



# Dispersion movements in ants: spatial structuring and density-dependent effects

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## Abstract

This paper examines whether the characteristics of individual dispersion movements in ants are changed when workers are moving solitarily or in a group. We analyzed the trajectories of workers of the species *Messor sancta* moving solitarily or in groups of different size (5, 10, 15 individuals), tested for density-dependent effects on their trajectory characteristics and investigated through resampling techniques whether ants are able to spatially structure their movements through direct (e.g. contact) or indirect (pheromone deposited on the ground) interactions. In addition to group size, the effects of the nutritional state of the colony and of the state of the area on which ants were dispersing were also examined.

Solitary ants moved faster and had more sinuous trajectories than ants moving in a group. We found however no significant differences in trajectory characteristics between groups of different size. Whatever the group size, ants from starved colonies moved more slowly and had more direct trajectories than their counterpart coming from fed colonies. On the other hand, the state of the area on which ants were moving had no direct significant effect on dispersion movement. Ants dispersing in a group moved independently and did not coordinate their movements through direct or indirect interactions. However, the geometry of their path was changed not only through the effect of random encounters with other workers but also through an active modification of their movement when they perceived directly or indirectly the presence of nearby workers.

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## 1. Introduction

Dispersion in biology describes the process by which a group of organisms spreads in the environment from a small region of space. Dispersion is central to all spatial ecological processes and is a key feature of the mathematical diffusion models investigating the dynamics of aggregation and dispersion in animals (Skellam, 1951; Okubo, 1980, 1986; Holmes,

1993; Parrish and Hamner, 1997). The dispersion movements of animals may be influenced by various biotic and abiotic factors. Current interest in landscape ecology has focused a great deal of attention on the physical structure of the environment, e.g. on the relationship between animal dispersion movements and vegetation cover (Fewell, 1988a,b) or the degree of spatial heterogeneity of the environment (With, 1994). Yet, other factors such as the physiological state of the animal, its motivation, degree of familiarity with the environment and the presence of other individuals of its own or of a different species may also be important. All these factors may in particular

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affect the risk-averse or risk-prone tendency of an animal (McNamara and Houston, 1992) and therefore its tendency to stay at the same place or move away from its current position.

Arthropods, because of their small size, provide good biological models for the study of dispersion because their movements can be easily studied both on a large scale, by collecting data on population fluxes (Eulerian approach, see Turchin, 1997), and on a small scale by collecting data on the movement of individuals (Lagrangian approach: Turchin et al., 1991; Wiens et al., 1993). In social insects, in addition to the aforementioned factors, interactions with nestmates may greatly affect the dispersion movements of individuals. For example, in the ant *Solenopsis invicta* the path shape of a worker exploring an area depends on the path shape of neighboring workers (Gordon, 1988) and in the Argentine ant *Linepithema humile*, the path shape of exploring ants is influenced by ant density (Gordon, 1995). Interactions may also affect the internal state of a worker and thus its pattern of movement (Pacala et al., 1996; Bonabeau et al., 1998; Gordon and Mehdiabadi, 1999).

In this paper we investigate the dispersion movements of ants moving on an area devoid of any food sources or physical obstacles. Groups of ants of various sizes are placed in a container in the center of an arena and are released simultaneously. The colony from which the ants are sampled is starved or satiated and the area on which they are moving is marked or not by their colony. With this simple protocol we want to address specifically three questions:

first, we want to examine in which way ants' dispersion movements are influenced by the nutritional state of their colony and by the state of the area on which they are moving;

second, we want to investigate whether the dispersion movements of a worker depend on the presence of nearby workers in the arena and whether this effect, if it exists, is density-dependent. As stated by Turchin (1989) density-dependent effects in dispersion movements have received too little attention in ecological and behavioral studies. Yet, they may greatly influence the outcome of the interactions of a group of organisms with potential competitors and predators, as well as the rate of resource discovery;

third, using resampling techniques, we want to examine whether ants move independently of each other, or whether they modify dynamically their trajectories in order to coordinate their movements with other workers. This coordination, if it exists, could be achieved through mutual attraction or repulsion forces (Couzin et al., 2002) and would lead to a spatial organization of the dispersion movement at the collective level, e.g. to congregation and gregarious movements in the case of mutual attraction, or to a partitioning of the area among workers in the case of mutual repulsion. As a complement to this question we also investigated whether the rate of physical interactions between workers is random or whether, on the contrary, ants actively monitor their rate of interactions, e.g. by seeking contact or by trying to avoid each other.

## 2. Materials and methods

### 2.1. General methods

We used the Mediterranean seed-harvesting ant *Messor sancta*. As most species of its genus, *M. sancta* generally forage collectively by forming temporary or permanent trunk-trails leading to areas of abundant food sources (Cerdan, 1989). Once they have reached the end of a trunk-trail however, foragers disperse and search solitarily on the foraging area. Solitary workers can also be observed dispersing directly from the nest.

The same colony, collected near Narbonne (Languedoc-Roussillon, France), was used in all experiments. The colony was housed in several glass test tubes placed in a 27 cm × 27 cm plastic box whose sides were coated with Fluon<sup>®</sup> to prevent ants from escaping. Ants were provided with water in the form of moist cotton and fed ad libitum with a mixture of seeds and twice a week with bits of crickets.

