

Amplification of individual preferences in a social context: the case of wall-following in ants

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Amplification processes are an essential component of the collective phenomena observed in social and gregarious species. In this paper, we tested the hypothesis that a weak individual wall-following tendency in ants can be amplified by communication through chemical trails, leading to a response to the spatial heterogeneities at the collective level. In our experiments, ants had to cross a diamond-shaped bridge along either of two branches of equal length to get from their nest to a food source. Two types of bridge were used: control bridges without a wall, and experimental bridges equipped with a wall along the inner edge of one of their branches. On the control bridges, ants collectively chose either branch of the bridge in most experiments, whereas on the experimental bridges, the branch with the wall was selected almost systematically. A mathematical model is proposed to assess, in various conditions, the importance of the amplification effect of the chemical trail on the wall-following tendency observed at the individual level. The model highlights the fact that the amplification process can lead to an overestimation of individual capabilities and, thus, that the results of experiments investigating individual preferences at group level in animals must be interpreted with caution.

Keywords: ants; Formicidae; preference; amplification; recruitment; wall-following

1. INTRODUCTION

Amplification processes through positive feedback mechanisms are widespread in group-living organisms from unicellulars to human (see reviews in Deneubourg & Goss 1989; Bonabeau *et al.* 1997; Theraulaz & Spitz 1997; Detrain *et al.* 1999; Parrish & Edelstein-Keshet 1999; Camazine *et al.* 2001; Krause & Ruxton 2002; Hemelrijk 2002; Couzin & Krause 2003). Amplification is an essential component of many self-organized collective phenomena observed, in particular, in social and gregarious arthropods, for example, aggregation of individuals (Deneubourg *et al.* 1990; Saffre *et al.* 1999; Depickère *et al.* 2004; Amé *et al.* 2004; Jeanson *et al.* 2005), collective defence (Franks & Partridge 1994; Millor *et al.* 1999), synchronization of activities (Buck 1988; Cole & Trampus 1999), trail and recruitment to a food source (Pasteels *et al.* 1987; Seeley *et al.* 1991; Fitzgerald 1995) or to a new nest (Camazine *et al.* 1999; Visscher & Camazine 1999; Pratt *et al.* 2002) or the building of complex nest structures (Theraulaz *et al.* 1999). In all these phenomena, collective behaviours emerge because an individual behaviour or tendency is amplified by the action of many other individuals. For example, in mass-recruiting ants, the trail-laying behaviour of a forager returning to the nest loaded with food is amplified by the response of the other ants to the trail it has just laid. Owing to the amplification processes, slight differences in the tendency of individual animals to display a given behaviour can lead to very different results at the collective level (Camazine *et al.* 2001). This may have important evolutionary

consequences when these differences are expressed between species because the phenotype of a species is composed as much of the behaviours of its individuals as of the collective behaviours they display or the collective artefacts they build (e.g. the nests of social insects; Dawkins 1999). This paper presents a case study of amplification phenomena in ants. We take the wall-following tendency as a behavioural target and investigate how differences in this tendency can translate into differences in the dynamics of recruitment and in the choice of a path to a food source.

Many species of animal present a strong tendency to follow the linear physical heterogeneities of the environment, such as walls or edges (Fraenkel & Gunn 1961; Schöne 1980). This behaviour is frequently observed in animals such as rodents or insects that move in a human-built environment. Wall-following can be based on mechanical, tactile stimuli (thigmotaxis; Creed & Miller 1990; Okada & Toh 2000; Jeanson *et al.* 2003a), but also on visual stimuli (Collett *et al.* 2001; Pratt *et al.* 2001; Graham & Collett 2002; Heusser & Wehner 2002). The high occurrence of wall-following behaviour in animals suggests that it has a strong adaptive value. There are several possible reasons for animals to prefer to move along walls. First, walls can be used as structural guidelines to orient and navigate in the environment, for example, ants (Topoff & Lawson 1979; Hölldobler & Taylor 1983; Klotz *et al.* 1985; Klotz & Reid 1992, 1993; Klotz *et al.* 2000; Collett *et al.* 2001; Pratt *et al.* 2001; Graham & Collett 2002; Heusser & Wehner 2002) and termites (Jander & Daumer 1974; Pitts-Singer & Forshler 2000). Second, animals are more likely to

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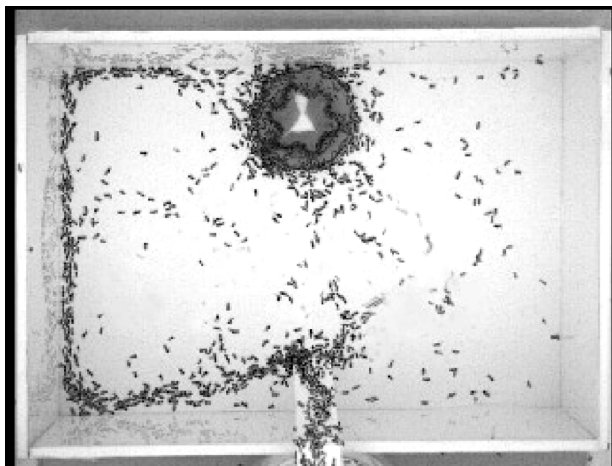


