

Research article

Dynamics of aggregation in *Lasius niger* (Formicidae): influence of polyethism

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Summary. Polyethism is a well-known phenomenon in social insects. How this phenomenon influences interactions among individuals, the spatial distribution in the nest is, on the other hand, very rarely documented. Therefore, we conducted experiments on the ant *Lasius niger* to observe the influence of polyethism on aggregation, by distinguishing two groups of ants: the brood-tenders and the foragers. We show a great difference in their self aggregation level. Brood-tenders are characterized by a rapid and dense gathering in one main stable cluster while foragers gather in several small unstable clusters. We show experimentally and verify with a model that this difference in behaviour is based on a smaller probability of leaving a cluster for the brood-tenders. Aggregation in the mixed case (groups composed of brood-tenders and foragers) is very close to that of the pure forager case, showing a decrease in the level of aggregation of the brood-tenders respecting to the pure group of brood-tenders. Nevertheless, experimental results supported by the results of the model, show that ants do not change their own behaviour when the two groups are together. Therefore, the decrease of the aggregation of brood-tenders in the mixed case can be explained by a difference in the dynamics between brood-tenders and foragers.

Key words: Ants, aggregation, polyethism, *Lasius niger*, pattern.

Introduction

In social species, many activities are concerned with aggregation which benefits either the individual or the group (Magurran, 1990; Wiley, 1991; Parrish and Edelstein-Keshet, 1999; Aron and Passera, 2000; Boinski and Garber, 2000; Krause and Ruxton, 2003). In social insects, many

activities are related to aggregation phenomena such as defence (Millor et al., 1999; Hölldobler and Wilson, 1990) or building behaviour (Franks and Deneubourg, 1997). The organisation of the nest may also be seen as a gathering of groups of individuals which must cooperate. The spatial distribution of the insects affects their activities, but also the activities affect the spatial organisation (Sendova-Franks and Franks, 1993, 1995; Backen et al., 2000). However, little work has been done on the spatial organisation of the nest and its functionality as well as the behaviours leading to these patterns (Aarab et al., 1990; Camazine et al., 1990; Fresneau and Corbara, 1990; Franks and Sendova-Franks, 1992; Sendova-Franks and Franks, 1994; Boi et al., 1999).

The insects can be distinguished according to their stage of development or their specialization (polyethism). This individual specialization correlates with the age of the insects. For many species, it was shown that workers perform different tasks during their life: a young worker is a brood-tender or nurse and takes care of the queen and of the brood; then it becomes a domestic worker and attends to the nest; and at the end of its life, it is a forager (Sorensen et al., 1984; Wilson, 1976). Moreover, many examples are known showing that the polymorphism, when it exists, strongly affects the specialization (see for example Wilson, 1978, 1980; Espadaler et al., 1990; Stapley, 1999). Finally, the specialization is function of the individual genetic (Stuart and Page, 1991; Fraser et al., 2000) and life history, including learning (Deneubourg et al., 1987; Weidenmuller et al., 2002). The different groups of specialists are characterised by different responses to social or environmental stimuli (Beshers and Fewell, 2001).

Aggregation of the individuals of the same caste (brood-tenders, foragers, etc.) may result in a similar response to a spatial heterogeneity or from attraction between individuals (Ceuster, 1977; Camazine et al., 2001). Empirical knowledge suggests that the inter attraction plays an important role in insect societies and may vary from caste to caste. The inter-

individual attraction can be a corner-stone of the spatial distribution of ants inside the nest. We investigate in this paper the influence of polyethism on the dynamics and patterns of aggregation resulting from attraction between individuals. Firstly, we will characterise the patterns of aggregation of brood-tenders, foragers and mixed group (brood-tenders and foragers). Secondly, we will identify the individual behaviours at the origin of the differences between the patterns of aggregation. Thirdly, we will analyse how foragers and brood-tenders influence each other in a mixed group. Experiments are carried out on *Lasius niger* because of its monomorphic character and also because many of its activities are well documented (foraging: Beckers et al., 1992, 1993; Devigne and Detrain, 2002; Portha et al., 2002, 2003; Maillieux et al., 2003; division of labour: Lenoir 1979; aggregation: Depickère et al., in press).

Material and methods

Four colonies (500–1000 workers) of *Lasius niger* were collected in Brussels (Belgium) on the campus of the ULB. They were reared using tube nests (10 cm length, 1 cm diameter, water and red paper) under $23 \pm 1^\circ\text{C}$, photoperiod of 12 h. They were fed with *Tenebrio molitor* larvae, and with a special food (Bhatkar and Whitcomb, 1970), three times a week.

The experimental setup was an arena made up of a PVC ring of 2 cm height and 19.8 cm in diameter, put on a black paper sheet. The inside edge was coated with Fluon®. A dark cylinder surrounding wall and a dark cover (30 cm above the arena) closed the setup in order to avoid any visual signals. In the cover, a first centred hole was used to illuminate the setup by a black chamber bulb (PF712E, 15W) and a second one, not centred, allowed us to put a digital camera and record the activity of the ants for 90 min.

