

A Basis for Spatial and Social Patterns in Ant Species: Dynamics and Mechanisms of Aggregation

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*Aggregation is usually studied in functional terms, forgetting mechanisms. In this paper, experimental results on the ant *Lasius niger*, complemented by a model, allow us to understand the mechanisms responsible for aggregation and to study the influence of the population density on this phenomenon. The results show (1) a high level of aggregation and the emergence of a large cluster; (2) that aggregation results from an amplification mechanism—the greater the number of ants inside a cluster, the greater the time spent by one ant in this cluster; and (3) that population density has only a weak influence on the aggregation process. This method of analysis and these results can certainly be extended not only in social insects but also in other species, like subsocial arthropods.*

KEY WORDS: ants; *Lasius niger*; aggregation; density; dynamics; mechanisms.

INTRODUCTION

Aggregation is a common phenomenon in both invertebrate and vertebrate species (Parrish and Edelstein-Keshet, 1999). In social insects, aggregation plays an essential role in the organization of their social behavior. The tendency to aggregate eggs, larvae, and pupae into separate piles is a nearly

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universal trait in ants (Franks and Sendova-Franks, 1992; for similar phenomena in honeybees, see Camazine *et al.*, 1990; Camazine, 1991). The formation of bivouacs in army ants (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995) and of swarms in *Apis mellifera* (Visscher and Camazine, 1999) are examples of aggregation and self-assembling. Moreover, in social insects, most activities are related to aggregation phenomena: e.g., defense in honeybees (Millor *et al.*, 1999) and food recruitment in ants (Wilson, 1962; Gordon, 1996). Aggregation also acts as a regulator of collective activities in nest digging (Rasse and Deneubourg, 2001).

Two dynamics are distinguished. First, animals gather because of heterogeneity of the environment (Fraenkel and Gunn, 1961; for ants see, e.g., Ceuster, 1977). Second, animals group through social interattraction (Allee, 1931; Ledoux, 1945; Grassé, 1952; Camazine *et al.*, 2001; Parrish and Edelstein-Keshet, 1999). However, for social species in natural situations, both mechanisms (response to heterogeneities and interattraction) are involved. These patterns emerge from interactions among individuals and between individuals and the environment (Dambach and Goehlen, 1999). They are sensitive to many environmental or social factors, such as the available space or the density of insects, and can be understood by analysis of individual behavior patterns (Pasteels *et al.*, 1987; Bonabeau *et al.*, 1997; Camazine *et al.*, 2001).

Communication in gregarious and social insects is mainly based on pheromones. Cuticular hydrocarbons act as recognition signals allowing tolerance between individuals of the same group (Jaffe, 1987; Lenoir *et al.*, 1999) and also act as aggregation pheromones (e.g., Vander Meer *et al.*, 1998; in *Blattella germanica*, Rivault *et al.*, 1998). Other aggregation pheromones have been identified, secreted by mandibular glands (*Blaberus craniifer* and *Eublaberus distanti* [Brossut and Sreng, 1985]), by Dufour's gland (*Camponotus* species [Ayre and Blum, 1971]), and by the sternal gland (*Oecophylla longinoda* [Hölldobler and Wilson, 1978]).

In this paper, we analyze the influence of density on aggregation of the ant *Lasius niger* (L.). After a study of the aggregation dynamic and the global structure of ants that appears, individual behavior patterns are analyzed and quantified in order to understand how collective behavior emerges. The experimental study is complemented by a model, developed to test whether patterns of individual behavior allow us to explain the collective pattern observed for the different densities.

MATERIALS AND METHODS

The black garden ant, *L. niger*, is a common Palaearctic species, which is monogynous and monomorphic with a narrow size distribution centered

on a length of 5–6 mm (with antennae). Colonies were collected in Brussels, Belgium. They were reared under laboratory conditions: using tube nests (5–10 tubes covered with red paper, 1.5 cm in diameter); $T^{\circ}\text{C}$, = 26 ± 2 ; and photoperiod, 12 h. Colonies were fed with *Tenebrio molitor* larvae and special food (Bhatkar and Whitcomb, 1970) three times a week. The experimental device was composed of a ring 98.2 cm² in area formed from a small petri dish (10 cm in diameter) placed in the center of a larger one (15 cm in diameter). The edges of the ring were coated with Fluon. Wet cotton wool placed inside the small petri dish maintained humidity. The setup was surrounded with a white sheet in a dark room. It was closed with a red transparent cover and lit by a dark chamber bulb hung 80 cm above the ring. The ants were removed from inside the tube nests, near the brood, and were therefore referred to as brood-tenders. They were chilled during 30 s in order to allow them to be placed regularly on the ring. A camera, mounted above the setup, recorded the activity of the ants for a period of 90 min.