Figure 1. Illustration of the wall-following tendency in ants. A colony of the ant *Lasius niger* is given access through a bridge (bottom part of the photograph) from their nest to a food source (upper part of the photograph) placed in a 29.7 cm × 21.0 cm box. The photograph shows the superimposition of 30 snapshots (one snapshot every minute). Note that most ants do not use the direct path from their nest to the food source but prefer to follow the left edge of the box.

encounter crevices that they can use as shelters when moving along walls than when moving on a plain surface. Walls can therefore provide protection against adverse abiotic conditions or potential predators. Third, animals often form clusters along walls because they actively search to maximize the amount of body area in contact with a solid surface (Schank & Alberts 1997; Lorenzo & Lazzari 1999).

In this paper, we investigate the extent to which the wall-following tendency of individual workers can influence the strategies used by a colony of ants to exploit food sources. The attraction of walls to ants is sometimes so strong that it can lead them to make long detours instead of travelling the straight line to reach a given point in space (figure 1). We carried out a series of laboratory experiments with a simple experimental set-up consisting of a diamond-shaped bridge offering the choice to the ants between two branches of equal length placed between their nest and a food source. To investigate the influence of a spatial heterogeneity, we compared the recruitment dynamics and the choice of a path by the ants when tested with a bridge with or without a small wall installed along one of its branches. Based on different behaviours measured at the individual level (velocity, branch choice in absence of pheromone), we then propose a model to assess the intrinsic degree of attraction of the wall for individual ants and to quantify the amplification of the thigmotactic tendency by the chemical trail in various conditions.

2. MATERIAL AND METHODS

(a) *Species studied and rearing conditions*

We used the black garden ant *Lasius niger*, a common Palearctic species that feeds mainly on aphid honeydew (Flatt & Weisser 2000). This species uses mass recruitment through scent trails; once a forager has found an abundant source of liquid food it lays a scent trail on its way back to the

nest and this trail is then used by its nest-mates to localize the food (Beckers *et al.* 1992b).

We used 15 queenless colonies collected in Toulouse, France. Each of these colonies contained 1000 workers and was housed in a plastic box of 100 mm diameter, the bottom of which was covered with a layer of plaster moistened by a cotton plug soaking in a water reservoir located beneath the nest. The nest-box was connected to another circular plastic box (diameter, 130 mm), which was used as a foraging area and 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 °C) with a 12 h light : 12 h dark photoperiod. Ants were supplied with water and a mixed diet of vitamin-enriched food (Bhatkhar & Withcombs 1970), as well as maggots (*Calliphora erythrocephala*) three times a week.

(b) *Experimental set-up and protocol*

In each experiment, a colony of *L. niger* starved for 5 days was given access to a food source through a diamond-shaped bridge offering the choice to the ants at each branch fork between two branches of equal length (figure 2). The food consisted of 5 ml of a 1 M sucrose solution contained in a small cavity carved in a block of paraffin wax. To prevent crowding effects, the cavity had a star-shaped form with dented edges so that a very large number of ants had access simultaneously to the food. The entire experimental set-up was isolated from any sources of disturbance by surrounding it with white paper walls.

Experiments were performed with two kinds of bridge: a bridge with two identical branches (control bridge), and a bridge with a wall running along the whole length of one of its branches. The wall consisted of a strip of white paper (80 g cm⁻²) of 2 mm height (corresponding roughly to the height of a *L. niger* worker) taped along the internal edge of the branch. With the control bridge, 15 experiments were conducted, while 19 were conducted with the experimental bridge.

(c) *Data collection and analysis*

In all experiments, the traffic on the bridge was filmed from above for 60 min. The data were collected both at the collective and at the individual level.

(i) *Collective level*

At the collective level, the traffic on the bridge was measured at intervals of 1 min every 3 min for 1 h. Counting began as soon as the first ant discovered the bridge and climbed onto it. We measured on both branches, at 1 cm from each choice point, the flow of ants leaving the nest and that leaving the food source. A two-way ANOVA with repeated measures on time was used to test for the effect of experimental set-up and time-interval on the flow of workers. An experiment could have two kinds of outcome. Either the traffic of ants was distributed symmetrically on the bridge or most of the ants selected one branch and the traffic was asymmetric. The binomial test was used for each experiment performed to test whether a significant choice for a branch was made by the ants. The binomial test compares the proportion of ants observed on each branch with that expected from a binomial distribution, assuming that each ant chooses either branch with equal probability (Siegel & Castellan 1988).

