in pheromone concentration between the two branches. They are observed just after the branch forks. These U-turns occur when an ant chooses the less used of two branches and immediately turns back because it has perceived a large difference in the concentration of the trail pheromone before and after the fork. Most of the time trail-based U-turns occur before the ants pass 1 cm onto the selected branch. Unlike intrinsic U-turns, these U-turns cannot by themselves cause the selection of the shorter branch. However, they increase the rate at which initial differences, such as those generated by other mechanisms like intrinsic U-turns, are amplified.

In our experiment we observed in addition a third category of U-turns, which we called induced U-turns (Dussutour et al. 2004). We consider that an ant makes an induced U-turn if it has already entered onto a branch and turns back to the branch fork after colliding with another ant coming from the opposite direction. Note that these U-turns, contrary to those previously described, do not occur spontaneously because they are a direct consequence of a contact. Induced U-turns are bound to be more frequent on highly congested branches because of the higher rate of contacts. In our experiment they could give an initial advantage to the longer branch.

To measure the frequency of the different categories of U-turns, we followed all ants leaving the nest and the food source during the 6 min that followed the return of the first ant to the nest. We noted which branch they selected first and if they crossed it completely. We also measured the number of each category of U-turns. To compute the probability of induced U-turns we counted the number of contacts between ants that were followed by a U-turn along the whole length of the branch. For the first treatment (first bridge type), we chose two replicates characterized by the selection of the wide branch and for the second treatment (second bridge type) we chose two replicates characterized by the selection of the long and wide branch.

Model

The relative contribution of the two mechanisms (travel duration and U-turns) to the selection of the wider branch was explored by an analytical model describing the change in the concentration of the trail pheromone and the resulting traffic of ants over each branch (see Appendix). The different types of steady-state solutions were identified, allowing us to construct the full bifurcation diagram.

The model is based on a previous model we developed to account for the symmetrical traffic observed at high traffic volumes on diamond-shaped bridges (Dussutour et al. 2004). It assumes that the flow of ants has reached equilibrium, i.e., that the flow is equal in both directions. This occurs in a matter of minutes in the experiments.

Initially, the branches have the same probability to be chosen, but they differentiate as soon as at least one individual has chosen a branch and laid a quantity of pheromone. The choice of branch 1 or branch 2 at either choice point of the bridge is governed by P_1 and P_2, respectively, in the equation

$$P_1 = \frac{(k_1 + C_1)^n}{(k_1 + C_1)^n + (k_2 + C_2)^n} = 1 - P_2 \tag{1}$$

Equation 1 is a simple choice function, which quantifies the way an ant makes its decision at a choice point, depending on the values of C_i, the concentration of the pheromone on the branches (Goss et al. 1989; Beckers et al. 1992a). The parameter n determines the degree of nonlinearity of the choice: A high value of n means that if the amount of pheromone is slightly higher on one branch, the next ant that arrives at the branch fork will have a very high probability of choosing it. k_i corresponds to the intrinsic degree of attraction of the unmarked branch i. Based on a previous study with a similar set-up in which a relationship was established between the proportion of ants choosing a branch and the frequency of their trail deposition, Beckers et al. (1992a) fitted Eq. 1 for *L. niger* with $n=2$ and $k_1=k_2=6$.

The analytical model was implemented in the form of Monte-Carlo simulations (Gillespie 1992). The advantage of this type of approach is that one can directly simulate the process of interest by modeling it at a probabilistic level, rather than solve master type equations (Van Kampen 1981). In such a numerical experiment the random aspects of the process are thus automatically incorporated. We can summarize the different steps of our simulation model as follows:

In the initial conditions the pheromone concentration and number of ants over each trail are fixed to zero. The first decision concerns whether an ant arrives at the choice point or not. This probability is given by the normalized value of the flux ϕ measured in the experiments. A random number is sampled from a uniform distribution between 0 and 1. If its value is less than or equal to ϕ, an ant comes to the choice point. The second decision is the choice of a branch. The choice of a branch is governed by Eq. 1 and is implemented by sampling a random number from a uniform distribution between 0 and 1. If this number is less than or equal to the value of P_1, the ant will follow and lay a trail on branch 1. If this number is greater than P_1, it will follow and mark on branch 2. When an ant chooses branch i, it lays a quantity q_i of pheromone that gradually disappears through the parameter ν, νC_i being the rate of pheromone evaporation. Hence, the probabilities given by Eq. 1 are updated at each simulation step according to the actual pheromone concentrations. The process is repeated for a number of steps sufficient to reach the stationary state where the total quantity of pheromone over the two branches is constant.

All statistical tests were conducted with SPSS for Windows (version 10, SPSS, Chicago, USA). All means in the text are given $\pm\mathrm{CI}_{0.95}$. The probabilities given in the text are always two-tailed.

Results

Collective level

The traffic volumes in both directions and the recruitment dynamics were not significantly different between the two treatments (Fig. 2; two-way ANOVA with repeated measures on time interval: treatment effect $F_{(1,28)}=0.001$ and $P=0.974$, and interaction treatment × time effect $F_{(19,28)}=0.497$ and $P=0.964$) and were typical of a trail-recruitment process (Pasteels et al. 1987). The flow reaches a peak after about 12 min (Fig. 2; time effect $F_{(19,28)}=17.268$ and $P<0.001$).