At the beginning of an experiment ants were captured in the plastic box housing the nest and placed either alone or by groups of 5, 10 or 15 individuals in a small circular container (height: 5 cm; diameter: 5 cm). The container was then immediately turned upside down in the center of an 80 cm diameter arena whose floor was made of plywood. This procedure allowed us to maintain a constant overall den-

sity on the experimental area, which is an essential consideration for our study. After a latency time of 2 min the container was lifted and the trajectories of the ants filmed during 5 min by a camera placed directly over the center of the arena. To avoid edge effects as much as possible only the first minute of the recording was used in the analysis. The floor of the arena was either washed with diluted alcohol (90%) just before the experiment began (condition: unmarked area) or previously marked by the colony which had access to it from the nestbox during 1 or 2 days (condition: marked area). The colony was either fed as usual (condition: fed colony) or starved during 1 week before the experiment (condition: starved colony). For each four combination of experimental conditions 25 individuals were tested alone and the experiment was replicated five times for the groups of 5, 10 and 15 individuals. In total 700 ants were thus tested. Ants were chosen randomly among the medium and major workers; minor workers were avoided because they were too small to be clearly visible on the TV screen. Several experiments could be done on the same day. However, the same ant was never tested twice on the same day. Because we did not mark ants we cannot exclude that we tested the same ant several times. However, since the experimental colony contained several thousand workers this should have occurred very rarely on two consecutive days.

## 2.2. Trajectory acquisition and analysis

We used a GrafBar GP-7 sonic digitizer (Science Accessories Corporation, Southport, USA) to digitize the ants' trajectories. We put a glass plate over the active area of the digitizer and placed behind it a 13 in. video monitor. As an ant moved on the screen, it was followed with the digitizer cursor and its path was input into a microcomputer as a series of  $X$ – $Y$  Cartesian coordinates at a rate of five points per second. The trajectories were thus initially defined as a series of 300 moves of 0.2 s duration. When an experiment was run with several ants we used a time counter inserted in the image to start the digitizing process for each ant exactly at the same video frame. As the speed at which the ants were moving on the screen was relatively slow, they could be followed with the videotapes played at normal speed. When confusion occurred because of a high encounter rate between ants, the videotapes were

first played in slow motion and the trajectories were drawn on an overhead which was then used as a guide to follow the ants.

The following characteristics were computed on the digitized trajectories:

running speed, defined as the ratio of total trajectory length over the time the animal spent moving during the trajectory;

turning index, defined as the standard deviation of the absolute value of the changes of direction between straight-line segments. This parameter was computed after smoothing the digitized trajectories as a series of straight-line segments according to the method described in Fig. 1. This procedure allows us to remove the artifacts due to hand wobble during the digitizing process (Tourtellot et al., 1991). It filters out the moves whose length was lower than or equal to 2 mm and the changes of direction whose absolute values was less than  $5^\circ$ . A similar turning index has been used in previous studies dealing with ant's patterns of movement (Adler and Gordon, 1992; Gordon, 1995). When the distribution of the changes of direction is centered on  $0^\circ$ , i.e. when there is no turn bias towards the left or right direction, it gives a good estimation of the sinuosity of a path. A low value indicates a linear movement; a high value, a high propensity to change direction;

maximum net displacement, which represents the maximum distance an ant traveled from the center of the arena and is thus directly related to dispersion movements (Wu et al., 2000).

All values in the text are given as mean  $\pm$  S.D.

## 2.3. Statistical analysis

To test for the effect of the state of the area, the colony nutritional status and the size of the group on each trajectory characteristic, we pooled in a single group all the trajectories from the five replicates performed for each combination of experimental conditions. Theoretical work shows that, as long as the sample size in each replicate is the same, pooling is as reliable a method as aggregating the individual scores of ants within replicate into a mean score to estimate population means and variances (Leger and Didrichsons, 1994). Since our experimental design