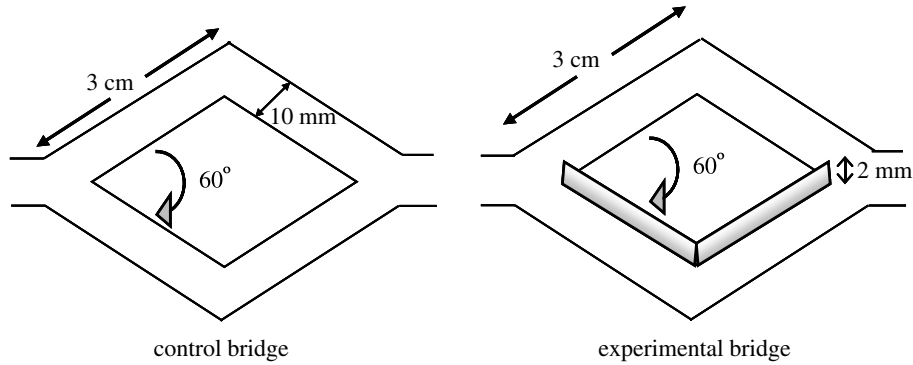


Figure 2. Bridges used in the experiments.

(ii) *The model*

The model we used describes the evolution of the concentration of trail pheromone and, consequently, the traffic of ants over each trail. It has already been successfully applied to different types of binary-choice experiment (Goss *et al.* 1989; Beckers *et al.* 1992a, 1993; Dussutour *et al.* 2004).

The model assumes that the flow of ants has reached equilibrium, that is, that the flow is equal in both directions. This occurs in a matter of minutes in the experiments. In this model, ants are faced with three types of decision: (i) staying or leaving the nest, (ii) choosing one of the branches of the bridge and (iii) laying a trail or not. The first decision is based on the probability p (s^{-1}) to leave the nest or the food source per unit of time. It is set to the value of the flux measured in the experiments. The second decision is the choice of a branch; an ant arriving at a branch fork on the bridge chooses branch 1 or 2 with probabilities P_{1j} and P_{2j} , depending on the trail pheromone concentration C_{1j} and C_{2j} at the choice point j ($j=1,2$):

$$P_{1j} = \frac{(k_1 + C_{1j})^n}{(k_1 + C_{1j})^n + (k_2 + C_{2j})^n} = 1 - P_{2j}, \quad (2.1)$$

or without pheromone on the branches:

$$P_{1j} = \frac{k_1^n}{k_1^n + k_2^n} = 1 - P_{2j}. \quad (2.2)$$

Equation (2.1) is a simple choice function, which quantifies the way an ant makes its decision at a choice point, depending on the values of C_{ij} , the concentration of the pheromone on each branch (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, then 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 (two identical branches without wall), 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 equation (2.1) for *Lasius niger* with $n=2$ and $k_1=k_2=6$. If a branch is characterized by a high degree of attraction, then its k will thus be greater than 6.

Note that equation (2.1) can be generalized for s possible paths:

$$P_{ij} = \frac{(k_i + C_{ij})^n}{\sum_{l=1}^s (k_l + C_{lj})^n} \quad i = 1, \dots, s \quad j = 1, 2. \quad (2.3)$$

We performed Monte Carlo simulations based on the following rules. At time $t=0$, the pheromone concentration over each trail is fixed to zero. When ants are offered a sucrose solution (as in our experiments), the model considers that each ant walking on the bridge deposits a quantity q of pheromone immediately after entering the branch, and another quantity q , t seconds later (corresponding to the average time to cross a branch), just before reaching the second choice point at the end of the branch. Moreover, each second, a quantity νC_{ij} ($i=1, 2; j=1, 2$) evaporates. The evaporation constant ν is equal to the inverse of the mean lifetime of the trail pheromone (i.e. $1/2400 s^{-1}$; Beckers *et al.* 1992a; Detrain *et al.* 2001).

The probabilities represented by equation (2.1) are updated at each simulation step (each second) according to the actual pheromone concentrations and the process is repeated for an hour corresponding to the duration of the experiment. For every simulation, we calculated the fraction of traffic using the branch with the wall. The simulations were run for 1000 realizations and the results observed in the simulations were then compared with those observed in the experiments.

(iii) *Individual level*

Two behaviours were measured at the individual level: the duration of travel on a branch and the intrinsic attractivity of the wall.

Travel duration. Goss *et al.* (1989) have shown through a mathematical model that a small difference in the time taken to cross a branch and bidirectional trail laying are enough to generate the selection of the shorter of two branches of unequal length. Although the bridges that we used in our experiments had two branches of equal length, ants may travel more rapidly on the branch equipped with a wall than on the other branch because they could use the wall as an orientation guideline. If this were the case, the branch equipped with a wall would be systematically selected.