Collective Level

Influence of the Total Population. Four populations were studied: 10 ants, corresponding to a density of 0.10 individuals/cm², 25 ants (0.25/cm²), 50 ants (0.51/cm²), and 100 ants (1.02/cm²). These four densities are very close to those found in a natural nest (Rasse and Deneubourg, 2001). Twenty experiments for each population were carried out (23 for the 25-ant case). Video recordings were made and observed on a computer, and a snapshot was taken after 1 min (3 min for the 100-ant population) and every 10 min thereafter. The Cartesian coordinates of the thorax of each ant were recorded using a special processing program.

The length of a *L. niger* ant with antennae is about 5–6 mm. We observed that when a cluster reorganized itself (e.g., after the arrival of an individual), an ant was able to leave the cluster by a distance of some millimeters and subsequently return to the cluster. Such an ant was considered to remain aggregated. Therefore, in our analysis, ants were considered to be aggregated when two or more individuals (identified by their thorax position) were at a distance less than 1 cm from each other, and a cluster was taken to consist of a group of aggregated ants that were interconnected by a distance of at most 1 cm.

A computer program was used to calculate the number of aggregated ants, and thus the aggregated fraction, defined to be the number of aggregated ants divided by total population; the number of clusters; and, for each cluster, its population (or “cluster size”), area (the “surface area”), and centroid. We calculated the surface area by drawing a circle around each ant. The surface area covered by all of the circles represented the cluster surface.

This was calculated for circles 10 mm in radius (which could be considered to represent the perceptual field for one ant). Finally, the angular distribution of ants at 90 min was also analyzed: after having calculated the angular position of each ant, all experiments were centered on the centroid of the largest cluster (see results). This last result gave us a preliminary indication about the final structure which appeared.

Individual Level and Model

A hypothesis concerning the mechanisms of emergence of the pattern of aggregation, based on individual behavior of ants and their interattraction, was proposed. It was based on four types of behavior: (1) stops following a meeting with another ant; (2) spontaneous stops from which cluster nucleation can originate; (3) spontaneous U-turns without touching the edges of the setup or another individual, which influence the probability of encountering nestmates; and (4) the time spent by an ant inside a group (which indicates the probability of leaving the cluster).

Calculation of Probabilities. The probability of each type of behavior occurring was extracted from observations of individual ants for the population of 10 ants. Probability (1) was equal to 1: an ant always stopped when a nestmate is encountered. To find the probability of making a spontaneous stop or U-turn, we recorded the durations of the paths ending in a spontaneous U-turn or a spontaneous stop. These durations were then arranged in increasing order. For each of these times, the fraction of ants still moving was plotted on a graph. This survival curve for moving ants was found to follow an exponential law:

$$F_c = \alpha \cdot e^{-\beta t} \quad F_c : \text{the fraction of ants still moving at time } t, \beta > 0 \quad (1)$$

β is the sum of the constant probabilities of making a spontaneous stop (p_S) and a spontaneous U-turn (p_U) ($\beta = p_S + p_U$). In this case, where one behavior (here: moving) ends in two different ways (stop or U-turn), it is easy to show that $p_S/p_U = N_S/N_U$, where N_U is the number of movements ending in spontaneous U-turns ($N_U = 40$) and N_S the number of movements ending in spontaneous stops ($N_S = 75$). Knowing that $\beta = p_S + p_U$ and p_S/p_U , we can calculate p_S and p_U . Finally, the probability of leaving a stop (p_L) was calculated in the same way, by recording the durations of stops according to the number of ants involved in these stops. For each number of ants involved in the stop, the survival curve of stops was observed to follow an exponential law similar to (1) where F_c represents the fraction of stops still present at time t . For each number of ants involved in the stop, the exponent represents the constant probability of leaving the stop. All these probabilities of leaving

a stop were then represented in relation to the cluster size. This curve was fitted by a power law:

$$p_L = a \cdot A^{-b} \quad A: \text{number of ants involved in the stop}; b > 0 \quad (2)$$

If A is equal to 1, p_L gives the probability of leaving a spontaneous stop. Equation (2) shows that the individual probability of leaving a cluster decreases with the number of ants in it.