L. niger (monogynous, polyandric) is characterized by a typical age polyethism (Lenoir and Mardon, 1978; Lenoir, 1979; Lenoir and Ataya, 1983). Young ants take care of the brood. So, we call them brood-tenders. The majority of foragers are old individuals. In our experiments, we used these two groups of ants: brood-tenders were picked up inside the nest near the brood, and foragers were taken outside the nest. At the beginning of the experiments, ants were dropped on the centre of the arena. Three situations were studied: two pure cases, with only one ant group (20 brood-tenders ($n = 24$) or 20 foragers: ($n = 12$)) and a mixed case: 10 brood-tenders/10 foragers ($n = 13$). In this last case, the abdomen of the ants of one group was painted with white gouache. In each replication of the mixed case, all the foragers or all the brood-tenders were painted. Moreover, experiments with 10 brood-tenders ($n = 12$) were carried out to verify the influence of a decrease of the density of brood-tenders, related to the study of the mixed case.

Collective level

The length of a *L. niger* ant is about 5–6 mm (with antennae). We observed that when an aggregate reorganised itself (e.g. after the arrival of an individual), an ant could leave the cluster over some millimetres and then come back to the aggregate. Therefore, we determined that this ant had not left the aggregate and that ants were aggregated when two or more individuals were at a distance (thorax to thorax) of less than 1 cm from each other.

The video recordings of each experiment were analysed on a computer: a snapshot was taken at 30 s, at 1 min and after every min up to 40 min and then every 5 min (51 snapshots in total). A program allowed the cartesian position of the thorax of the ants to be recorded. Then, with some processing programs, we calculated:

- the radial distribution of the ants in the arena: the arena has been divided into five rings of 2 cm; the external ring corresponds to the edge of the arena. The fact that the rings do not have the same areas is taken into account by the measurement of the ant density in each that we will use later in the analysis;
- the number of aggregated ants and so the aggregated fraction (number of aggregated ants/total number of ants);
- the number of clusters and their size (number of ants inside): clusters were ranked in a decreasing order for each experiment and for each time. Then, for each rank, a mean size of cluster was calculated;
- the spatial stabilization of the biggest cluster: the distance between the centroid of the biggest cluster at time t and the centroid of the biggest cluster at time $t+1$ was calculated for each experiment and then a mean distance was calculated.

The aggregation will be confirmed by a comparison of the experimental fraction of aggregated ants and the experimental size of clusters with results obtained from a random distribution of the ants respecting the experimental radial distribution in the setup. Moreover, this aggregation is not due to an external environmental cue but to the ants themselves, as is shown by the test verifying the homogeneity of the angular distribution of the ants in the setup at 90 min (Chi square test: $N = 240$, $\chi^2_2 = 3.1$, N.S.).

We verified the absence of any effect of paint marks on the ants by comparing the behaviour of each caste between experiments where individuals were painted and experiments where they were not painted. For all the tests, no difference was observed between painted and non painted individuals of the same caste. For example, in the seven experiments where brood-tenders were painted, they represented 59.7% of the total aggregated population, while in the six experiments where foragers were painted (and not brood-tenders) brood-tenders represented 60.2% of the total aggregated population.

Individual level

Our goal is to identify the individual behaviours that can explain how aggregation emerges. Three types of behaviours were particularly studied because of their influence on contacts between ants: 1) spontaneous stops, which can be at the origin of a cluster; 2) stops by encounter; 3) the time spent by an ant in a cluster, which depends on cluster size and which shows us the probability of leaving a cluster. This study has been done for the both pure cases.

We calculate the probability associated with each behaviour. Firstly, the probability of making a spontaneous stop (p_s) has been found by an analysis of the life times of ant paths that end with a spontaneous stop ($N = 18$ paths for brood-tenders and $N = 49$ for foragers). The survival curve of still moving ants obeys an exponential law (1), indicating that the probability of making a spontaneous stop (β) is constant.

$$F_c = e^{-\beta t} \quad F_c: \text{fraction of still moving ants at time } t \quad (1)$$

Secondly, the probability of leaving a cluster or a spontaneous stop (p_L) is researched: for each size of clusters (i.e. the ant number in the cluster), we analyse the time spent by an ant in the cluster (size = 1 corresponds to a spontaneous stop). Again, for each size of clusters, the survival curve of those clusters obeys an exponential law (1) where F_c represents the fraction of still surviving clusters and β the constant probability of breaking a cluster which can be due to the arrival or the leaving of one ant. Then, as we know the numbers of clusters that end with the arrival of another ant in the cluster (N_A) and by the leaving of one ant of the considered cluster (N_L), and the relations $N_A/N_L = p_A/p_L$ and $\beta = p_A + p_L$, we calculate the probability of leaving a stop p_L and the probability that an ant meets a cluster p_A for each size of clusters. All these probabilities found for each cluster size (size = 1: spontaneous stop) obey a power law:

$$p_L = a \cdot N^{-b} \quad N = \text{number of ants involved in the stop} \quad (2)$$

We consider that the probability of stopping by encounter is always equal to 1. Due to the exponential law, the stop time is the inverse of the probability of leaving the aggregate (precision level of the video recorder: 0.04 s). Finally, the speed of the ants is calculated: 80 paths of 3 s in duration were measured in two experiments (40 for each) for brood-tenders and for foragers.

An algorithm of individual behaviour process was formulated (Fig. 1) and was the basis of a Monte-Carlo simulation (1000 simulations). This model was used to validate our hypothesis on the mechanisms of aggregation explained previously. Almost all clusters are in the external ring of 2 cm at the end of the experiments (see Results). Therefore, our theoretical setup has the shape of this external ring divided into square cells 3 mm in length where the ants can move with the experimental speed in the eight directions, each cell having eight neighbours. From the interior edge of this ring, the ants can go to the centre of the arena, represented by only one large cell, where ants cannot be stopped or aggregated. The probability of going to the centre of the arena p_C is naturally equal to $3/8$, corresponding to the probability of going to three cells. The mean resting time in the centre (outside the ring) is estimated at 1 second and so the probability of going to the ring is equal to $1/\text{the mean resting time in the centre}$.