To test this hypothesis, we measured the average time taken for a sample of ants to travel the whole length of a branch without interactions (so that its course was not impeded by other ants) at three different periods of time during the experiments: at 0 min (before a chemical trail was laid), at 15 min (when the recruitment reaches a peak) and at 60 min (end of the experiment). Because there were not enough ants travelling on the branch without the wall on the experimental bridge, we compared the travel duration of the ants walking on the branch with the wall on the experimental bridge to that of the ants walking on the branches without wall

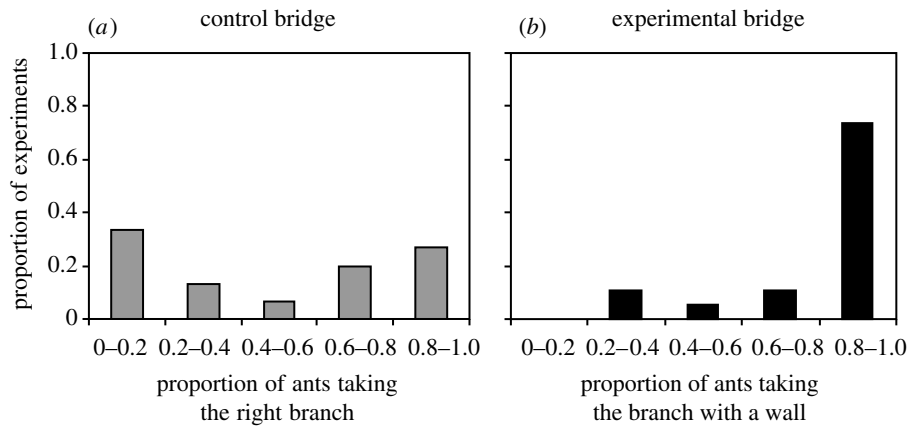


Figure 3. Experimental frequency distribution of the proportion of ants taking (a) the right branch of the control bridge ($n=15$) and (b) the branch of the experimental bridge equipped with a wall ($n=19$), 1 h after the beginning of the experiment.

of the control bridge. For the control bridge, we chose an experiment characterized by the selection of one branch, and for the experimental bridge, we chose an experiment characterized by the selection of the branch with the wall. For both bridges, we considered only the ants walking on the branch that was eventually selected and we computed a three-way ANOVA to test for the effect of the bridge (control versus experimental), direction of travel (nestbound versus outbound) and the time since the beginning of the experiments (0, 15 or 60 min) on the travel duration.

Intrinsic degree of attraction of the branch with the wall. To test the attractiveness of the wall for the ants, we followed all ants leaving the nest during the first 3 min of the experiments, in the absence of the chemical trail, and we noted which branch they selected first. During this period, we can reliably assume that there was no chemical trail that could influence the choice of the ants because: (i) in *L. niger* trail-laying behaviour is observed only in individuals that have been in contact with the food (Beckers *et al.* 1992b), and (ii) Mailleux *et al.* (2003) have shown that ants spend more or less 3 min at the food source before returning to their nest. Therefore, it can be assumed that no ants had returned to the nest within the time window we chose for our observations.

To investigate whether the attractiveness of the branch with wall could correspond to a thigmotactic tendency, we analysed the behaviour of the first 50 outbound and nestbound ants towards the wall and the other edge of the bridge at three points during the experiments: 0, 15 and 60 min. First, we counted the number of ants contacting the wall at the branch fork before selecting a branch. Second, we measured the frequency of contacts with either edge of a branch along its whole length. A contact was considered to occur each time any parts of the ant's body came into contact with the edge. These behaviours were measured from the videotapes of the two experiments that were used in the analysis of the travel duration. We used a four-way ANOVA to test for the effect of the bridge (control versus experimental), the direction of travel (nestbound versus outbound), the presence of a wall (edge with versus without a wall) and the time of the experiments (0, 15 and 60 min). As the number of contacts with either edge of the branch was measured on each ant followed, the edge factor was treated as a repeated measure.

All statistical tests were conducted with SPSS for Windows (v. 10, SPSS Incorporated, Chicago, USA).

All means in the text are given ± 1 s.e. The probabilities given in the text are always two-tailed.

3. RESULTS

(a) Collective level

The recruitment dynamics and the traffic volumes were comparable on the control and experimental bridge (two-way ANOVA with repeated measures on time-interval: experimental set-up effect: $F_{1,32}=0.003$, $p=0.955$; mean flow in ants per minute: 91.55 ± 2.11 and 90.71 ± 3.15 , for the control and experimental bridge, respectively; interaction time \times experimental set-up: $F_{19,32}=0.003$, $p=0.841$) and were typical of a trail-recruitment process (Pasteels *et al.* 1987). The flux reaches a peak 10 min after the beginning of the experiments (time effect: $F_{19,32}=9.946$, $p<0.001$). The similarity in the recruitment dynamics suggests that the trail-laying frequency did not depend on the experimental set-up.

On the control bridge, we found that, after 1 h, most ants travelled on only one branch in 14 out of 15 experiments (figure 3a). The left branch was selected as often as the right one, indicating that no environmental bias interfered with the ants' choice. When a wall was present, most experiments led to asymmetrical traffic on the bridge (figure 3b). In 16 out of 19 experiments, the ants showed a clear preference for the branch with the wall (binomial test: $p<0.05$ in all cases) and the number of experiments in which ants significantly chose the branch with the wall was significantly different from random (χ^2 goodness-of-fit: $\chi^2=8.895$, d.f. = 1, $p=0.003$).