In both treatments most ants traveled on only one branch of the bridge after 1 h (in 14 out of 15 replicates in the first treatment, and in all 15 replicates in the second treatment). Thus, in only one replicate did the ants choose neither of the branches. In 12 out of the 15 replicates of the first treatment and in 11 out of 15 replicates of the second treatment, ants showed a significant preference for the wide branch (binomial test $P<0.05$ in these cases; Fig. 3a).

The total number of ants crossing the bridge after 1 h was significantly higher when the wide branch was selected than when the narrow branch was selected (Mann–Whitney U test $U=34$ and $P=0.049$). When the total number of ants crossing the bridge was higher than 5,000 individuals, all replicates of the experiment ($n=15$) ended with the selection of the wide branch.

Individual level

Collective choice generated by travel duration

We used a multiple regression model with dummy variable coding (Aiken and West 1991) to study the effect of branch width and branch length on the probability to contact another ant.

We first tested the effect of branch width and took the short and narrow branch as the branch of reference in the analysis. This branch was compared to the short and wide branch with a first dummy variable, D_1, and to the long and wide branch with a second dummy variable, D_2. The number of encounters per ant was centered on its mean. This procedure is recommended in multiple regression analysis to prevent multicolinearity problems (Aiken and West 1991). The general equation of the model, the coding for the dummy variables, and the results of the analysis are indicated in Table 1.

The multiple regression model was significant ($F_{(5,471)}=1{,}932.61$ and $P<0.001$) and accounted for 95% of the total variance. The regression line describing the relationship between the number of contacts and the number of encounters for the branch of reference had a slope ($b_3=0.76$) and intercept ($b_0=5.78$) significantly different from 0. The slope of this regression line was significantly different both from that computed for the short and wide branch (slope difference $b_4=-0.44$) and from that computed for the long and wide branch (slope difference $b_5=-0.44$). Owing to the difference in ant density, the number of contacts for the mean number of encounters was much higher on the branch of reference than both on the short and wide branch (intercept difference $b_1=-2.81$) and on the long and wide branch (intercept difference $b_2=-3.05$). We conclude that there was a significant effect of branch width on the probability to contact another ant.

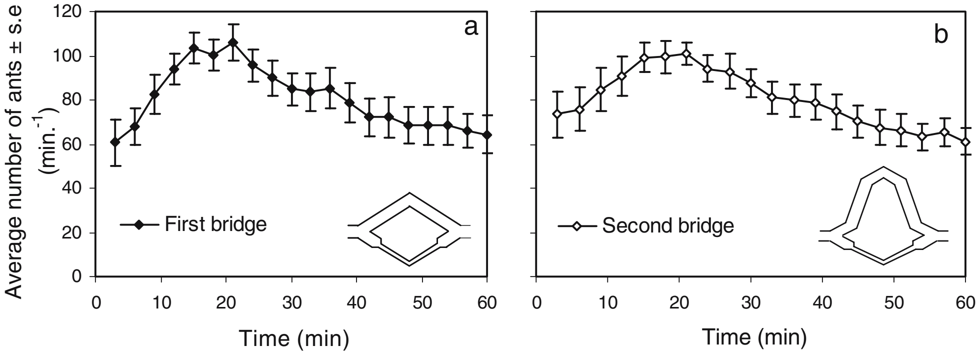

Fig. 2 Average number of ants per minute crossing **a** the first and **b** second type of bridge in both directions every 3 min. n=15 replicates for both bridges

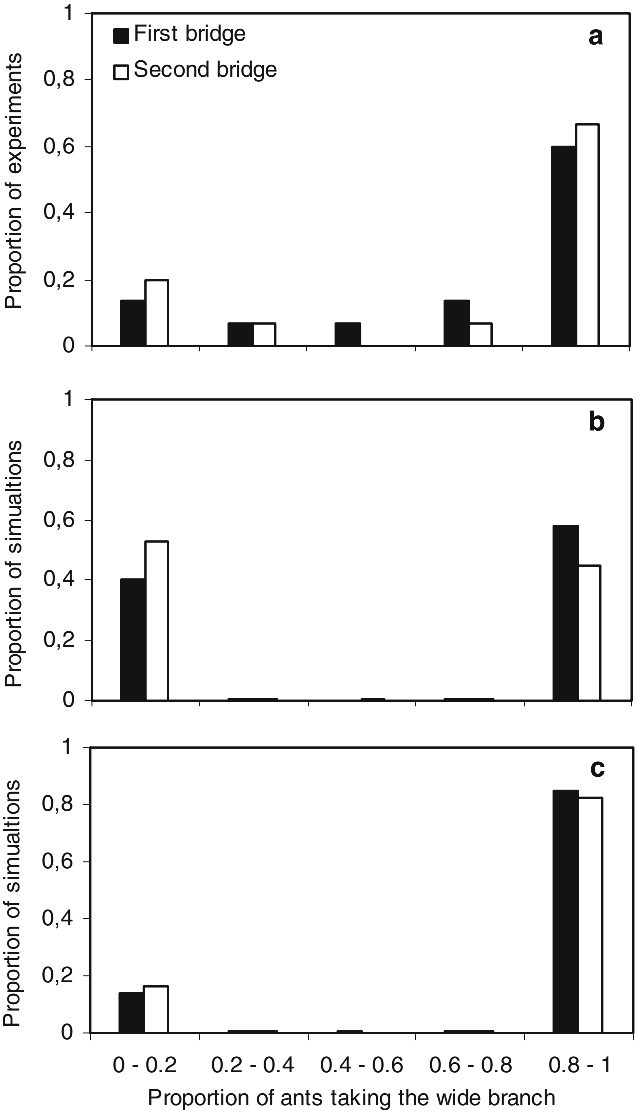

Fig. 3 **a** Experimental frequency distribution of the proportion of ants taking the wide branch in the first treatment (n=15) and the long and wide branch in the second treatment (n=15) 1 h after the beginning of the experiment. **b**, **c** Results of the Monte-Carlo simulations, which take into account **b** only the travel duration on each branch and **c** the U-turn probability on each branch. The simulations are averaged over 1,000 runs

The slopes of the simple regression lines describing the relationship between the number of contacts and the number of encounters for each branch (Fig. 4) indicate that the probability to contact another ant was indeed significantly higher for the short and narrow branch (0.71±0.18) than for the short and wide (0.31±0.19) or the long and wide (0.29±0.13).