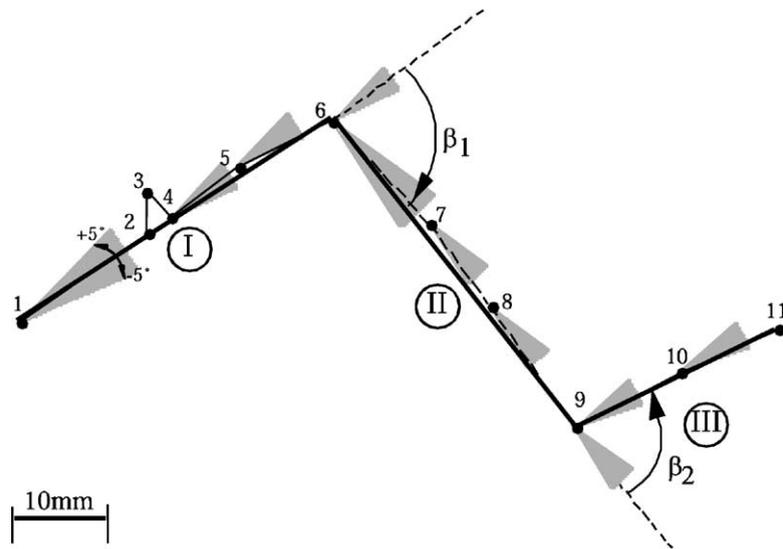


Fig. 1. Procedure used to smooth the trajectories. After being digitized, the trajectories consisted of a series of moves of 0.2 s duration. In order to remove the artifacts due to hand movement during the digitizing process, they were smoothed as a series of straight-line segments composed of one or several moves. Moves equal to or less than 2 mm length were considered as due to hand wobble and were filtered out by the procedure. The direction of a straight-line segment is given by the direction of its first move and its end point corresponds to the origin of the first move encountered whose direction lies outside the interval  $\pm 5^\circ$  of the direction of the segment. In the figure is represented the first 11 points of a path. The grey zone represents the angular tolerance in the direction of the moves composing the segments. Moves [2, 3] and [3, 4] were ignored in the smoothing process because their length was less than 2 mm. After the smoothing process was applied three straight-line segments labeled I, II, III were defined. The computation of the turning index is based on the values  $\beta_i$  of the changes of direction between straight-line segments.

was unbalanced (different sample size for each combination of experimental conditions due to the different group sizes tested in the experiment) and the assumptions of normality was not verified for most trajectory characteristics, non-parametric statistics were used. This restriction prevented us from analyzing interaction effects.

#### 2.4. Coordination among workers

We tested whether there was any coordination among workers moving in a group by measuring the amount of area covered *per capita* in each group. This parameter was assessed by dividing the area of the arena in  $1 \text{ cm}^2$  cells and by computing the number of cells in which at least one point of any of the digitized trajectories of the group could be found. This number was then divided by the number of ants in the group. Because of the overlap between trajectories the amount of area covered *per capita* for ants moving in a group should therefore always be lower

than the average amount of area covered by each trajectory. The side of the cells was about twice the size of the average move length of all paths (mean  $\pm$  S.D.:  $4.41 \pm 1.10 \text{ mm}$ ,  $N = 700$ ), which ensures that almost all cells crossed by a trajectory were taken into account. Since we do not know the actual perception range of *M. sancta* workers, the amount of area covered should not be considered as a measure of the surface scanned by an ant. It is merely an assessment of the area covered by its trajectory. This measure is then used in resampling techniques (see Section 3) in order to reveal a spatial organization of the dispersion movement at the collective level.

A computer program was used to assess the frequency of interactions between ants moving in a group. Interactions were considered to occur when the distance between two ants at the same time step was equal to or less than 1 cm. A visual check of the videotapes shows that more than 90% of the interactions between ants were detected with this criterion. Because all ants started from the center of the

arena, interactions occurring within the first 2 s of the experiment were ignored. For each experiment, interactions were only counted once, whether two or more individuals were involved in it. The effect of experimental conditions on the number of interactions was tested by using a three-way ANOVA with group size, state of the area and state of the colony as the three main factors and the number of interactions in each experiment as the dependent variable. The data were log-transformed to improve homoscedasticity. For each interaction detected, the time step at which the interaction began, the duration of the interaction and the distance at which the two ants began to converge continuously were recorded. To compute this latter parameter, we started at the time step at which the beginning of the interaction occurred and backtracked along the trajectories until reaching a time step  $t$  for which the distance between the two ants began to shorten. The process was stopped if the distance between the two ants at time step  $t - 1$  was shorter than that at time  $t$ . The distance at time  $t$  was then considered as the distance at which the ants began to converge monotonically. If encounters between individuals do not occur at random but are triggered by some kind of perception between ants, we should be able to detect a critical distance of attraction by this method.

### 3. Results

The mean values of the trajectory characteristics obtained for each group size and each experimental condition are given in Table 1. The mean value of the changes of direction between segments for the 700 trajectories recorded was equal to  $-0.34 \pm 8.20^\circ$  and was not different from zero indicating that there was no turn bias in the ants' movement. Therefore, according to Gordon (1995) the turning index we used gave a good estimation of the sinuosity of the paths.

#### 3.1. Influence of the colony nutritional state and of the state of the area on dispersion movements

There was no direct effect of the state of the area on which the ants were moving: whether the area was previously marked or not by ants did not affect any of the trajectory characteristics (Table 2). The nutritional state of the colony however did have an influence on the running speed of the workers, the sinuosity of their trajectories and their maximum net displacement: on the whole, ants belonging to a fed colony moved slightly faster than ants belonging to a colony that had been starved for a period of 8 days ( $22.81 \pm 5.84$  mm/s versus  $21.05 \pm 5.12$  mm/s), their

Table 1  
Trajectory characteristics of the ants in the different experimental conditions<sup>a</sup>

Area state	Colony state	Group size	Running speed (mm/s)	Turning index (degrees)	Maximum net displacement (mm)
Marked	Starved	1	22.80 ± 4.54	47.88 ± 5.40	229.22 ± 87.65
		5	19.66 ± 3.70	46.83 ± 4.99	173.44 ± 79.19
		10	20.34 ± 5.11	44.30 ± 9.27	213.46 ± 102.92
		15	21.07 ± 3.85	45.16 ± 6.83	238.20 ± 104.74
	Fed	1	26.39 ± 4.54	51.53 ± 5.48	237.95 ± 102.87
		5	23.95 ± 6.61	50.34 ± 5.37	206.72 ± 127.07
		10	21.11 ± 3.94	49.69 ± 7.13	229.57 ± 107.45
		15	21.26 ± 5.55	48.90 ± 5.88	219.54 ± 115.74
Unmarked	Starved	1	26.19 ± 6.30	49.23 ± 4.54	163.74 ± 85.38
		5	22.40 ± 6.73	44.84 ± 6.34	237.34 ± 104.55
		10	20.42 ± 4.79	45.07 ± 6.22	242.65 ± 115.30
		15	19.66 ± 4.63	45.73 ± 7.30	237.64 ± 114.23
	Fed	1	25.68 ± 6.29	50.64 ± 5.29	145.97 ± 78.48
		5	20.45 ± 4.75	48.85 ± 4.52	135.59 ± 69.87
		10	22.91 ± 6.70	47.82 ± 5.61	213.37 ± 97.70
		15	23.70 ± 5.63	47.80 ± 5.21	197.24 ± 79.31