(b) Individual level

(i) Travel duration

There were no significant differences in the time required to cross a branch between the control and experimental bridge, and between the outbound and nestbound direction (table 1; three-way ANOVA on log-transformed data: experimental set-up effect: $p=0.062$; 4.85 ± 0.22 and 4.46 ± 0.21 s, for the control and experimental bridge, respectively; direction effect: $p=0.723$; 4.68 ± 2.51 and 4.59 ± 1.79 s, for the outbound and inbound direction, respectively). Therefore, the selection of the branch with the wall was not a consequence of a difference in travel time. In addition, the travel time measured at the beginning of the experiment was higher than that

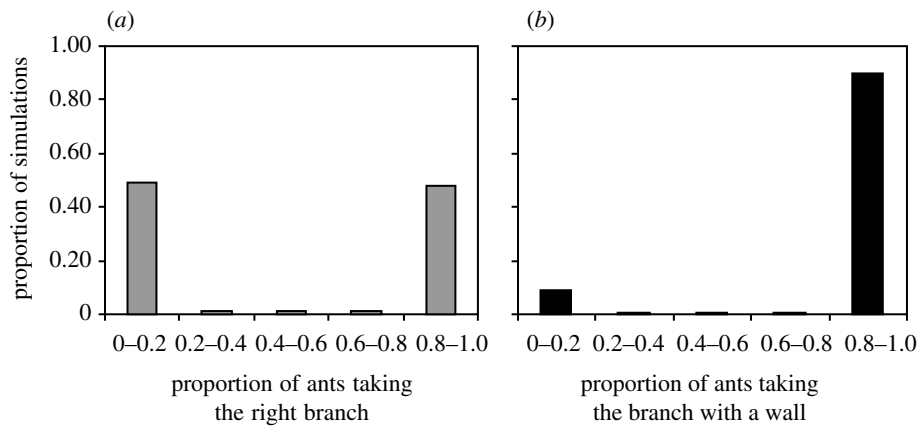


Figure 4. Frequency distribution of the proportion of ants taking the right branch or the branch with the wall in the simulations run with different intrinsic degrees of attraction of the branches (a) $k_1=k_2=6$. (b) $k_1=8.5$ and $k_2=6$, where k_1 is the intrinsic degree of attraction of the branch equipped with a wall ($n=1000$ realizations of the simulation in each case).

Table 1. Results of a three-way ANOVA to test for the effect of experimental set-up (control bridge versus experimental bridge), direction of travel (inbound versus outbound) and time of the experiments at which the measures were done (0, 15 and 60 min) on the duration of travel. (The data were log transformed to comply with the assumption of normality.)

source of variation	mean squares	d.f.	F	p
time	0.222	2	7.62	0.001
experimental set-up	0.103	1	3.53	0.062
direction	0.003	1	0.13	0.723
experimental set-up \times direction	0.014	1	0.49	0.486
experimental set-up \times time	0.024	2	0.84	0.436
direction \times time	0.070	2	2.40	0.094
experimental set-up \times direction \times time	0.035	2	1.21	0.299

measured after 15 min, at the peak of recruitment, or at the end of the experiment (table 1; time effect: $p=0.001$; 5.61 ± 0.04 , 4.09 ± 0.21 and 4.21 ± 0.15 s at $t=0$, 15 and 60 min, respectively). This difference in travel time could be a result of the absence of chemical trail guiding the ants at the beginning of the experiment.

(ii) *Intrinsic degree of attraction of the branch with the wall*

In the absence of a wall, ants chose both branches equally during the first 3 min of the experiments (the binomial test was non-significant in all experiments). Moreover, the choice an ant made at the branch fork was not influenced by the choice of the preceding ant (one sample runs tests of randomness computed on one experiment: $n=60$ ants, $z=1.715$, $p=0.086$; Siegel & Castellan 1988). On the other hand, when a wall was present, ants chose a branch in 15 out of 19 experiments, and in 14 out of those 15 experiments, the branch chosen was the one equipped with a wall. A significant preference for the branch equipped with a wall was thus already expressed by the ants during the first 3 min of the experiments, in the absence of a recruitment trail.

To determine the intrinsic degree of attraction of the branch with the wall, we computed the value of k for which our model yielded approximately the same proportion of ants choosing the branch with the wall as that observed during the first 3 min of the experiments, i.e. 0.66 ± 0.03 ($n=2438$ choices pooled over 19 experiments). Applying equation (2.2) with k_1 representing the intrinsic degree of attraction of the branch with the wall, we obtain

$$P_1 = 0.66 = \frac{k_1^2}{k_1^2 + 6^2}, \quad (3.1)$$

which yields a value $k_1 \approx 8.5$.

To test the hypothesis that a small individual preference for the branch with the wall is sufficient to explain the collective choice we observed in our experiments, we performed Monte Carlo simulations with the values measured in our experiments assigned to the parameters of our model.

Assuming the two branches are equally attractive (i.e. $k_1=k_2=6$), the situation corresponding to the control bridge, most simulations ended with the selection of one branch, either the left or the right (figure 4a). However, when we assigned the value $k_1=8.5$ to the branch with the wall, most of the simulations ended with the selection of the branch with the wall (figure 4b). The results of the simulations are comparable with that of the experiments (compare figure 3 with figure 4), confirming that a difference in the intrinsic degree of attraction of the branch is sufficient to induce the systematic choice of the branch with the wall observed in our experiments.