At the beginning of the simulations, the ants were placed at the centre. For each simulation, at each time step, an ant could be at the centre or on the ring of the setup. If it was at the centre, it has a probability p_R of leaving and going to the ring randomly on the first free row of cells (interior edge of the ring). If the ant was on the ring, it can be in two states: a stopped ant or a walking ant. If it was a stopped ant, it had a probability p_L of leaving its cell. Then, it had a probability p_{Ud} of changing its original direction and going to the next cell (equal probability between the eight possible directions). If another ant was on the next cell, then it stopped. If it was a walking ant, it could make an encounter and then stopped. If it did not make an encounter, if it was on the interior edge of the setup, it could go to the centre with the probability p_C . If not, or if it was not on the interior edge of the ring, it could make a spontaneous stop with a probability p_S and then stop. If not, it moved on one cell. The results of the simulations are then analysed in the same way as the experimental results and are compared with experimental ones issued also from a ring of 2 cm.

Results

Collective level

When ants are dropped onto the centre of the arena at the beginning of the experiments, they explore the environment and quickly reach the edge of the setup. Then, because of encounters, some small aggregates appear, they rapidly grow and stabilise for brood-tenders while for foragers, they stay small and unstable.

Radial distribution

In the pure cases, the majority of brood-tenders ($\approx 90\%$) and foragers ($\approx 60\%$) are in the external ring that is characterised by a high density of workers. The density of brood-tenders in this external ring is 1.5 the corresponding foragers' density suggesting that brood-tenders are more thigmotactic than foragers (Fig. 2, Table 1). In the mixed case, the radial distribution of the two groups of ants is similar to these of pure cases, considering the relative ant number (Fig. 2, Table 1). This radial distribution appears early in the experiments and is stable: for each condition, the radial distribution at 15 min is similar to this at 90 min (Table 1).

Aggregated fraction

For brood-tenders in the pure case (Fig. 3), aggregation is fast: after a quick rise, the plateau value is reached and in five minutes 70% of the total population is gathered. For foragers (Fig. 3), the aggregation level is lower: 35% of the total population is gathered, during the entire experimental time. For the mixed case, the attempted aggregation level is close to pure forager levels: 40% of the mixed population is aggregated. If these results are compared with those that issue from a random distribution of the ants in the arena, we observe in each case a difference showing the existence of an active aggregation (Table 2). There is no difference in the aggregation level of foragers (number of aggregated foragers/total number of foragers) between the pure and the mixed situation while for brood-tenders the fraction is lower in the mixed case than in the pure case (Table 2). This weaker level of aggregation can be due to the smaller number of brood-tenders in the mixed case (10 ants) compared with the pure case (20 ants). Therefore, 12 experiments in the same conditions, with 10 brood-tenders in the arena were performed. No difference appears neither in the aggregation level nor in the radial distribution, showing that this hypothesis does not explain the decrease (radial distribution (Fig. 1, Table 1), fraction of aggregated ants (Table 2) and pattern similar: χ^2 test: $X^2 = 7.6, p < 0.05$). Therefore, this difference in the aggregated level is due to the presence of the foragers. The comparison between the fraction of aggregated ants in the total arena and the ring suggests that the few individuals situated in the central part of the arena are not aggregated. The mean number of aggregated individuals in the centre at the end of the experiments (between 60 and 90 min) is on average 0.48 ants for brood-tenders, 1.86 for foragers and 1.26 for the mixed case. Therefore, most of the aggregated ants are in the external ring.

Size of clusters

For brood-tenders, the evolution of the mean size of the largest cluster (Fig. 4) obeys a power law ($\text{Size} = 0.17 \cdot t^{0.25}$, Pearson correlation coefficient, $r = 0.92, N = 51, p < 0.005$), with a strong increase during the first 10 min (at 10 min, 35% of the total population is involved in the main cluster) and then a weaker increase (Fig. 4). At the end of the experiments, the main cluster gathers almost 50% of the ants and some satellites are observed (Fig. 4). This pattern obeys a power law ($\text{Size} = 0.55 \cdot \text{rank}^{-2.38}$, Pearson correlation coefficient, $r = 0.99, N = 4, p < 0.05$). For the forager and mixed cases (Fig. 4), during the entire experimental time, the size of the biggest cluster is almost constant and respectively only gathers 15% and 20% of the ants. For both cases, some other small clusters are also observed (Fig. 4). Figure 5 shows the mean fraction of brood-tenders inside the clusters according to their size. The greater the cluster size, the greater the fraction of brood-tenders inside: for duos, 50% of ants are brood-tenders while for clusters of 8–10 ants, 80% of the individuals are brood-tenders.