A model was developed to account for the experimental observations, implemented by Monte Carlo simulations. For each population, 1000 simulations were conducted, which were analyzed as for the experiments. The setup was divided into square cells 3 mm in length. The ants were randomly distributed at $t = 0$ and were initially stationary. The average ant speed used in the simulations was determined experimentally by an analysis of the length of 40 paths 3 s in duration in two experiments. A direction of movement was chosen from eight possibilities. At each time step (Fig. 1), a worker could be in two states: moving or stationary. A walking ant could encounter another individual and then stop. If it did not meet another ant, it had a probability of making a spontaneous U-turn (p_U) or a spontaneous stop (p_S). A stationary ant had a probability (p_L) of moving again, which decreased with the number of ants surrounding it. The number of neighbors involved in p_L was eight at most (in the eight cells around the stationary ant). When the ant left the aggregate, it had a probability p_{Ud} of leaving in another direction than its arrival direction (equal probability among the eight possible directions). The decrease in probability p_L with the number of surrounding nestmates was the basis for an amplification process leading to clustering. Indeed, the greater an aggregate, the greater was the probability that it would grow.

RESULTS

Influence of the Total Population

Collective Level. The mean numbers of aggregated ants, and hence the mean aggregated fractions, increase sharply during the first 10 min and then grow slowly (Fig. 2). After 10 min, for the four populations, both are significantly different from those obtained with a homogeneous distribution of ants (Table I). For each population, except for 100 ants where aggregation is faster, the aggregated fractions are different between 10 and 90 min (Table I). At 10 min, the four aggregated fractions are different: the greater the total population, the greater the aggregated fraction (Kruskall–Wallis test: $\chi_3^2 = 55.6$, $P < 0.001$, nonparametric multiple comparison test; see Table I). Nevertheless, there is no difference at 90 min between the