Exploration of the model with increasing values of k_1 shows that the value of k_1 we observed is in the range of values for which the amplification of the thigmotactic tendency by the chemical trail is maximum (figure 5a). If the intrinsic degree of attraction were too strong, then most ants would choose the branch with the wall right from the beginning of the experiment, and the chemical trail would play only a small role in the collective choice. If it were too weak, on the other hand, then the amplification of the individual preference by the recruitment process would be small and not enough to select most often the branch with the wall.

The model also shows that the effect of the amplification of the intrinsic preference by the chemical trail is more

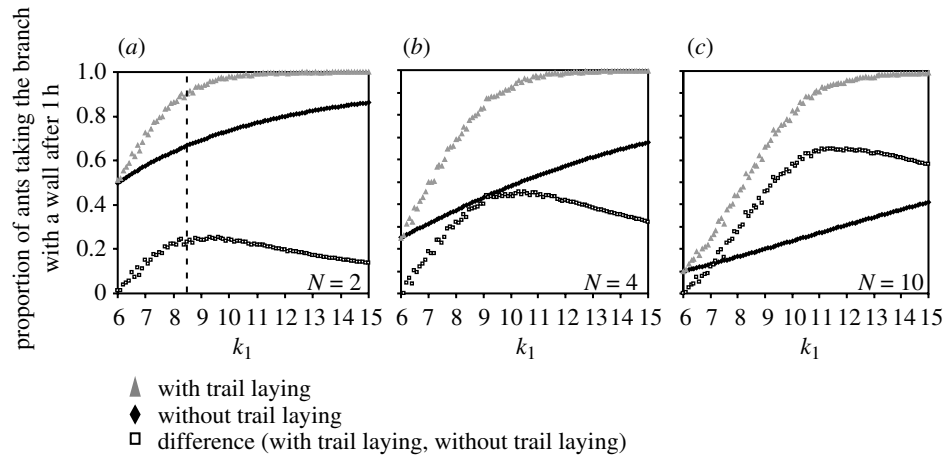


Figure 5. Proportion of ants selecting the branch equipped with a wall after 1 h as a function of the intrinsic degree of attraction k_1 of the branch equipped with a wall, in presence or absence of trail laying behaviour. The difference between the proportions predicted by the model in the two conditions is also represented. N corresponds to the number of possible paths (a) $N=2$ (b) $N=4$ and (c) $N=10$. Each data point corresponds to the mean of 1000 realization of the simulation. The vertical dashed line shows the value of k_1 observed in our experiments for the branch with the wall.

Table 2. Results of a four-way ANOVA to test for the effect of experimental set-up (control versus experimental bridge), direction of travel (inbound versus outbound), edge of the branch (inner versus outer) and time of the experiments at which the measures were done (0, 15 and 60 min) on the number of times individual ants contacted either edge of the branch. (Because the number of contacts with either edge of the branch was counted on each ant that was followed, this factor was treated as a repeated measure.)

source of variation	mean squares	d.f.	F	p
<i>between ants</i>				
experimental set-up	580.58	1	152.92	0.001
direction	2.54	1	0.67	0.413
time	25.62	2	6.75	0.001
experimental set-up \times direction	5.43	1	1.43	0.232
experimental set-up \times time	4.52	2	1.19	0.304
direction \times time	4.01	2	1.06	0.348
experimental set-up \times direction \times time	6.51	2	1.72	0.181
<i>within ants</i>				
edge	525.77	1	78.73	0.001
edge \times experimental set-up	698.36	1	104.58	0.001
edge \times direction	17.36	1	2.60	0.098
edge \times time	20.47	2	3.07	0.048
edge \times time \times direction	5.39	2	0.81	0.446
edge \times experimental set-up \times time	11.63	2	1.74	0.176
edge \times experimental set-up \times direction	13.75	1	2.05	0.152
edge \times experimental set-up \times direction \times time	12.10	2	1.81	0.164

pronounced when the number of possible paths increases. The higher the number of possible paths, the stronger the effect of the amplification by the chemical trail (figure 5*b,c*). Moreover, for a given number of possible paths, one can always find a value of k_1 for which the effect of the amplification is maximum and this value increases with the number of possible paths. For example, for 10 paths, when $k=11$, the amplification by the chemical trail is responsible for a 60% increase in the choice of the branch with the wall (figure 5*c*).