All the experiments with brood-tenders ($n = 24$) are characterized by the presence of the biggest cluster at the end of the experiments in the external ring of 2 cm. For the for-

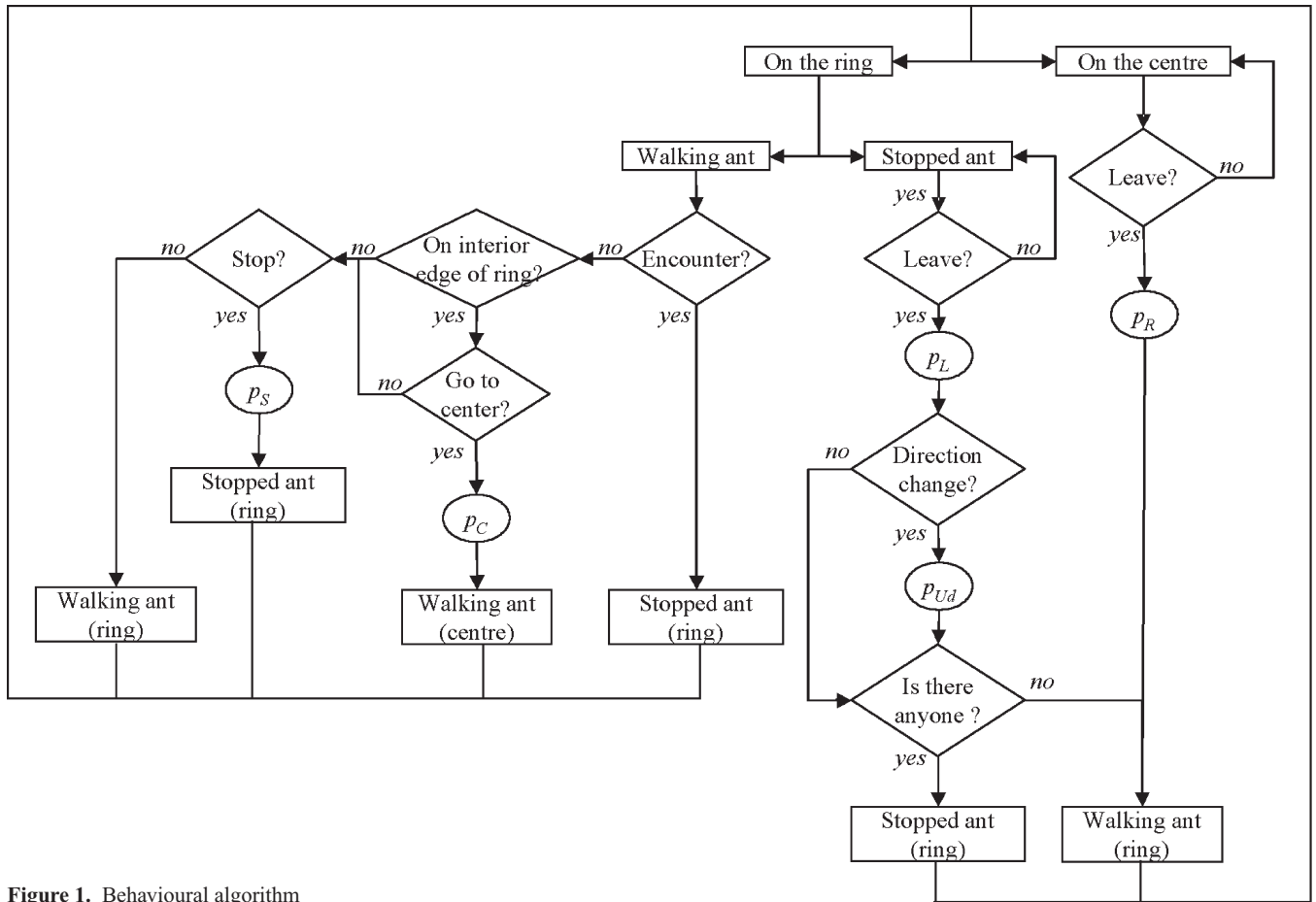


Figure 1. Behavioural algorithm

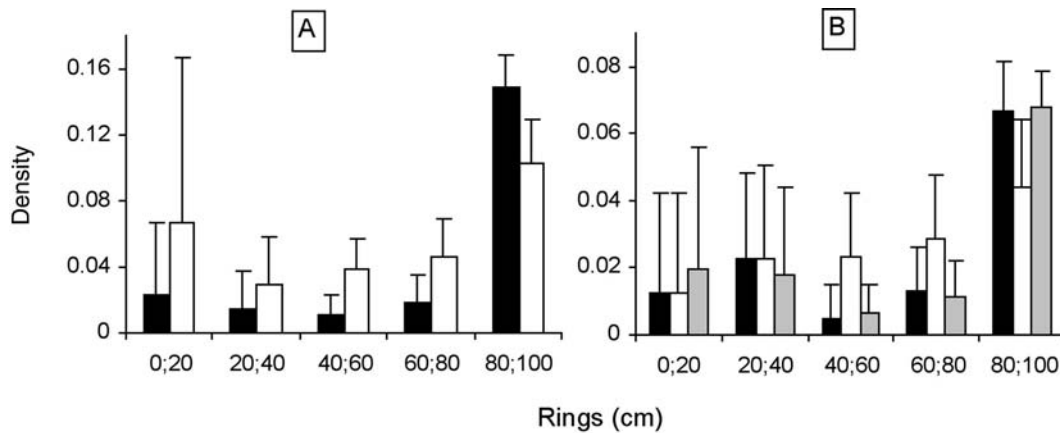


Figure 2. Radial distribution of the ants at 90 min in the arena divided in five rings (0 = centre of the arena). A) Density of brood-tenders (black) and foragers (white). B) Density of brood-tenders (black) and foragers (white) in the mixed case, and density of brood-tenders in experiments with only 10 ants in the arena (grey)

Table 1. Comparisons (Mann Whitney U tests) between the densities of ants in the pure case (except if it is noted ‘mixed’) in the external ring of 2 cm at 90 min (except if another time is noted)