We then tested the effect of branch length and took the long and wide branch as the branch of reference in the analysis. This branch was compared to the short and wide branch with a first dummy variable, D_1, and to the short and narrow branch with a second dummy variable, D_2 (Table 1). This model is similar to the previous one and is used only to compare the probability to contact another ant between the long and wide branch and the short and wide branch. The two results of interest here are the fact that the slope and intercept of the regression line describing the relationship between the number of contacts and the number of encounters for the branch of reference are not significantly different from that computed for the short and wide branch (slope difference b_4=−0.01 and intercept difference b_1=0.24; Table 1). We thus conclude that there was no significant effect of branch length on the probability to contact another ant.

Because the range of the number of contacts for the different types of branches were quite different, we were not able to use a multiple regression model to test the relationship between the gross travel duration and the number of contacts across the different types of branches. We therefore conducted a simple regression analysis on the data for each branch type.

Whatever the branch type, travel duration increased significantly with the number of contacts. The regression analysis yielded a significant relationship for the three types of branches ($F_{(1,127)}$=798.42 and P<0.001, $F_{(1,180)}$=849.73 and P<0.001, and $F_{(1,162)}$=529.22 and P<0.001 for the short and narrow, the short and wide, and the long and wide branches, respectively) and accounted for 86.3, 82.5, and 76.9% of the variance. The mean gross travel duration, i.e., the travel duration with contacts, differed significantly among the three types of branches (one-way ANOVA

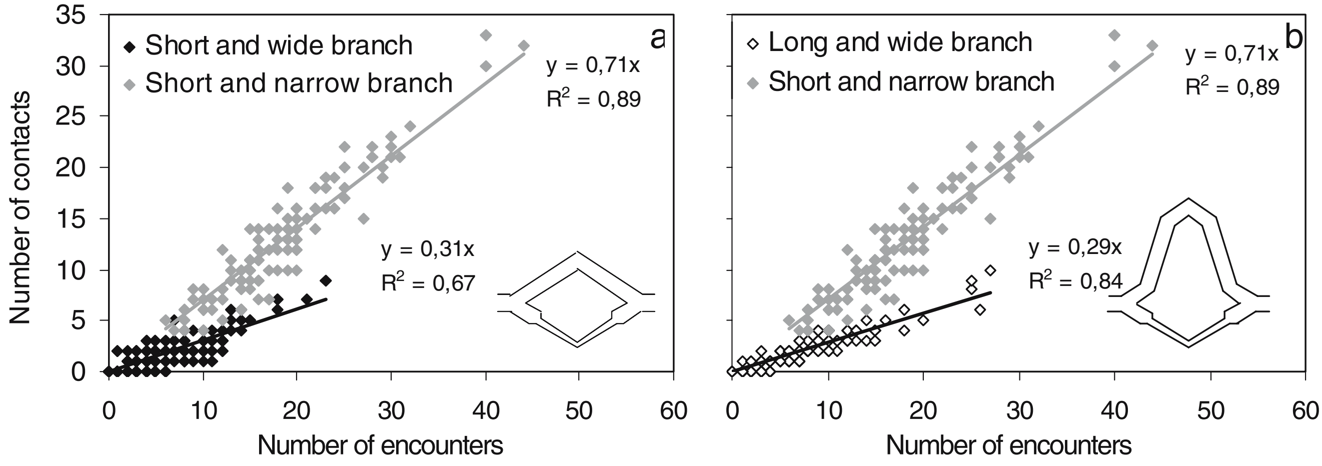

Fig. 4 Relationship between the number of encounters with a physical contact and the total number of encounters per ant with or without a contact for each of the three branches used in the experiment in **a** the first and **b** the second treatment. The *slopes* of the *lines* correspond to the probability for an ant traveling on the bridge to be contacted by another ant during an encounter. n=183, n=130, and n=164 for the short and wide branch, the short and narrow branch, and the long and wide branch, respectively

Table 1 Multiple regression analyses with dummy coding testing the relationship between the number of encounters with physical contact and the number of encounters with or without physical contact across the three types of branches used in the experiment