Sample size:  $N = 25$  (group size: 1 and 5 individuals),  $N = 50$  (group size: 10 individuals),  $N = 75$  (group size: 15 individuals). Five replicate experiments were run for each group size and each combination of experimental conditions.

<sup>a</sup> Values are mean ± S.D.

Table 2  
Effects of experimental conditions on individual trajectory characteristics

	Group size <sup>a</sup>	Area state <sup>b</sup>	Colony state <sup>b</sup>
Running speed	<0.001	0.609	<0.001
Turning index	<0.001	0.327	<0.001
Maximum net displacement	0.001	0.060	0.018
Amount of area covered <i>per capita</i>	<0.001	0.198	0.432

The table gives the probability associated with the test statistics computed.

<sup>a</sup> Kruskal–Wallis one-way ANOVA.

<sup>b</sup> Wilcoxon–Mann–Whitney test.

trajectories were characterized by a higher value of the turning index ( $49.03 \pm 5.83^\circ$  versus  $45.73 \pm 7.01^\circ$ ) and they remained slightly closer to the center of the arena ( $204.46 \pm 103.85$  [range: 7.08–426.36] mm versus  $224.53 \pm 107.22$  [range: 17.56–519.57] mm).

### 3.2. Influence of group size on dispersion movements

Table 2 shows that group size had a highly significant effect on all trajectory characteristics. Whatever the experimental conditions, isolated ants moved faster (Fig. 2a) and their trajectories were characterized by a higher turning index than ants moving in a group (Fig. 2b). The maximum net displacement increased markedly when group size went from 5 to 10 individuals (Fig. 2c).

### 3.3. Coordination among workers

There was a significant difference among group size in the amount of area covered *per capita* (Table 2). As predicted, the amount of area covered *per capita* by ants moving solitarily was higher than that of those moving in groups of 5, 10 or 15 ( $105.52 \pm 33.01$ ,  $78.06 \pm 15.91$ ,  $76.55 \pm 9.70$ ,  $61.58 \pm 12.60$  cm<sup>2</sup>, respectively; Kruskal–Wallis:  $\chi^2 = 47.60$ ,  $P < 0.001$ ). The amount of area covered by ants moving in groups of 5, 10 and 15 ants however did not differ statistically. There was no effect of either the state of the area or the nutritional state of the colony on the amount of area covered.

To test for the existence of coordination among workers we examined whether the amount of area cov-

ered *per capita* in our experiments was the same as that we would have obtained if each ant of the group were moving on the area independently. This was done by using the following resampling method:

- (1) as the amount of area covered *per capita* did not depend of either the state of the area or the nutritional state of the colony, we considered the results of the 20 experiments performed with each group size and computed the frequency distribution of this variable;
- (2) we created a set of 20 resampled groups for each group size. Each resampled group was created by drawing randomly ants from distinct experimental groups. We then computed the amount of area covered *per capita* in each resampled group and calculated the frequency distribution of the amount of area covered for the 20 resampled groups created for each group size;
- (3) using a Kolgomorov–Smirnov (KS) test, we compared the distribution of the amount of area covered *per capita* in the 20 experimental groups with that computed for the set of 20 resampled groups created at step (2);
- (4) we repeated steps (2) and (3) 200 times and computed the median value of the KS statistic and its associated probability.

Using this method, we found that the distribution of the amount of area covered *per capita* in experimental groups was almost identical to that obtained in resampled groups. The probability associated with the median value of the KS statistic was higher than 0.05 and the average amount of area computed for the resampled groups was very close to that observed in experimental groups (resampled versus experimental groups:  $80.40 \pm 16.33$  cm<sup>2</sup> versus  $78.06$  cm<sup>2</sup>,  $78.53 \pm 11.31$  cm<sup>2</sup> versus  $76.55$  cm<sup>2</sup>,  $67.60 \pm 8.30$  cm<sup>2</sup> versus  $61.58$  cm<sup>2</sup> for groups of 5, 10 and 15 individuals, respectively).