Three kinds of evidence show that the attraction for the branch with the wall is based on a strong thigmotactic behaviour. First, many ants contacted the wall at the branch fork before selecting a branch. The overall proportion of ants contacting the wall before entering a branch was equal to 0.44 and this was not significantly

different over the three times that the experiment was conducted ($\chi^2=3.26$, d.f. = 1, $p=0.071$, values pooled for the three times of the experiment) and for the two directions of travel ($\chi^2=0.80$, d.f. = 2, $p=0.669$ and $\chi^2=4.66$, d.f. = 2, $p=0.097$, for outbound and nestbound ants, respectively). Ninety-nine per cent of the ants (253 out of 256) that contacted the wall at the branch fork eventually selected the branch with the wall. Second, ants contacted significantly less the edges of the branch on the control bridge than on the experimental bridge (table 2; experimental set-up effect: $p<0.001$; 1.60 ± 0.06 and 3.15 ± 0.15 contacts for the control and experimental bridge, respectively). Moreover, irrespective of the experimental set-up, the two edges of the branch were not equally contacted (table 2; edge effect, $p<0.001$; 3.20 ± 0.14 and 1.60 ± 0.08 contacts for the inner and the outer

edge of the branches, respectively). These effects were mainly a result of the fact that on the experimental bridge, ants contacted significantly more the edge equipped with a wall than the edge without wall (table 2; interaction experimental set-up \times edge effect: $p < 0.001$; 4.79 ± 0.23 and 1.52 ± 0.13 contacts for the edge with and without a wall, respectively). On the control bridge, both edges were equally contacted (1.51 ± 0.08 and 1.68 ± 0.10 contacts for the inner and outer edge, respectively). Ants also had significantly more contact with the edges at the beginning than at the end of the experiment (table 2; time effect: $p = 0.001$; 2.77 ± 0.15 , 2.25 ± 0.16 and 2.06 ± 0.15 contacts at $t = 0, 15$ and 60 min, respectively), suggesting that the importance of the wall as a guideline slowly decreases with time as the chemical trail is reinforced.

4. DISCUSSION

Our experiments clearly show that a small environmental heterogeneity can strongly influence path choice in *Lasius niger* and, consequently, the geometry of recruitment trails. When given the choice between a branch with a wall and a branch without wall, ants selected the branch with a wall in 16 out of 19 experiments. On the other hand, in accordance with previous studies with *L. niger* (Goss *et al.* 1989; Beckers *et al.* 1992a; Portha *et al.* 2002; Dussutour *et al.* 2004) and *Monomorium pharaonis* (Sumpter & Beekman 2003), in the absence of heterogeneity, either branch was equally selected.

Two types of hypothesis can be proposed to account for the almost systematic choice of the ants for the branch equipped with the wall. The first hypothesis is based on a modification of the trail signal or on a modification of the amplification process in the presence of a wall, whereas the second hypothesis is based on an intrinsic preference of individual ants for the wall.

The first hypothesis relies on a modulation of the trail-laying behaviour of the ants. Ants may have a higher propensity to deposit trail pheromone when walking near a wall than when walking on a plain area. This could be checked by quantifying the trail-laying behaviour of the ants (see method in Portha *et al.* 2002). However, two experimental results show that this hypothesis does not sufficiently explain the ant choice. First, the preference for the branch with the wall in our experiments appeared during the first 3 min of the experiment, in the absence of chemical trail. Second, the dynamics of recruitment was the same for the two experimental set-up. If ants were to trail-lay more frequently near the wall, then one would expect the peak of recruitment to be higher and to occur sooner when the branch with the wall was selected, which was not the case in our experiments.

One could also hypothesize that the efficiency of the trail signal could be increased in the presence of the wall. The atmospheric conditions near the wall could be slightly different from on a plain area, inducing some modifications in the properties of the trail signal. For example, if the trail near the wall were to evaporate less rapidly because of a slightly cooler temperature then it would be amplified faster than the trail on the branch without wall. The properties of the trail could thus be modified by the properties of the environment and this in turn could affect the dynamics of information transfer and the choice of a

path. This effect would be comparable to that observed when chemical trails are laid on different types of substrate. Ants behave in the same way when walking on different substrate but the properties of the substrate affect the properties of the trail signal (evaporation and adsorption rate), which, in turn, modifies the recruitment dynamics (Wilson 1962; Detrain *et al.* 2001; Jeanson *et al.* 2003b). Unfortunately, we have no way of knowing the extent to which the atmospheric conditions near the wall are modified. However, the same reasoning we used to disprove the modification of the trail-laying behaviour still holds in this case. This hypothesis does not adequately account for either the preference for the branch with the wall in absence of chemical trail, or the fact that the dynamics of recruitment are identical for either a branch equipped with a wall or without a wall.

The choice of the branch with the wall at the colony level in our experiments could result from a slight reduction in the travel time (Goss *et al.* 1989). As with other insects, ants can use the linear heterogeneities of the environment as guidelines to orient on their foraging area (Klotz *et al.* 2000), and this could result in a decreased travel time on the branch with the wall. However, our analyses show that the travel time of individual ants was not significantly affected by the presence of a wall (table 1). Moreover, regardless of whether ants walk on a branch with or without a wall, the travel time decreases gradually over time. This may be explained either by an increase in ant velocity owing to the arousal properties of the trail pheromone or, most likely, to its use as an additional guideline.