General equation for the two multiple regression models: $NC = b_1D_1 + b_2D_2 + b_3NEA + b_4(NEA \times D_1) + b_5(NEA \times D_2) + b_0$		
Multiple regression models	D_1	D_2
a. Short and narrow branch as reference branch		
Dummy variable coding		
Short and narrow branch	0	0
Short and wide branch	1	0
Long and wide branch	0	1
Solution equation $NC = -2.81D_1 - 3.05D_2 + 0.76\,NEA - 0.44(NEA \times D_1) - 0.44(NEA \times D_2) + 5.78$		
Joint test of b_1–b_5: R^2=0.95, $F_{(5,471)}$=1932.61, P<0.001		
Test of b_0: t(471)=31.82, P<0.001		
Test of b_1: t(471)=−12.79, P<0.001		
Test of b_2: t(471)=−14.28, P<0.001		
Test of b_3: t(471)=47.04, P<0.001		
Test of b_4: t(471)=−16.35, P<0.001		
Test of b_5: t(471)=−17.34, P<0.001		
b. Long and wide branch as reference branch		
Dummy variable coding		
Short and narrow branch	0	1
Short and wide branch	1	0
Long and wide branch	0	0
Solution equation $NC = 0.24D_1 + 3.05D_2 + 0.32\,NEA - 0.01(NEA \times D_1) + 0.44(NEA \times D_2) + 2.73$		
Joint test of b_1–b_5: R^2=0.95, $F_{(5,471)}$=1932.61, P<0.001		
Test of b_0: t(471)=24.15, P<0.001		
Test of b_1: t(471)=1.40, P<0.161		
Test of b_2: t(471)=14.28, P<0.001		
Test of b_3: t(471)=16.61, P<0.001		
Test of b_4: t(471)=−0.31, P=0.754		
Test of b_5: t(471)=17.34, P<0.001		

Model a is used to test the effect of the width of the branch whereas model b is used to test the effect of the length of the branch

NC Number of encounters with contact and *NEA* number of encounters per ant (centered values) with or without physical contact

$F_{(2,469)}$=335.49 and $P<0.001$). The highest value observed was for the short and narrow branch (13.47±0.98 s), followed by the long and wide branch (6.13±0.26 s), and by the short and wide branch (4.14±0.20 s).

The time lost per contact did not differ significantly between the three types of branches (0.83±0.06, 0.82±0.05, and 0.81±0.07 s for the short and narrow, the short and wide, and the long and wide branches, respectively). The regression analysis indicates that in the absence of contacts, there was no effect of branch width on the time required to cross the bridge (intercept of the regression lines with the null axis 2.96±0.82 and 2.71±0.13 for the short and narrow and the short and wide branches, respectively). Under the same conditions there was, however, as could be expected because ants walked at similar speed, a significant effect of branch length on travel duration (4.67±0.17 and 2.71±0.13 for the long and wide branch and the short and wide branch, respectively).

To test the hypothesis that a difference in travel duration alone is able to generate the collective choice we observed, we performed Monte-Carlo simulations with the average values of net travel duration (without contacts, see values given above) assigned to the parameters of our model, i.e., τ=3 s for the short and narrow branch, τ=2.7 s for the short and wide branch, and τ=4.7 s for the long and wide branch. Similarly, the values of the probabilities of contact ς in the simulations corresponded to those measured in the experiment, i.e., ς=0.7 for the short and narrow branch and ς=0.3 for the short and wide branch and for the long and wide branch. At each time step a random number is sampled from a uniform distribution. If this number is less than or equal to the probability of contact ς, a contact occurs. The time lost per contact was set to 0.8 s and the value of the flow to 0.8 ant s^{-1}. When using such values we found that the proportion of replicates of the simulations in which ants selected the narrow branch was higher than that observed experimentally (Fig. 3b). Therefore, the difference in travel duration alone cannot explain the collective response observed.

Collective choice generated by U-turns

Close examination of the flow on each branch of the two types of bridges used in the treatments shows that up to around 150 s after the onset of a replicate, both branches of the bridges were equally used. A bifurcation occurred afterwards and the majority of ants used the same branch. We thus defined two periods where the first encompassed the time from the return of the first ant to the nest (time 0 s) to 150 s (before the choice), and the second encompassed the time from 150 to 350 s (after the choice) (see Table 2). Because the results for the two replicates of each treatment that were analyzed were not significantly different, we pooled the data of each treatment.

Before the choice point the proportion of ants making a trail-based U-turn differed at most between the narrow and wide branches for the two types of bridges (Table 2). On the second type of bridge, before the choice points, the ants made more intrinsic U-turns on the long and wide branch compared to the short and narrow branch

Table 2 Proportion of ants taking each branch and proportion of ants making different types of U-turns on the branches (pooled for outbound ants) in each treatment, before and after a collective choice occurred for a given branch

	Before the choice (0–150 s)				After the choice (150–350 s)			
	First treatment		Second treatment		First treatment		Second treatment	
Type of branch	Short narrow	Short wide	Short narrow	Long wide	Short narrow	Short wide	Short narrow	Long wide
Branch choice	0.49 P=0.809NS	0.51	0.50 P=0.882NS	0.50	0.17 P<0.001*	0.83	0.17 P<0.001*	0.83
Induced U-turn	0.69 P<0.001*	0.06	0.63 P<0.001*	0.04	0.75 P<0.001*	0.01	0.68 P<0.001*	0.04
Trail-based U-turn	0.51 P=0.672NS	0.51	0.52 P=0.672NS	0.51	0.53 P=0.672NS	0.51	0.54 P=0.672NS	0.51
Instrinsix U-turn	0.03 P=0.636NS	0.02	0.06 P<0.001*	0.33	0.09 P<0.001*	0.02	0.17 P=0.01NS	0.10

Trail-based and intrinsic U-turns were distinguished by the fact that the former occur immediately after the branch forks while the latter occur on the subsequent sections. For each treatment the results of two replicates were pooled. The proportions of ants taking each branch were compared with a binomial test (theoretical probability to take either branch of the bridge=0.5) For the two treatments the proportions of ants making U-turns on each branch were compared with a chi-square test for contingency tables

NS Nonsignificant

*Significant (type I error for each category of U-turn corrected by a standard Bonferroni method; level of significance 0.05/4=0.0125)

(Table 2) because the longer branch deviated more from the source–nest axis than the shorter branch. After the choice points, however, the proportion of ants making intrinsic U-turns on the long and wide branch decreased while it increased on the shorter branch. As for the proportion of induced U-turns, it was always higher on the narrow branch than on the wide branch, whatever the type of bridge and the period of time considered (Table 2). More than half of the foragers made at least one induced U-turn on the narrow branch.