Interactions were observed in 59 out of 60 experiments. The only experiment where we did not observe interactions was with a group of 5 ants belonging to a starved colony and moving on an unmarked area. In total, 1392 interactions were censused. Interactions were short and lasted in general less than 1 s ( $0.44 \pm 0.46$  s; range: 0.2–4.2 s). Predictably, we found that there was a significant effect of group size on the frequency of interactions in groups of moving ants ( $F_{2,47} = 65.10$ ,

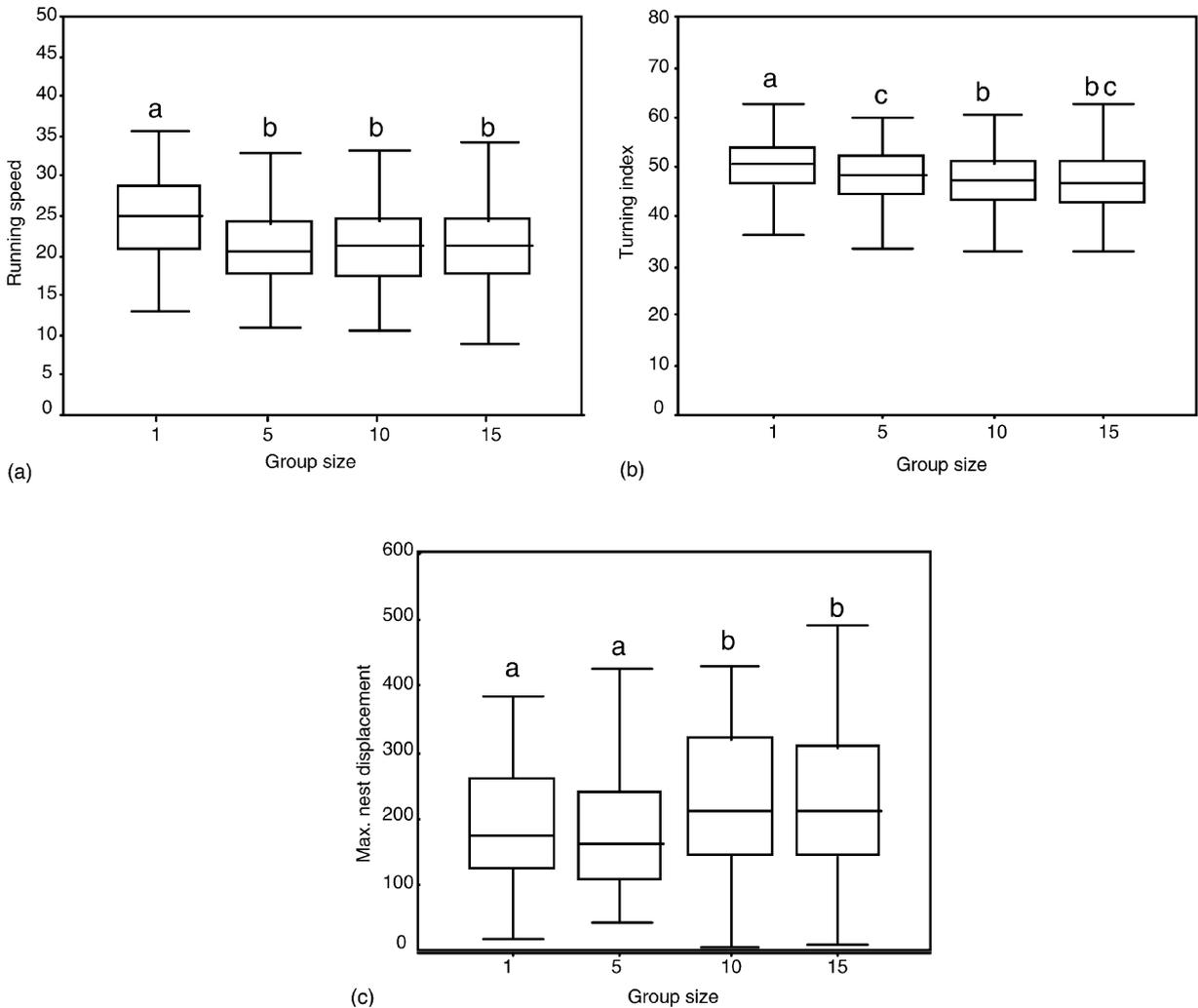


Fig. 2. Effects of group size on the trajectory characteristics of individual ants. The distributions are represented as boxplots. Each box is divided at the median of the distribution and the bottom and the top of the box represent respectively the lower and upper quartiles of the distribution. A vertical line extends from the top and the bottom of the box to the 1.5 interquartile range of the distribution. (a) Running speed in mm/s. (b) Turning index in degrees. (c) Maximum net displacement in mm. Mean  $\pm$  S.D. for all graphs. Bars sharing the same letter do not differ significantly at  $P = 0.05$  (Kruskal–Wallis followed by a Dunn's test). Sample size:  $N = 100$  (group size: 1 and 5),  $N = 200$  (group size: 10),  $N = 300$  (group size: 15).

$P < 0.001$ ). There was also a slight effect of the state of the area ( $F_{2,47} = 4.80$ ,  $P = 0.03$ ) but none of the colony nutritional status ( $F_{2,47} = 0.54$ ,  $P > 0.05$ ). The number of interactions occurring along the path of an ant did not have a significant effect on its characteristics. There was a significant negative correlation between the number of interactions occurring along the trajectory of an ant and the maximum net displacement ( $r = -0.354$ ,  $N = 600$ ,  $P < 0.01$ ) and a

significant positive correlation with the turning index ( $r = 0.227$ ,  $N = 600$ ,  $0.05 > P > 0.01$ ). Running speed however was not significantly correlated with the number of interactions occurring along the path of an ant ( $r = 0.069$ ,  $N = 600$ ,  $P > 0.05$ ). Interestingly, the trajectory characteristics of ants moving in a group but for which no interactions with other workers were recorded differed significantly from those of ants moving solitarily (Table 4).