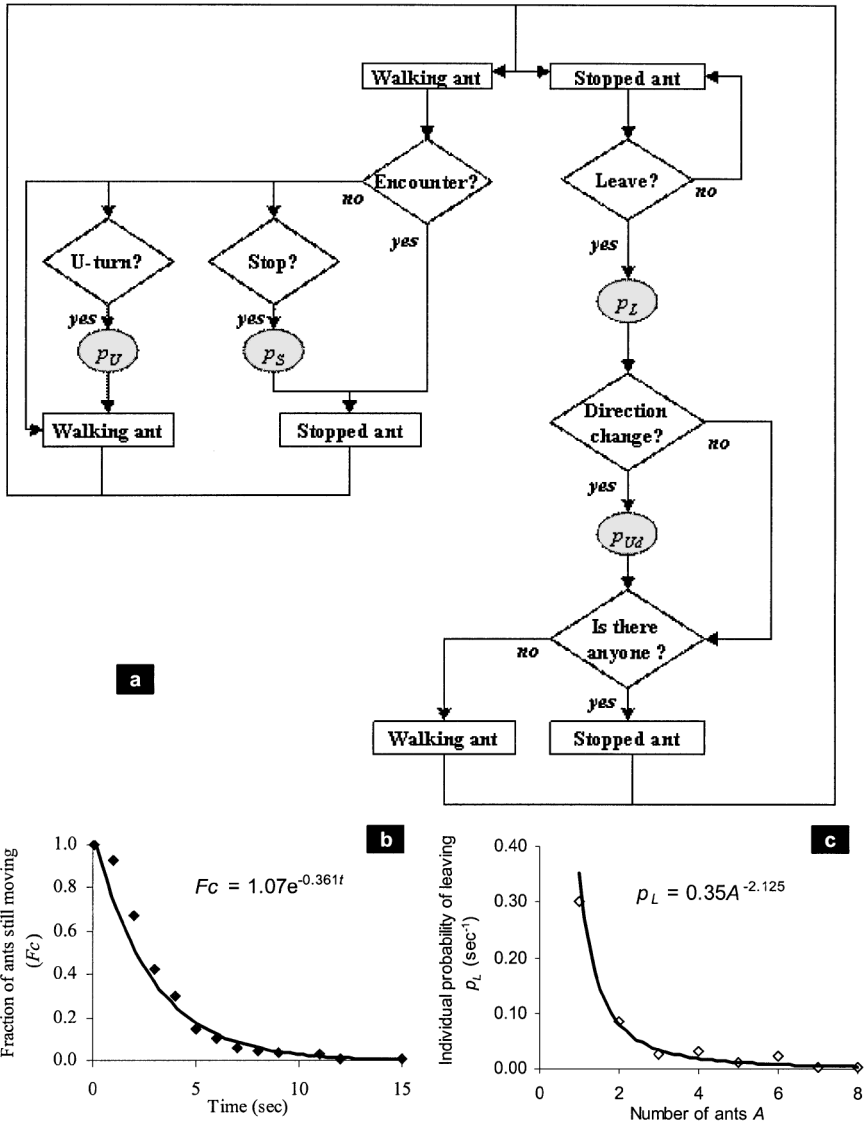


Fig. 1. Individual behaviors and probabilities. (a) Behavioral algorithm, basis for the simulations. (b) Fraction of ants still moving as a function of time (Pearson correlation coefficient, $r = 0.98$, $N = 13$, $P < 0.005$). (c) Individual probability of leaving a stop as a function of the number of ants A involved in the stop (Pearson correlation coefficient, $r = 0.94$, $N = 8$, $P < 0.005$)

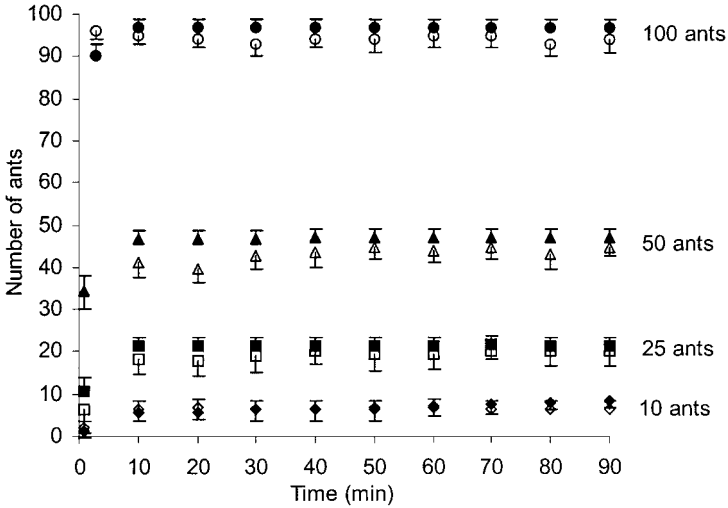


Fig. 2. Dynamics of the mean number of aggregated ants (mean \pm SD) for each total population (10 ants, diamond; 25 ants, square; 50 ants, triangle; 100 ants, circle) for experiments (white) and simulations (black).

aggregated fractions of the different population conditions, except for the 100-ant case, which has a higher fraction ($\chi^2_3 = 25.3$, $P < 0.001$, nonparametric multiple comparison test; see Table I).

The angular distribution of ants at 90 min follows a unimodal curve, suggesting the dominance of one aggregate (Fig. 3). The greater the total population, the flatter this angular distribution and the greater the number of sectors with a high number of ants: 70% of the total population is in one sector for 10 ants, in three sectors for 25 and 50 individuals, and in five sectors for 100 ants. However, despite the growth of the cluster surface, the mean density in these sectors grows with the total population.

A finer analysis shows that the ants are gathered in a single main aggregate (the main cluster), as well as a number of smaller ones (Fig. 4a). For each experiment, we rank the clusters as a function of their size and calculate the mean size (number of ants) for each rank. A big cluster appears very early in the experiments (Fig. 4b): after 10 min, the biggest cluster includes 20 to 40% of the total population and, hence, can be called the main cluster. Its dimension increases with time until it includes 80–100% of the ants at 90 min. The total density does not influence the evolution of the pattern. The mean size of the main cluster grows according to a power law which is similar in form across the four total populations (Fig. 4b). At 90 min, the size of the main cluster is proportional to the total population (Fig. 4a): the

Table 1. Statistical Results: (a) Comparison Between Experimental Fractions of Aggregated Ants and Those Obtained with a Uniform Distribution of Ants, at 10 and 90 min, for the Four Populations (Wilcoxon Mann–Whitney Test Using U for $N \leq 20$ and z for $N > 20$); (b) Nonparametric Multiple-Comparisons Test (Based on N.S.K.) After a Significant Kruskal–Wallis: Comparison Among the Four Experimental Fractions of Aggregated Ants, at 10 and 90 min; and (c) Comparison Between the Fraction of Aggregated Ants at 10 and 90 min for Each Total Population (Wilcoxon Signed-Ranks Test)