To test the hypothesis that a difference in the frequency of induced U-turns alone was able to generate the collective choice we observed in our experiment, we performed Monte-Carlo simulations with the values of induced U-turn probabilities measured in our experiments assigned to the parameters of our model, i.e., γ=0.7 and γ=0.05 for the narrow and wide branches, respectively. We used the same values as in the preceding simulations for the travel duration, the probability of contact, and the overall flow on each branch.

The results of the simulations are comparable to that of the experiment, confirming that a difference in the probabilities of induced U-turns is sufficient to generate the choice of the wide branch, whatever its length (Fig. 3c).

Analytical model

The analytical model was used to explore the effect of induced U-turns on branch choice at different flows. We explored the model for bridges with branches of equal length but with different induced U-turn probabilities on the two branches, corresponding to what we observed in our experiment in the first treatment. To simplify the model, the probability of making an induced U-turn on the wide branch was assumed to be zero. We explored the stationary solutions of the model for different probabilities to make an induced U-turn on the other branch (the narrow one) for two different values of the overall flow of ants: low (0.1 ant s^{-1}) and high (0.8 ant s^{-1}). These values correspond to the lowest and mean flow of ants, respectively, as observed in the experiment.

Whatever the probability of induced U-turns on the narrow branch, the model gives three stationary solutions at low traffic volume (Fig. 5): one unstable and two stable solutions. The unstable solution corresponds to symmetrical traffic, i.e., the absence of choice, and the two stable solutions correspond to asymmetrical traffic, i.e., the choice of either the wide or the narrow branch. When the wide branch is chosen it captures almost all traffic, whatever the value of the probability of induced U-turns on the narrow branch. The choice of the narrow branch on the other hand depends on the probability of induced U-turns: The percentage of traffic on the narrow branch declines slowly when the probability of induced U-turns increases.

At high traffic volumes the model gives three stationary solutions (two stable and one unstable) up to a threshold probability of induced U-turns on the narrow branch; after which only one solution is possible: the choice of the wide branch. This latter solution is unaffected by the probability of induced

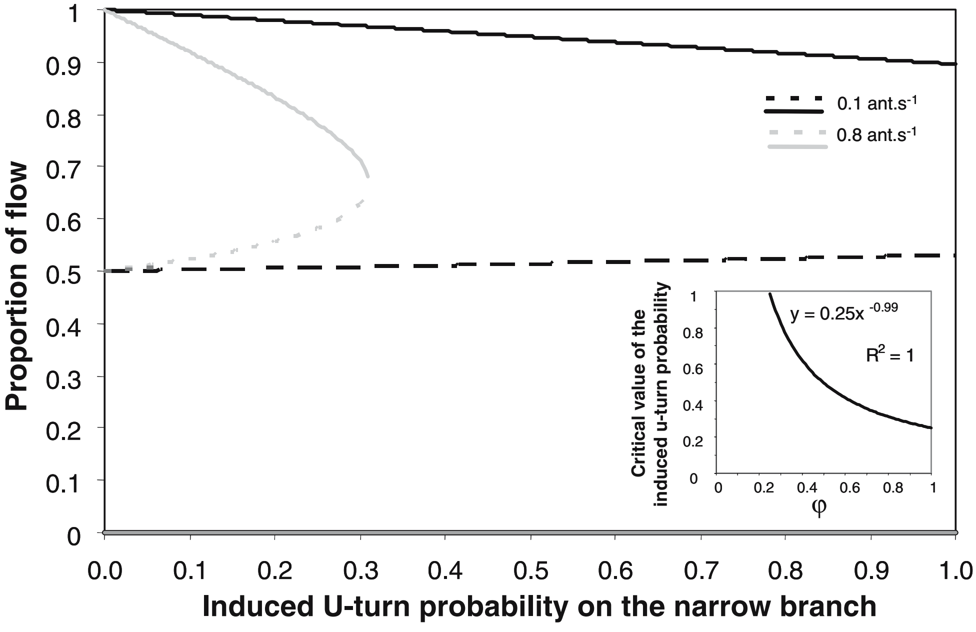

Fig. 5 Results of the analytical model. The curves show the proportion of the overall flow of ants on the narrow branch of the bridge as a function of the probability of making an induced U-turn on this branch in the stationary state. The solutions of the analytical model (see Appendix) are given for two values of the flow intensity, φ, used in the equations. φ represents half of the total flow of ants crossing the bridge. The *dashed lines* represent the unstable solutions and the *continuous lines* the stable ones. The *inset* shows the critical value of the probability of induced U-turns as a function of φ. The model admits two stable solutions *below* and only one stable solution *above the curve*

U-turns on the narrow branch as it is the same for values below or above the threshold. For the other stable solution corresponding to the choice of the narrow branch, the percentage of traffic on the narrow branch declines steeply with increasing probability of induced U-turn. However, the narrow branch should never be chosen above the threshold value of induced U-turn. For the unstable solution (absence of choice—symmetrical traffic) the percentage of traffic on the narrow branch increases slowly for increasing values of the probability of induced U-turns. The threshold probability of induced U-turns above which only one stable solution is found is an inverse function of the flow intensity (Fig. 5, inset).