Finally, an alternative explanation of the branch selection with the wall could be related to the intrinsic attractiveness of the wall for individual ants. Our results strongly suggest that this was indeed the case. First, in the absence of trails during the first 3 min of the experiments, the majority of ants chose the branch with the wall in 14 out of the 15 experiments in which a significant preference for a branch was expressed at the colony level. Second, all ants that contacted the wall at the branch fork proceeded on the branch with the wall, showing that the wall was indeed very attractive. Third, while walking on the branch with the wall, ants contacted significantly more the edge with the wall than the edge without wall, showing that they displayed an active and not just a passive thigmotaxis (Cred & Miller 1990).

The hypothesis that an intrinsic preference for the branch with the wall explains the collective choice of the ants is further supported by our model of branch choice. This model is the same as that used in previous studies in ants with similar experimental set-ups (Goss *et al.* 1989; Beckers *et al.* 1992a, 1993; Detrain *et al.* 2001; Dussutour *et al.* 2004), except that a difference in the intrinsic preference of the two branches, represented by the parameter k in equation (2.1), was introduced. The results of our simulations show that a 40% difference in the value of k_1 between the two branches was enough to generate the choice we observed in our experiments. At the beginning of the experiment, in absence of a chemical trail, the choice of most ants is determined by their thigmotactic tendency. About 65% of the workers selected the branch with the wall. As the recruitment proceeds, the intrinsic preference for the branch with the wall is amplified by

the chemical trail and after 1 h, 85% of the traffic is concentrated on this branch. The amplification by the chemical trail is thus responsible for a 20% increase in the choice of the branch with the wall. In our case, the difference in intrinsic attractiveness between the two alternative paths was a result of the presence of a wall along one of the branches. However, one could assume that the intrinsic attractiveness of a path could vary for other reasons, for example, type of substrate (organic, mineral), substrate coarseness (smooth versus rough), presence of visual stimuli along the path, and so on.

In our experiments, we showed that the effect of an individual preference (a thigmotactic tendency) could be considerably amplified by the interactions between individuals through olfactory cues (the trail pheromone), leading to the collective choice of a path along a wall by the ants. Moreover, the model suggests that any individual preference that modifies the value of k would also be amplified. The model also shows that the larger the number of choices, the greater the amplification of the individual preference by the trail. Similar processes may be at work in aggregation phenomena in many insects, even when it does not depend on any type of olfactory cues or trail. For example, when workers of various species of ants are placed in an arena illuminated by a dim red light they tend to rapidly cluster along its edge (Depickère 2003; Depickère *et al.* 2004). The location of the cluster is determined by the thigmotactic tendency of individual workers, while its stability is ensured by the fact that the probability of a worker leaving a cluster decreases with its size. The cohesive forces of the cluster thus act as a mechanism amplifying the individual preference of the workers for the wall. The same kind of explanation can be provided to account for the formation of clusters in the German cockroach *Blattella germanica* (Amé *et al.* 2004; Jeanson *et al.* 2005). Similar mechanisms could also probably explain the aggregation in natural cavities or crevices observed in various species of animals, for example, in the Heteroptera *Dysdercus cingulatus* (Farine & Lobreau 1984), the sandy beach isopod (Odendaal *et al.* 1999) or the spiny lobsters (Childress & Herrnkind 2001). Note that any kind of spatial heterogeneity can be the basis of an individual preference. For example, in the German cockroach *Blattella germanica*, the individual preference for high humidity values may determine the location of the aggregates in patches of high humidity (Dambach & Goehlen 1999). Similarly, slight differences in habitat preference between sexes in ungulates can be amplified by social attraction and may be a possible explanation for the sexual segregation observed in many species (Bon *et al.* in press).

Our study also has some methodological consequences as it illustrates a common pitfall in experiments measuring preferences in animals displaying behaviours liable to amplification (recruitment, aggregation, imitation, allelomimeticism, etc.). For example, Olabarria *et al.* (2002) examined the preferences for microhabitats in several species of intertidal microgastropods by placing several individuals of the same species in a core divided into three equal sections, each containing a different or the same microhabitat. The preference for one of the microhabitats over the others was assessed after three days by comparing the proportion of individuals in each of the microhabitats

when presented together or alone. What this careful experimental procedure fails to take into account, however, is the gregarious character of some of the species of microgastropods they studied. The preferences measured may therefore be the result of both individual preferences for a given microhabitat and of an amplification process owing to the trail-laying and trail-following behaviour observed in many gregarious microgastropods (Chelazzi 1992). Consequently, the individual preferences measured are probably overestimated. Conversely, without testing animals individually, the importance of weak individual preference (e.g. for food, environmental conditions) is probably underestimated when studying collective choice at the group level in many social species.

In conclusion, this paper shows how a simple mathematical model describing the dynamics of the collective choice of a path in a social species can be used to assess, in various circumstances, the relative importance of individual preferences for an environmental factor, and of the amplification process resulting from the direct or indirect interactions between individuals. The model could be easily applied to the study of decision-making process of other gregarious animals in different contexts (e.g. choice of food, aggregation site or habitat). Our results highlight the fact that weak individual preferences may be at the heart of decision-making processes involving seemingly complex mechanisms. Finally, our study also suggests that common preferences between individuals coupled to amplification processes through communication may have played an important role in the evolution of social life and cooperation.

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