Group and condition	Mean density ± SD (n)	Group and condition	Mean density ± SD (n)	p
Brood-tenders	0.149 ± 0.019 (24)	Foragers	0.102 ± 0.027 (12)	$U = 17.5, p < 0.001$
Foragers	0.102 ± 0.027 (12)	Mixed foragers	0.044 ± 0.030 (13)	$U = 62.5, N.S.$
Brood-tenders	0.149 ± 0.019 (24)	Mixed brood-tenders	0.067 ± 0.015 (13)	$U = 107.5, N.S.$
Brood-tenders: 15 min	0.135 ± 0.028 (24)	Brood-tenders: 90 min	0.149 ± 0.019 (24)	$U = 205.5, N.S.$
Foragers: 15 min	0.094 ± 0.023 (12)	Foragers: 90 min	0.102 ± 0.027 (12)	$U = 55.5, N.S.$
Mixed: 15 min	0.105 ± 0.029 (13)	Mixed: 90 min	0.120 ± 0.022 (13)	$U = 77, N.S.$
20 Brood-tenders	0.149 ± 0.019 (24)	10 Brood-tenders (pure)	0.068 ± 0.011 (12)	$U = 95, N.S.$
10 Brood-tenders (pure)	0.068 ± 0.011 (12)	Mixed brood-tenders	0.067 ± 0.015 (13)	$U = 75.5, N.S.$

Table 2. Comparisons (Mann Whitney U tests) of the fractions of aggregated ants in the total arena between the two groups and conditions (the random distribution of ants respects the experimental radial distribution of the considered caste at 90 min)

Group and condition	Mean ± SD (n)	Group and condition	Mean ± SD (n)	Result
Brood-tenders	0.68 ± 0.16 (24)	Brood-tenders (Random)	0.28 ± 0.12 (100)	$U = 65, p < 0.001$
Foragers	0.33 ± 0.15 (12)	Foragers (Random)	0.18 ± 0.12 (100)	$U = 272, p < 0.005$
Mixed	0.36 ± 0.12 (13)	Mixed (Random)	0.20 ± 0.12 (100)	$U = 238, p < 0.001$
20 Brood-tenders	0.68 ± 0.16 (24)	10 Brood-tenders (pure)	0.65 ± 0.16 (12)	$U = 131.5, N.S.$
20 Brood-tenders	0.68 ± 0.16 (24)	10 Brood-tenders (mixed)	0.43 ± 0.1 (13)	$U = 48.5, p < 0.001$
20 Foragers	0.33 ± 0.15 (12)	10 Foragers (mixed)	0.29 ± 0.06 (13)	$U = 75.0, N.S.$

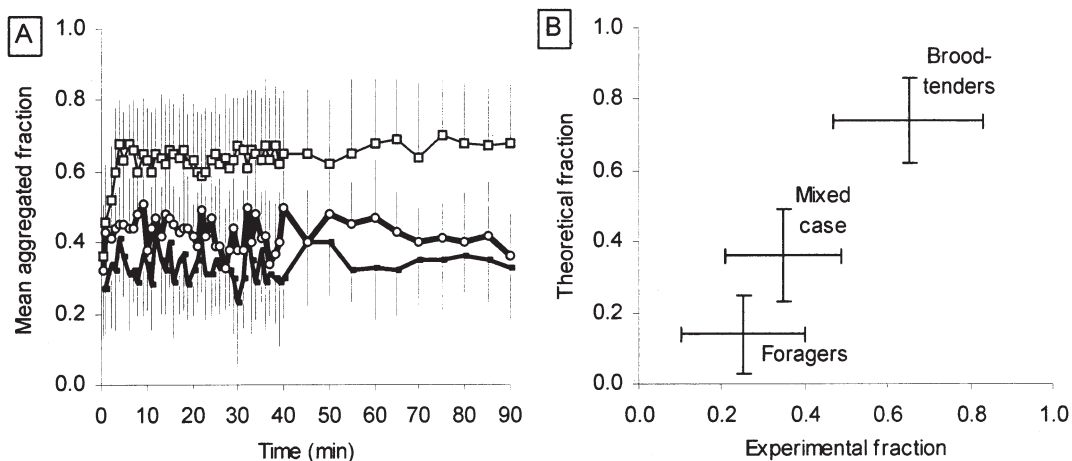


Figure 3. Fractions of aggregated ants. A) Evolution of the mean (\pm SD) experimental fraction of brood-tenders (white square), foragers (black) and in mixed case (white circle); B) Comparison of the mean fractions (\pm SD) of aggregated ants between experiments and theory in the three cases at 90 min

ager ($n = 12$) and the mixed cases ($n = 13$), in all the experiments except one in each case, this cluster is also in the external ring. The distribution of the size of clusters, whatever the caste, is different from this issued from a random distribution (χ^2 test: brood-tenders: $X_3^2 = 255.0, p < 0.001$; foragers: $X_3^2 = 22.4, p < 0.001$; mixed case: $X_3^2 = 29.5, p < 0.001$).