The analytical model shows that the symmetrical solution is always unstable. This solution differed from that observed in experiments where ants were offered the choice between two narrow branches of equal length (Dussutour et al. 2004). In this case ants were redirected to the other branch with the same probability for either branch when a head-on encounter occurred just after the branch fork. This leads to an equal use of the two branches. In our experiment, however, this redirection occurred almost exclusively on the narrow branch, leading to the selection of the wide branch.

The stationary solutions of the model at low and high traffic volume remain the same when a difference is introduced in the time required to cross each branch owing to a difference in branch length. However, Monte-Carlo simulations show that at high traffic and for the same probability of induced U-turns on the narrow branch, the percentage of simulations in which the wide branch is chosen slowly declines (Fig. 6a). The effect of induced U-turns is less pronounced with increasing value of the branch length ratio. For example, when the wide branch is four times longer than the narrow one, neither branch is favored in the simulations. Simulations also show that for the same branch length ratio, the effect of induced U-turns on the narrow branch becomes more important for increasing flow volumes (Fig. 6b).

Discussion

When presented with the choice between two paths of equal length and different width, *L. niger* workers almost always ended up selecting the wider branch. The fact that this result was observed only in the replicates characterized by a high traffic volume shows that overcrowding on the narrow branch plays an essential role in the mechanism underlying this selection process. Two mechanisms can be hypothesized to account for this result. The first is based on the interplay between the amplification process underlying the formation of a trail and the difference in travel duration between the two paths (Goss et al. 1989). The second is based on repulsive interactions between workers making head-on encounters (“induced U-turns”).

During the first minutes of the experiment when traffic volumes were low, the ants frequented both branches of the bridges equally. When the two branches are of equal width the traffic rapidly becomes asymmetric and only one branch is selected (Goss et al. 1989; Beckers et al. 1992b, 1993; Dussutour et al. 2004; Sumpter and Beekman 2003). When the branches are of different width, however, travel duration increases more rapidly on the narrow branch than on the wide branch, owing to a higher rate of contact generated by overcrowding. A reduction in travel time due to a shorter distance can thus be rapidly offset by a delay incurred by overcrowding. The situation thus becomes equivalent to that observed in the absence of overcrowding when ants have to choose between two branches of unequal lengths with a higher travel duration on the long branch compared to the short one (Goss et al. 1989; Beckers et al. 1992b). The difference in travel duration generated by overcrowd-

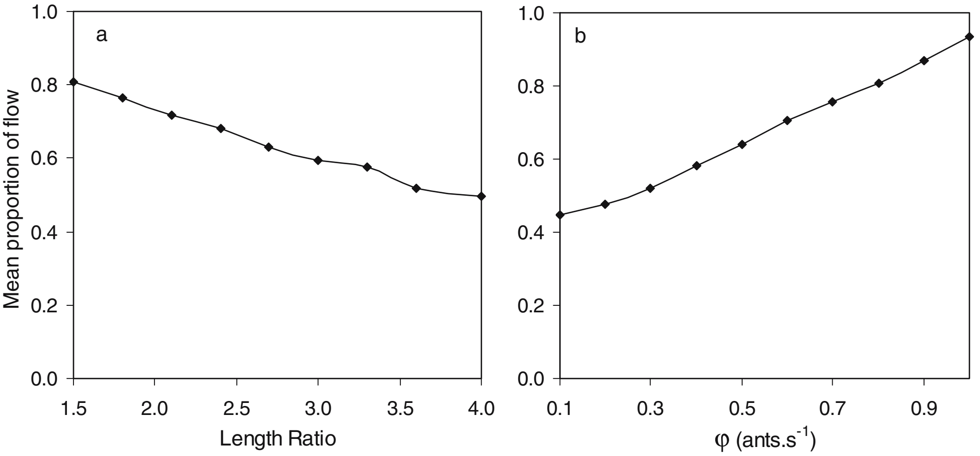

Fig. 6 Results of the Monte-Carlo simulations. Mean proportion of the overall flow of ants on the wide branch for **a** different length ratio of the branches (fixed φ=inbound or outbound flow 0.8 ant s^{-1}) and **b** different values of the half flow of ants crossing the bridge (fixed branch ratio 1.5). Each point on the graphs is the average value obtained for 5,000 runs of the simulation

ing, however, does not account for the wide branch selection because a model built on this sole mechanism was unable to reproduce the experimental results. This is in accordance with the theoretical results obtained by Beckers et al. (1992b) showing that short path selection in *L. niger* cannot be explained solely by a difference in travel duration when the branch length ratio is reasonably low ($\lessapprox 4$). The only ant species that are able to select the shorter path on this basis are those that lay a trail bidirectionally (Argentine ant: Goss et al. 1989; Pharaoh's ant: Fourcassié and Deneubourg 1994). This is not the case of *L. niger* in which only successful returning foragers lay a trail (Beckers et al. 1992a; Portha et al. 2004).