To test whether ants regulate the frequency of interactions by seeking or avoiding contacts with nest-mates, we used a resampling method analogous to that used to test for the amount of area covered *per capita*.

1. Since the major effect on the number of interactions was due to group size, we considered the 20 experiments achieved with each group size as a whole and computed the frequency distribution of the number of interactions observed.
2. We created a set of 20 resampled groups for each group size. The ants in each resampled group were drawn randomly from distinct experimental groups. We then computed the number of interactions occurring in each of the resampled groups and calculated the frequency distribution of the number of interactions for the set of 20 resampled groups.
3. Using a KS test, we compared for each group size the distribution of the number of interactions observed in the 20 experimental groups with that observed in the set of 20 resampled groups created at step (2).
4. We repeated step (2) and (3) 200 times and computed the median value of the KS statistic and its associated probability. If ants were moving independently on the area, the distribution of interaction frequencies in experimental groups and in resampled groups should be similar and one should obtain a probability greater than the 0.05 significance threshold.

Table 3 gives for each group size the mean number of interactions in the experimental and resampled

Table 3  
Number of interactions censused<sup>a</sup>

Group size	Experimental groups ( $N = 20$ )	Resampled groups ( $N = 4000$ )	$P$
5	$5.95 \pm 3.17$	$3.99 \pm 3.23$	$>0.05$
10	$17.75 \pm 10.92$	$11.77 \pm 5.78$	$>0.05$
15	$45.40 \pm 16.89$	$31.41 \pm 11.24$	$>0.05$

Two hundred simulations were run. In each simulation 20 resampled groups were created and the frequency distribution of the number of interactions observed in experimental groups and in resampled groups was compared with a Kolgomorov–Smirnov test. A total of  $200 \times 20 = 4000$  resampled groups was thus created.  $P$  gives the probability associated with the median value of the 200 Kolgomorov–Smirnov statistical values.

<sup>a</sup> Values are mean  $\pm$  S.D.

groups. The mean number of interactions in the experimental groups did not appear to be significantly different from that of the resampled groups for any of the group size.

Further evidence of the fact that ants did not seek interactions was provided by the study of the critical distance of attraction between ants. If interactions were actually actively sought by ants, one should be able to detect a critical distance at which two ants would perceive each other and converge monotonically until interacting. To test this, we created a null model by drawing randomly pairs of ants in distinct experimental groups of the same size and by using the algorithm described in the method section to detect interactions. Once 5000 interactions were obtained for each group size we compared the frequency distribution of the critical distances obtained by the null model with that observed in the experiments. We found that the relative frequency yielded by the observations was significantly higher than that yielded by the model only for distances within 10 and 15 mm (Fig. 3). This corresponds approximately to two or three times the size of a media worker.

#### 4. Discussion

While the state of the area on which the ants were moving had no direct effect on their movements, the nutritional state of the colony to which they belonged had one on several of their trajectory characteristics. Ants belonging to a starved colony moved significantly more slowly and had less sinuous trajectories than ants belonging to a colony that had been fed regularly. This result concords with that of Cosens and Toussaint (1985) who found that the running speed of non-replete workers of *Formica aquilonia* was significantly smaller than that of replete workers. A possible explanation for this difference could be that food depletion induces a decline of ants' energy reserves, resulting in a reduction of the energy they can expend in locomotion.

The number of individuals in the arena strongly affected the characteristics of the ants' movements. The main differences in trajectory characteristics were found between ants moving solitarily and ants moving in a group, whatever the size of the group. Ants moving in a group were slower and had less sinuous

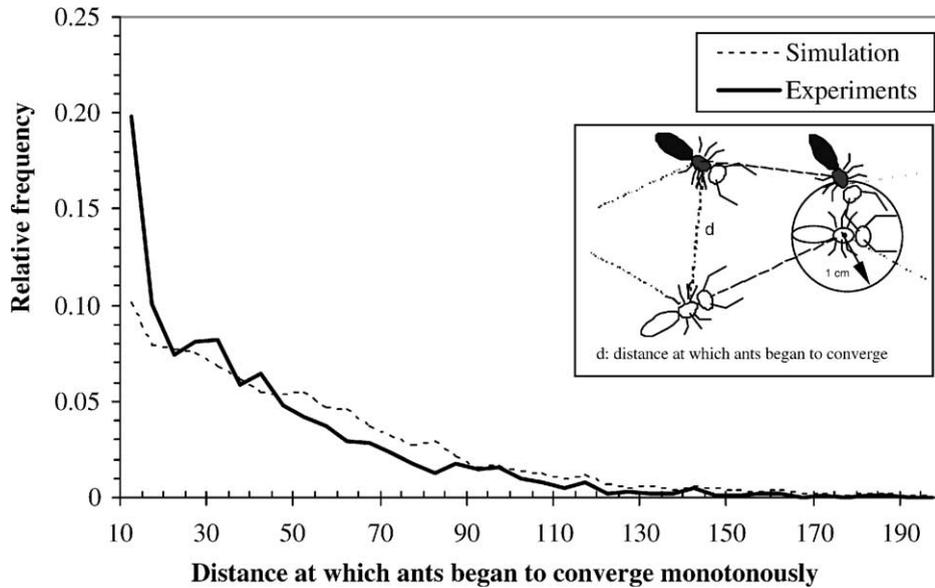


Fig. 3. Frequency distribution of the distance at which ants began to converge monotonously. A null model was created by simulation by drawing randomly pairs of ants in distinct experimental groups of the same size and by using the algorithm described in Section 2 to detect interactions.  $N = 1297$  interactions for the experimental group and 15,000 for the simulations (5000 interactions for each group size).