Stability in space of the biggest cluster

For brood-tenders, at the beginning of the experiments, a wide distance between the position of the centroid of

the biggest cluster at time t and the position of the centroid of the biggest cluster at time $t+1$ is measured, suggesting that clusters appear, disappear and reappear in another place (Fig. 4). With time, this distance decreases following an exponential law ($Distance = 48.7 \cdot e^{-0.014t}$, Pearson correlation coefficient, $r = 0.72, N = 51, p < 0.005$), until reaching 20 mm and so a relative stability. This can be related to the mean sizes of these clusters: big clusters are more stable than small ones. For foragers and mixed cases (Fig. 4), the distances are wide without any decrease over time, suggesting that no spatial stabilization appears. Again, this lack of stability is related to the small sizes of the biggest clusters in these cases. There-

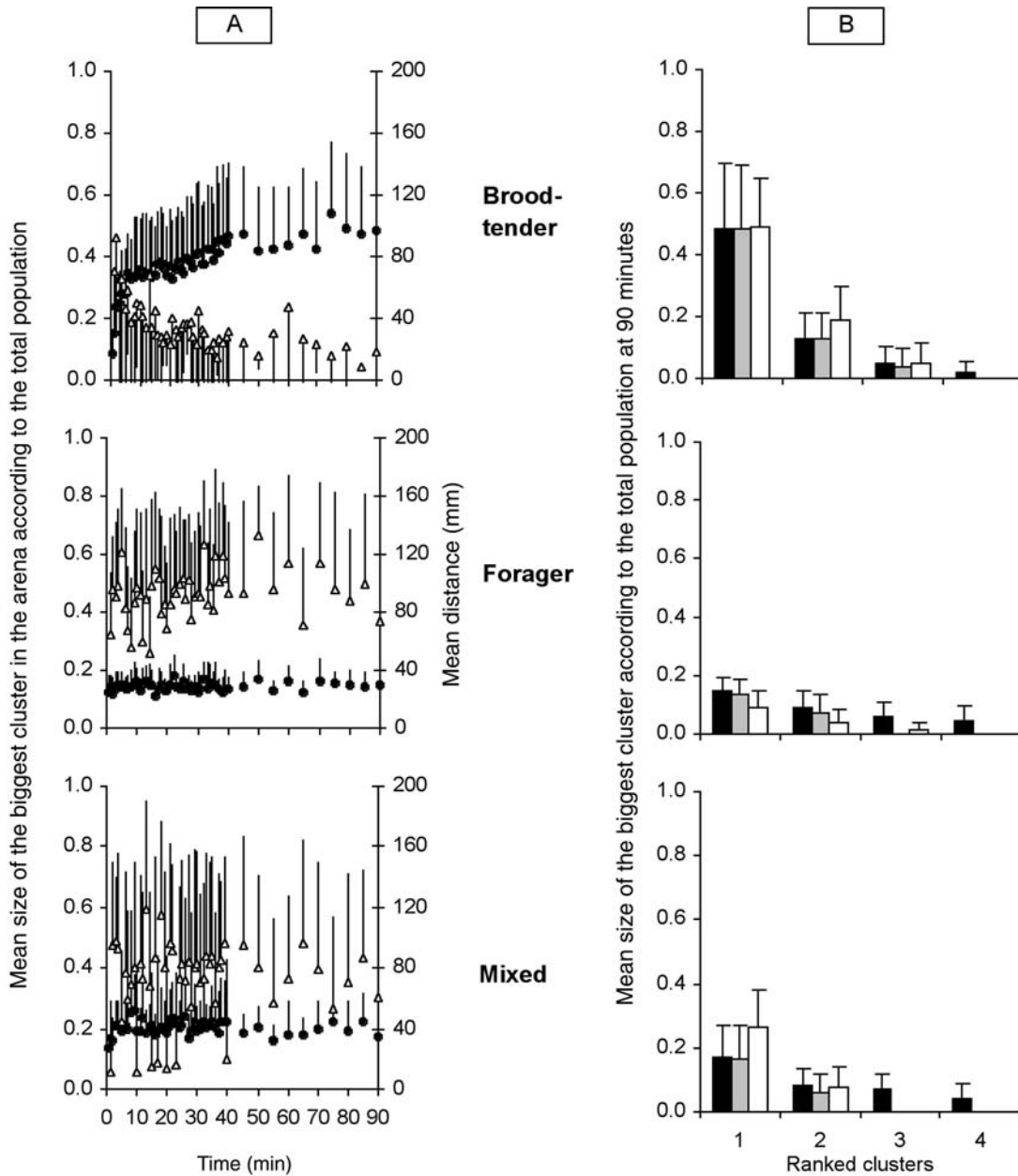


Figure 4. Mean (\pm SD) sizes of clusters and distances: A) Evolution of the mean sizes of the biggest cluster (circle) in the external ring of 2 cm and evolution of the mean distance between the centroids of the biggest cluster at t and $t+1$ (triangle) in the arena; B) Mean size (\pm SD) of the biggest cluster at 90 min for experiments in the arena (black), experiments in the ring (grey) and simulations (white)

fore, whatever the caste used, for clusters with a small size, a same weak stability is found, suggesting that the stability is more due to the size of the clusters than the caste of which they are composed.

In conclusion, in the brood-tender case, aggregation reaches a high level, with one main cluster, stable in space. For the forager and the mixed cases, aggregation is weak, with small and unstable clusters. In the mixed case, they are principally composed of brood-tenders, especially in the biggest clusters.