Along with an increase in travel duration, overcrowding on the narrow branch also generated a considerable number of induced U-turns. These occur after the choice point when ants enter in contact with the ants travelling from the opposite direction. Because the ants coming from the choice point have more space to maneuver, they give way to the other ants and turn back. Our model shows that induced U-turns are sufficient to explain the selection of the wide branch. Thus, the higher frequency of induced U-turns on the narrow branch redistributes the traffic over the wide branch. Induced U-turns can be considered as a dispersive force that counteracts the trail attraction. It is interesting to note that they originate from the trail attraction itself, as this causes crowding, which generates inhibitory interactions. The effect of dispersive mechanisms and inhibitory interactions on traffic regulation has already been shown under two different conditions in *L. niger*: when ants are faced with a choice between two narrow paths (Dussutour et al. 2004) and when only one narrow path is available (Dussutour et al. 2005b). Evidence of dispersive mechanisms based on repulsive pheromone signals was also recently provided in the Pharaoh's ant *Monomorium pharaonis* (Robinson et al. 2005).

We found that the wide branch was favored even at a 1.5-fold increase in length compared to the short branch. A different result was obtained in *L. niger* by Beckers et al. (1992b) in the absence of traffic congestion. These authors found that the higher frequency of intrinsic U-turns on the long branch due to its higher deviation from the nest–food axis was responsible for the short branch selection they observed in almost all cases. When overcrowding occurs, as in our experiment, the effect of intrinsic U-turns becomes negligible compared to that of induced U-turns. The model based on induced U-turns, therefore, still accounts for the selection of the wide and long branch. For higher length ratios, however, our model shows that the choice of the wide and long branch declines linearly and that the short and narrow branch is eventually selected. This is explained by the fact that the benefit of choosing the long branch in terms of travel duration progressively disappears. Our analytical model also shows that the choice of the wide branch after a few minutes occurs because the overall flow on the bridge becomes too high and the frequency of induced U-turns on the narrow branch reaches a threshold value. At this critical value, the energetic benefit of using the shorter branch does not offset the cost of additional travel time.

In a study related to energy maximization in the wood ant, Denny et al. (2001) offered alternative paths to the ants to compare between time and energy savings constraints. Their results show that ants prefer to cross a path on which they expended less energy, even if it took more time than an alternative path. They concluded that savings in energy was more important than savings in time to explain route preferences in ants. On the contrary, our experiment showed that ants prefer to trade time against energy. If one considers that ants expend energy on locomotion (Fewell 1988), leaving no energy for interactions with other ants, then the shorter branch, no matter the level of overcrowding, should always be favored. Ants could either go back to the nest or they could force their way onto the narrow path. Yet, this is not what we observed. Therefore, in *L. niger*, as in other ant species (seed-harvesting ant, *Messor barbarus*: Acosta et al. 1993; *Pogonomyrmex*: Fewell 1988; Weier and Feener 1995; *Paraponera clavata*: Fewell et al. 1996), the foraging strategies are better explained in terms of time than energy savings. *L. niger* workers thus behave more as time minimizers than as energy maximizers, as defined by Schoener (1971).

In species of ants characterized by mass recruitment, it is time and not energy that should be minimized. In fact, because of the nonlinear nature of the amplification mechanisms underlying the mass recruitment process, any delay experienced by ants in their trip back to the nest (e.g., due to adverse abiotic conditions, locomotion difficulties, aggressive encounters, or overcrowding) can slow down the recruitment process, exposing the ants to the risk of losing the food by desiccation or competition (de Biseau et al. 1997). When given the choice between paths of different lengths ants will thus choose the path that minimizes their travel time, which is not necessarily the shorter one.

Without excluding the possible existence of a more sophisticated decision-making process, our results emphasize the fact that adaptive foraging strategies can emerge out of simple behavioral rules and through the iterative process of trail-laying and trail-following behavior. Any parameter (e.g., food distance from the nest and level of traffic congestion), which can influence the recruitment dynamics, can also influence the decision-making process at the collective level. Yet, these parameters do not need to be specifically measured or coded by individual foragers. Ants, as other group-living animals (Camazine et al. 2001; Conradt and Roper 2005; Couzin et al. 2005), appear to have hit on a simple but effective means of making decisions. By interacting with each other and with the environment, ants, in spite of their limited and local individual perception, are able to choose the best path to establish their trail in the environment.

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Appendix

The concentration of the pheromone *Cij* on branch *i* (*i*=1, 2) immediately behind each choice point *j* (*j*=1, 2) changes with time *t* according to the equation:

$$dC_{ij}/dt = q\Phi_{ij}(t) + q\Phi_{ij'}(t-\tau) - \nu C_{ij}(t) \tag{2}$$

with $j' = 3 - j$,

where $\Phi_{i1}(t)$ represents the flow of foragers from the nest to the food source choosing branch *i* behind the choice point 1, $\Phi_{i2}(t)$ the opposite flow on branch *i* behind the other choice point, $j'=3-j=2$, τ the average time required for an ant to get from one choice point to the other, *q* the quantity of pheromone laid on the trail per forager, and νC_{ij} the dispersion rate of the pheromone (ν=1/mean life time of the pheromone).