trajectories than isolated ants. This result is in accordance with that of Gordon (1988) who found in the ant *S. invicta* that the path shape of a worker exploring an area depends on the path shape of neighboring workers. We found in addition that the difference in trajectory characteristics between ants moving solitarily and ants moving in a group was not due to a mere effect of the physical interactions because the trajectory characteristics of ants moving in a group but who did not interact with other workers were significantly different from those of ants moving solitarily (Table 4). One explanation could be that ants modify the geometry of their trajectories when they perceive

the presence of other workers on the area. This perception may be achieved directly, through visual interactions, or more likely, indirectly, through a chemical substance deposited on the ground as ants progressively expand on the area. Further experiments should help to investigate this phenomenon.

Ants moving in groups of 10 or 15 tended to move further away from the center of the arena than ants moving solitarily or in a group of 5 and this effect was accentuated for the ants coming from starved colonies. This result could be interpreted in the light of the theory of risk-sensitive foraging (McNamara and Houston, 1992). Ants moving in groups of 10 or 15

Table 4

Trajectory characteristics of ants moving solitarily and of ants moving in a group with or without interactions with other nestmates<sup>a</sup>

	Ants moving solitarily ( $N = 100$ )	Ants moving in a group	
		Without interactions ( $N = 88$ )	With interactions ( $N = 513$ )
Running speed (mm/s)	25.27 ± 5.66 a	21.84 ± 4.93 b	21.36 ± 5.36 b
Turning index (°)	49.65 ± 27.83 a	44.29 ± 6.30 b	47.57 ± 6.49 c
Maximum net displacement (mm)	196.40 ± 97.80 a	298.10 ± 98.23 b	203.92 ± 102.22 a

The values followed by different letters on the same line are statistically different at the significance threshold of 0.05 (Kruskal–Wallis one-way ANOVA followed by a Dunn’s test).

<sup>a</sup> Values are mean ± S.D.

may be more risk-prone than ants moving solitarily or in a group of 5 and thus may disperse further away; starvation may be an additional factor increasing this tendency.

While the overall area covered by a group of moving ants increased with group size, the amount of area covered *per capita* was higher for ants moving solitarily than for ants moving in a group, whereas the amount of area covered by ants moving in groups of different size was not statistically different. Considering the manner in which the amount of area covered *per capita* was computed, this can be explained by the simple fact that, in ants moving in a group, the increase in the overall area covered was balanced by the higher amount of overlap of individual workers' trajectories in the first seconds of the experiment. The amount of area covered *per capita* would be higher if there were some sort of regulatory mechanisms allowing a reduction of this overlap, e.g. through the exertion of repulsive forces leading to a partitioning of the area among individuals (Ruxton, 1995; Ruxton and Glasbey, 1995). Our simulation shows however that the amount of area covered *per capita* by workers moving in a group was not significantly different from that one would have obtained if ants were moving on the area independently of each other. We conclude therefore that there was no coordination among workers moving on the arena.

The mean number of interactions observed in ants moving in a group was not significantly different from that one would have observed if ants had been moving on the area independently of each other. This confirms the results discussed above: if ants had attempted to avoid contact with other nestmates, one would have observed a reduction in the number of interactions. In the Argentine ant *L. humile* Gordon et al. (1993) found that the rate of contact at high densities was the result of a pure random process whereas in *Lasius fuliginosus* (Gordon, 1995) and in the small workers of the species *Tapinoma nigerrimum* (Lopez et al., 1997), ants were found to be able to regulate their rate of contact at high densities by respectively curtailing or seeking contact with neighboring ants. However, the results of these authors are difficult to compare with ours for two reasons. First, the ant densities at which their observations were achieved were much higher than in our experiments, e.g. in Gordon's experiment on *L. fuliginosus* the lowest density was more than

three times higher than the highest density we used. And second, ants were observed while patrolling on an area several minutes to several hours after they had been allowed access to it, whereas in our experiments they were observed during the first minute of movement, after they had been passively displaced from the nest and released in the center of an arena. This could clearly influence the shape of their trajectories and the rate of interactions (Bonabeau et al., 1998). Another difficulty in comparing our experiments with those of other authors is also the fact that with the procedure we used we do not know whether ants are simply moving away from the center of the arena because they are alarmed or because they are searching for food or for their nest entrance. That ants were not dispersing simply because they were alarmed was shown however by the fact that, when seeds (*Brassica rapa*) were placed in the arena, they had the same probability to be handled by ants entering in contact with them, whether ants were captured in the nest and placed directly in the center of the arena as in our experiment, or whether they access the arena freely from their nest placed under the arena. However, the probability to seize a seed and to carry it was halved, which may indicate that ants were confused by the situation and were also looking for their nest entrance.