Individual level and mechanisms

Individual behaviour patterns are analysed to identify the mechanisms at the origin of the different level of aggregation and understand how in mixed groups, brood-tenders and foragers interact. The two groups of ants are not distinguished by their probability of stopping spontaneously (0.08 for foragers and to 0.11 for brood-tenders, Mann-Whitney U test: $U = 409.5$, N.S.). Their speeds are different: foragers move more rapidly than brood-tenders (Foragers $\bar{X} \pm SD = 3.67 \pm 1.48$ cm/s and brood-tenders $\bar{X} \pm SD = 2.91 \pm 0.96$ cm/s, Chi

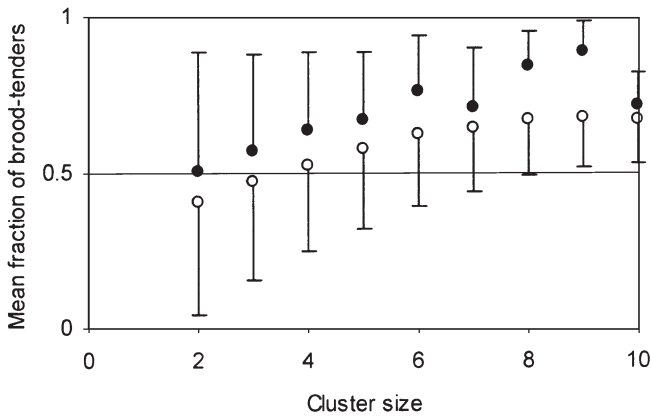


Figure 5. Mean fraction (\pm SD) of brood-tenders inside the clusters in mixed case for experiments (black) and simulations (white) according to the cluster size

square test: $\chi^2_5 = 17.8, p < 0.05$). However, the greater difference between the two groups of ants appears in the individual probability of leaving a stopping site according to the number of the ants involved at the stopping site (Fig. 6): a brood-tender remains stationary ten times longer than a forager.

The probability that a duo breaks (by an arrival or a leaving of one ant) is 0.38 s^{-1} for brood-tenders ($n = 108$) and

3.72 s^{-1} for foragers ($n = 148$) (Fig. 6). We calculate then the probability of leaving a duo by the same method that used for the calculation of the probability of leaving a cluster and we find that it is equal to 0.14 s^{-1} and 1.75 s^{-1} respectively. If there is no change in the behaviour of the ants when the two castes are together, the probability of breaking a mixed duo (1 brood-tender and 1 forager) would be equal to the sum of the individual probability of each caste: $0.14 + 1.75 = 1.89 \text{ s}^{-1}$. The value found experimentally (Fig. 6) for this probability in the mixed case ($1.70 \text{ s}^{-1}, n = 97$) is similar to the theoretical value, suggesting that individuals do not change their behaviour when they are together.

The model was used to test if these individual behaviours are able to reproduce the different patterns of aggregation. As suggested by the last individual result, the model assumes that a forager (brood-tender) shows the same behaviour when interacting with conspecifics of the same or of the other caste. Simulations are compared with experimental results obtained in a ring of 2 cm (see Material and method). For both brood-tenders and foragers, the comparison between experimental and theoretical results shows that a same evolution is found and so we limited the comparison to the plateau value. For the pure cases, a good agreement is found between theoretical and experimental results concerning the fractions of the aggregated ants (Fig. 3). Concerning the pattern observed at 90 min, a big cluster is also present in the simulations, with a size similar to the experimental size (Fig. 4). Therefore, this