At low density (without collision between ants) we have

$$\Phi_{ij}(t) = \phi_j(t)F_{ij}(t) \tag{3}$$

where ϕ_1 is the outbound flow of foragers traveling from the nest to the food source and ϕ_2 the opposite, nestbound flow. The function F_{ij} describes the relative attractiveness of the trail on branch *i* at each choice point *j* (Goss et al. 1989; Beckers et al. 1992a).

$$F_{ij} = \frac{\left(k + C_{ij}\right)^2}{\left(k + C_{1\,j}\right)^2 + \left(k + C_{2\,j}\right)^2} = 1 - F_{i'j} \tag{4}$$

Equation 3 describes the flow dynamics without interactions between ants. At high flow volumes, ants making an induced U-turn on a branch do not continue back to the nest or the food source when reaching the choice point but almost always turn to the other branch. The consequence of an induced U-turn is then essentially equivalent to a pushing behavior in which an ant that has just engaged on a branch after a choice point is pushed to the other branch by an ant coming from the opposite direction (Dussutour et al. 2004). Taking into account the probability to make an induced U-turn, the flow of ants arriving at choice point *j* and choosing branch *i* can then be expressed by the following formula:

$$\Phi_{ij}(t) = \phi_j(t)F_{ij}(t)\left[1 - \gamma_i\Phi_{ij'}(t-\tau)\right] + \phi_j(\mathrm{t})F_{i'j}(\mathrm{t})\gamma_{i'}\Phi_{i'j'}(t-\tau) \tag{5}$$

with $j'=3-j$ and $i'=3-i$; and with the proportionality factor γ_i quantifying the frequency of induced U-turns.

The first term on the right-hand side of Eq. 5 represents the flow of ants engaged on branch *i* $\left[\phi_j(t)F_{ij}(t)\right]$, diminished by the number of ants pushed toward the other branch $i'=3-i$ by the ants arriving from the opposite direction $\left[\Phi_{ij'}(t-\tau)\right]$. The second term represents the flow of ants that were engaged on branch *i′* and were pushed toward branch *i*.

If $\gamma_1=\gamma_2=0$, Eq. 5 agrees with Eq. 3 for the case of low traffic volume.

At the stationary state the conditions are defined by: $dC_{ij}/dt = 0, F_{ij}\ (t-\tau)=F_{ij}\ (t) = F_{ij}$, $\Phi_{ij}\ (t-\tau) = \Phi_{ij}(t) = \Phi_{ij}$, and $\phi_j(t-\tau) = \phi_j(t) = \phi_{j'}(t) = \phi$ (as the nestbound flow and the outbound flow should be equal). This implies for Eq. 2

$$dC_{ij}/dt = 0 = q\left(\Phi_{ij} + \Phi_{ij'}\right) - \nu C_{ij} \tag{6}$$

At equilibrium we get $\Phi_{ij} = \Phi_{ij'} = \Phi_i$, $\Phi_{i'j} = \Phi_{i'j'} = \Phi_{i'}$ and $F_{ij} = F_{ij'} = F_{i'}$.

From Eq. 5 we get:

$$\Phi_i + \Phi_{i'} = \left(\phi F_i[1-\gamma_i\Phi_i] + \phi F_{i'}\gamma_{i'}\Phi_{i'}\right) + \left(\phi F_{i'}[1-\gamma_{i'}\Phi_{i'}] + \phi F_i\gamma_i\Phi_i\right) \tag{7}$$

which gives

$$\Phi_i + \Phi_{i'} = \phi \tag{8}$$

Equation 6 can then be written as $2q(\Phi_i)=\nu C_i$ and $C_1 + C_2 = \frac{2q\phi}{\nu} = A$, taking into account Eq. 8, Φ_i can be rewritten as

$$\Phi_i = \phi F_i[1-\gamma_i\Phi_i] + \phi F_{i'}\gamma_{i'}(\phi - \Phi_i)$$
$$\Phi_i = \frac{\phi F_i + \phi^2 F_{i'}\gamma_{i'}}{1 + \phi F_i\gamma_i + \phi F_{i'}\gamma_{i'}}$$

If we take γ_1=0 for the wide branch and γ_2>0 for the narrow branch, we obtain:

$$\Phi_1 = \frac{\phi F_1 + \phi^2 F_2\gamma_2}{1 + \phi F_2\gamma_2} \text{ and } \Phi_2 = \frac{\phi F_2}{1 + \phi F_2\gamma_2}$$

The concentration of the pheromone on each branch immediately after either choice point of the bridge is proportional to the flow of ants passing on the branch

$$\frac{C_1}{C_2} = \frac{\Phi_1}{\Phi_2} = \frac{\phi F_1 + \phi^2 F_2\gamma_2}{\phi F_2} = \frac{F_1 + \phi F_2\gamma_2}{F_2}$$

taking $\gamma=\gamma_2$ and considering the choice function (Eq. 4), we get

$$C_1(k+C_2)^2 - C_2(k+C_1)^2 - \gamma\phi C_2(k+C_2)^2 = 0$$

or

$$k^2(C_1 - C_2) + C_1C_2(C_2 - C_1) - \gamma\phi C_2(k+C_2)^2 = 0 \quad (9)$$

Substituting $A=C_1+C_2$ in Eq. 9, we obtain

$$\begin{aligned} &k^2(A-2C_2) + (A-C_2)C_2(2C_2-A) \\ &\quad - \gamma\phi C_2(k+C_2)^2 = 0 \end{aligned} \quad (10)$$

which can be rewritten as

$$aC_2^3 + bC_2^2 + cC_2 + d = 0 \quad (11)$$

with

$$\begin{aligned} a &= \gamma\phi + 2; \\ b &= 2\gamma\phi k - 3A; \\ c &= \gamma\phi k^2 + 2k^2 + A^2; \\ d &= -k^2A \end{aligned}$$

Equation 11 is solved numerically giving us three stationary solutions. However, we are only interested by positive real solutions. Depending on the value of the parameters, Eq. 11 may have one positive solution (always stable) or three positive real solutions (two stable and one unstable).

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