In conclusion, our results show that the dispersion movement of an ant was strongly affected by the presence of nearby ants. The geometry of an ant's path is changed not merely through the effect of random encounters with other workers but also through an active modification of its movement when it perceives directly or indirectly the presence of other workers in the surroundings. There is however no coordination among workers leading to a gregarious movement or to a particular spatial organization of their dispersion movement. Providing the condition of constant overall density is met, the resampling technique we used in this paper could be easily applied to the study of the collective movement of other organisms, e.g. unicellulars and gregarious fish or mammals.

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## References

- Adler, F.R., Gordon, D.M., 1992. Information collection and spread by networks of patrolling ants. *Am. Nat.* 140, 373–400.
- Bonabeau, E., Theraulaz, G., Deneubourg, J.L., 1998. Group and mass recruitment in ant colonies: the influence of contact rates. *J. Theor. Biol.* 195, 157–166.
- Cerdan, P., 1989. Etude de la biologie, de l'écologie et du comportement des fourmis moissonneuses du genre *Messor* (Hymenoptera, Formicidae) en Crau. Thèse de 3<sup>ème</sup> cycle. University of Science and Technology, Languedoc, Montpellier.
- Cosens, D., Toussaint, N., 1985. An experimental study of the foraging strategy of the wood ant *Formica aquilonia*. *Anim. Behav.* 33, 541–553.
- Couzin, I.D., Krause, J., James, R., Ruxton, G.D., Franks, N.R., 2002. Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* 218, 1–11.
- Fewell, J.H., 1988a. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. *Behav. Ecol. Sociobiol.* 22, 401–408.
- Fewell, J.H., 1988b. Variation in foraging patterns of the western harvester ant, *Pogonomyrmex occidentalis*, in relation to variation in habitat structure. In: Jeanne, R.L. (Ed.), *Interindividual Variability in Social Insects*. Westview Press, Boulder, Colorado, pp. 257–282.
- Gordon, D.M., 1988. Group-level exploration tactics in fire ants. *Behavior* 104, 162–175.
- Gordon, D.M., 1995. The expandable network of ant exploration. *Anim. Behav.* 50, 995–1007.
- Gordon, D.M., Mehdiabadi, N.J., 1999. Encounter rate and task allocation in harvester ants. *Behav. Ecol. Sociobiol.* 45, 370–377.
- Gordon, D.M., Paul, R.E., Thorpe, K., 1993. What is the function of encounter patterns in ant colonies? *Anim. Behav.* 45, 1083–1100.
- Holmes, E.E., 1993. Are diffusion models too simple? A comparison with telegraph models of invasion. *Am. Nat.* 142, 779–795.
- Leger, D.W., Didrichsons, I.A., 1994. An assessment of data pooling and some alternatives. *Anim. Behav.* 48, 823–832.
- Lopez, F., Fungairiño, S.G., Serrano, J.M., Acosta, F.J., Reunanen, P., 1997. Allothetic efficiency in the patrolling networks of a polymorphic ant, *Tapinoma nigerrimum* Hymenoptera: Formicidae. *J. Insect Behav.* 10, 115–127.
- McNamara, J.M., Houston, A.I., 1992. Risk-sensitive foraging: a review of the theory. *Bull. Math. Biol.* 54, 355–378.
- Okubo, A., 1980. Diffusion and ecological problems: mathematical models. *Lecture Notes in Biomathematics*, vol. 10. Springer, New York.
- Okubo, A., 1986. Dynamical aspects of animal grouping: swarms, schools, flocks, and herds. *Adv. Biophys.* 22, 1–94.
- Pacala, S.W., Gordon, D.M., Godfray, H.C.J., 1996. Effects of social group size on information transfer and task allocation. *Evol. Ecol.* 10, 127–165.
- Parrish, J.K., Hamner, W.M., 1997. *Animal Groups in Three Dimensions*. Cambridge University Press, Cambridge.
- Ruxton, G.D., 1995. Foraging in flocks: non-spatial models may neglect important costs. *Ecol. Model.* 82, 277–285.
- Ruxton, G.D., Glasbey, C.A., 1995. Energetics of group foraging: analysis of a random-walk model. *IMA J. Math. Appl. Med. Biol.* 12, 71–81.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Tourtellot, M.K., Collins, R.D., Bell, W.J., 1991. The problem of movelength and turn definition in analysis of orientation data. *J. Theor. Biol.* 150, 287–297.
- Turchin, P.F.J., 1989. Beyond simple diffusion: models of not-so simple movement of animals and cells. *Comments Theor. Biol.* 1, 65–83.
- Turchin, P.F.J., 1997. Quantitative analysis of animal movements in congregations. In: Parrish, J.K., Hamner, W.M. (Eds.), *Animal Groups in Three Dimensions*. Cambridge University Press, Cambridge, pp. 107–112.
- Turchin, P., Odendaal, F.J., Rausher, M.D., 1991. Quantifying insect movement in the field. *Environ. Entomol.* 20, 955–963.
- Wiens, J.A., Crist, T.O., Milne, B.T., 1993. On quantifying insect movements. *Environ. Entomol.* 22, 709–715.
- With, K., 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecol.* 9, 25–36.
- Wu, H., Li, B.L., Springer, T.A., Neill, W.H., 2000. Modelling animal movement as a persistent random walk in two dimensions: expected magnitude of net displacement. *Ecol. Model.* 132, 115–124.