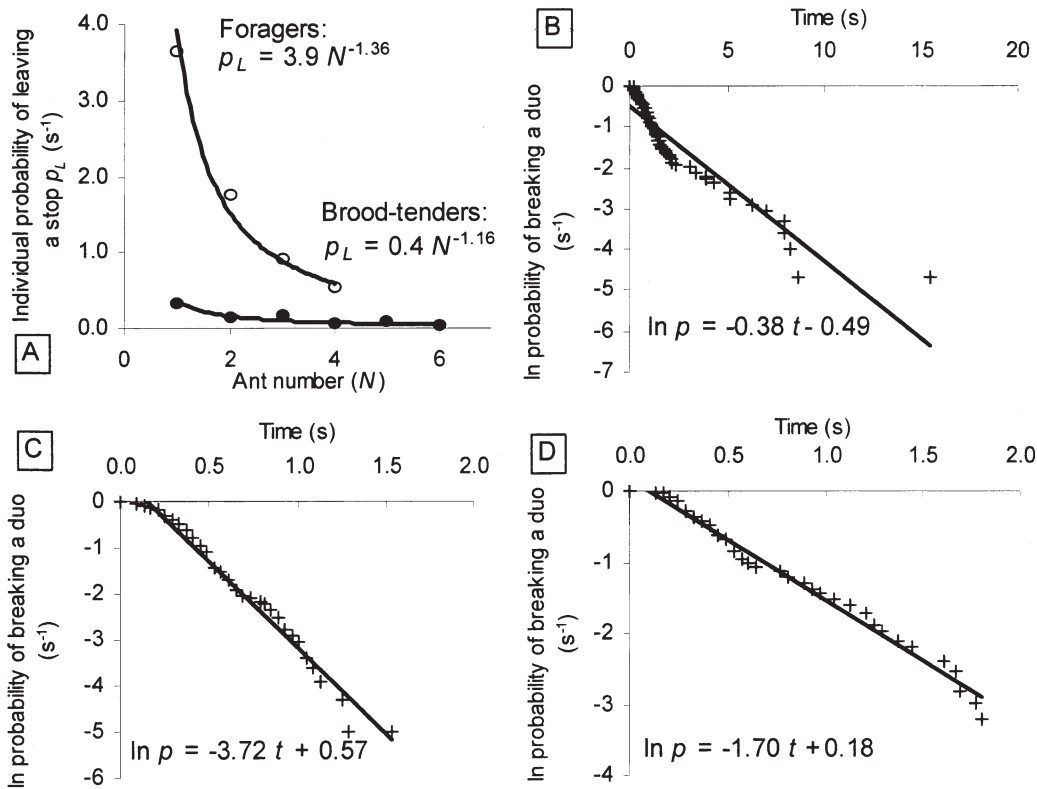


Figure 6. Individual probability of leaving a stop (A: Pearson correlation coefficient: foragers (white): $r = 0.99, N = 4, p < 0.05$; brood-tenders (black): $r = 0.91, N = 6, p < 0.05$); and of breaking a duo for brood-tenders (B); for foragers (C); for the mixed case (D) (Pearson correlation coefficient: B: $r = 0.93, N = 61, p < 0.005$; C: $r = 0.99, N = 31, p < 0.005$; D: $r = 0.99, N = 32, p < 0.005$)

agreement between theoretical and experimental results validates our hypothesis about the mechanisms of aggregation: the individual differences in the behaviour between brood-tenders and foragers are sufficient to generate the difference in the aggregation level observed.

For the mixed case, we also have a good agreement between theory and experiments. Similar levels of aggregation are found in simulations and in experiments (Fig. 3) with a similar size of clusters at 90 min (Fig. 4) and a similar proportion of brood-tenders inside the clusters (Fig. 5). The decrease of aggregated brood-tenders observed in experiments between the pure and the mixed case is also found in simulations. In fact, this decrease can be characterized by the calculation of the mean fraction of aggregated brood-tenders from 60 to 90 min between the experimental ring and the simulations. Both ratios (aggregated brood-tenders in the mixed case/aggregated brood-tenders in the pure case) are equal to 0.8. This result suggests that when brood-tenders and foragers are together, they do not change their behaviour, i.e. the value of probabilities related to their individual behaviour pattern.

Discussion

Brood-tenders and foragers are characterized by much wall-following: ants rapidly reach the edge of the setup and then move and aggregate in a ring of 2 cm. Brood-tenders and foragers of *L. niger* show a great difference in their aggregation level. Brood-tenders are characterized by rapid and dense gathering: 70% of the total population is aggregated and 50% of this total population is in one main cluster whereas only 33% of the foragers are clustered at 90 min in several small clusters. These results for brood-tenders confirm those of a previous study showing the stability of this behaviour (Depickère et al., submitted). The analysis of the individual behaviours shows that the main difference between the two castes appears in the time one individual stays stationary and isolated or inside a cluster. A brood-tender remains stopped ten times longer than a forager. The model, elaborated from individual data, strongly suggests that the difference between these resting times generate two levels of aggregation.

When foragers and brood-tenders are together, just 40% of the ants are aggregated, in small clusters, as in the case of the foragers. However, the greater the cluster size, the greater the proportion of brood-tenders inside. A decrease in the level of aggregation is observed for the brood-tenders in comparison with the pure case. The model, where the two castes do not change their behaviour when they are together, reproduces all the mixed case characteristics. Inter-attraction varies caste to caste but no influence appears from one caste to another. The response of an ant depends on its caste but does not depend on the caste of the attracting individual. It is an interesting result because some studies show a difference between ants performing foraging or nest maintenance in the composition of cuticular hydrocarbons, which are the basis of the individual recognition or of the task decisions (Lenoir

et al., 1999; Wagner et al. 1998, 2000, 2001; Greene and Gordon, 2003). Therefore, the origin of these differences has to be searched for in the dynamics of the system. As the foragers have shorter stops, they have a greater mobility. The brood-tenders begin to aggregate and some mixed and pure clusters appear. The foragers that encounter these clusters stop but rapidly leave them. This leaving, more frequent in the mixed experiments than in experiments with only brood-tenders, can generate the leaving of other ants of the cluster, causing a reorganisation of the cluster. This effect could be amplified by the higher speed of foragers, even if the increase of the ant speed in the model does not change the global results obtained. The model shows that this dynamical cause is dominant but we cannot exclude a weak presence of a change of behaviour.

This work gives a preliminary understanding of the spatial organisation of ants inside the nest. In social-insect colonies the different specialists are often spatially segregated and the density of individuals varies from one area of the nest to another (Sendova-Franks and Franks 1995, Tschinkel 1999). These spatial patterns are largely based on the social interactions. Supported by their experimental results on *Lep-tothorax*, Backen et al. (2000) propose a dynamic leading to the spatial segregation and based on the attraction between workers and the worker mobility. The latter is associated with their task specialisation. In this paper, we describe another mechanism also based on inter attraction: the probability of leaving a cluster decreases with the cluster size. We show that a quantitative difference between these probabilities of the brood-tenders and of the foragers leads to spatial patterns where the brood-tenders form large and stable clusters while foragers are more scattered. These patterns must facilitate the adaptive response of the colony. The foragers must be more scattered due to their external activities must move easily to leave the nest and/or to be recruited. Inversely, brood-tenders stay inside the nest, near the brood pile, more in contact with nestmates and therefore to aggregate. We hypothesise that this probability of leaving a cluster varies according to specialisation with the forager having the highest values and the brood-tender the lowest.

However, to explain the spatial organisation of colonies of social insects, many other questions must be addressed such as the difference between the responses of the castes to the spatial heterogeneity (Ceuster, 1977; Camazine et al., 2001). Also, a key question for future studies is how the synergy between the responses to the environmental and social factors and their changes govern the dynamics of spatial distribution of insects inside the nest (Cerdan, 1989; Maillieux, 2002).

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