(a)			
Population	10 ants	25 ants	50 ants
N	20	23	20
10 min	$U = 28.0, P < 0.005$	$z = 24.7, P < 0.05$	$U = 43.0, P < 0.005$
90 min	$U = 0.5, P < 0.005$	$z = 23.0, P < 0.05$	$U = 6.5, P < 0.005$
$U = 44.0, P < 0.005$			$U = 78, P < 0.005$
(b)			
Population	10 ants	25 ants	50 ants
Mean rank			
10 min	18.1	33.5	44.7
90 min	32.8	30.8	41.6
2×2 comparison:	10/100	10/25	25/100
	10/50	10/25	25/50
10 min	$q_{KW} = 14.8, P < 0.05$	$q_{KW} = 7.2, P < 0.05$	$q_{KW} = 4.0, P < 0.05$
90 min	$q_{KW} = 8.7, P < 0.05$	$q_{KW} = 2.4, NS$	$q_{KW} = 8.8, P < 0.05$
	$q_{KW} = 2.4, NS$	$q_{KW} = -0.5, NS$	$q_{KW} = 2.9, P < 0.05$
		$q_{KW} = 2.8, NS$	$q_{KW} = 2.8, NS$
			$q_{KW} = 6.2, P < 0.05$
(c)			
Population	10 ants	25 ants	50 ants
N	20	23	20
	$Z = -3.6, P < 0.01$	$Z = -1.9, P < 0.05$	$Z = -2.5, P < 0.05$
			$Z = -1.1, NS$

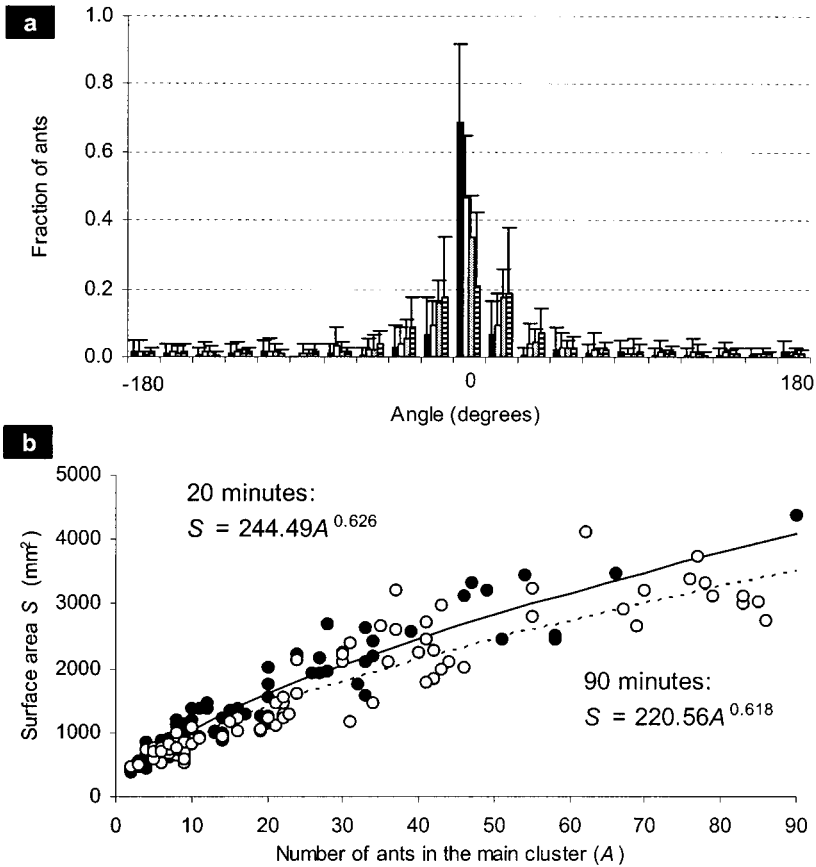


Fig. 3. Density in the main cluster. (a) Angular distribution of ants (mean \pm SD) at 90 min for the four total populations. Black, 10 ants; white, 25 ants; gray, 50 ants; hatched, 100 ants. (b) Surface of the main aggregate, at 20 min (●) and 90 min (○), calculated with circles of 10-mm radius, as a function of the size of the aggregate (number of ants). Pearson correlation coefficient: 20 min (—) $r = 0.96$, $N = 83$, $P < 0.005$; 90 minutes (---) $r = 0.95$, $N = 83$, $P < 0.005$.

fraction of ants in this cluster (60–70%) is not different among the four total populations (Kruskal–Wallis test: $H_3 = 2.363$, NS). The distribution of the mean sizes ranked in decreasing order at 90 min follows a similar power law (allometric law) for the four total populations (Fig. 4a). Nevertheless, the higher this population, the lower the exponent, due to the increase in the number of small satellite clusters.

The centroids of each main cluster in each experiment were calculated. First, they were used to test the homogeneity of the setup, to prove

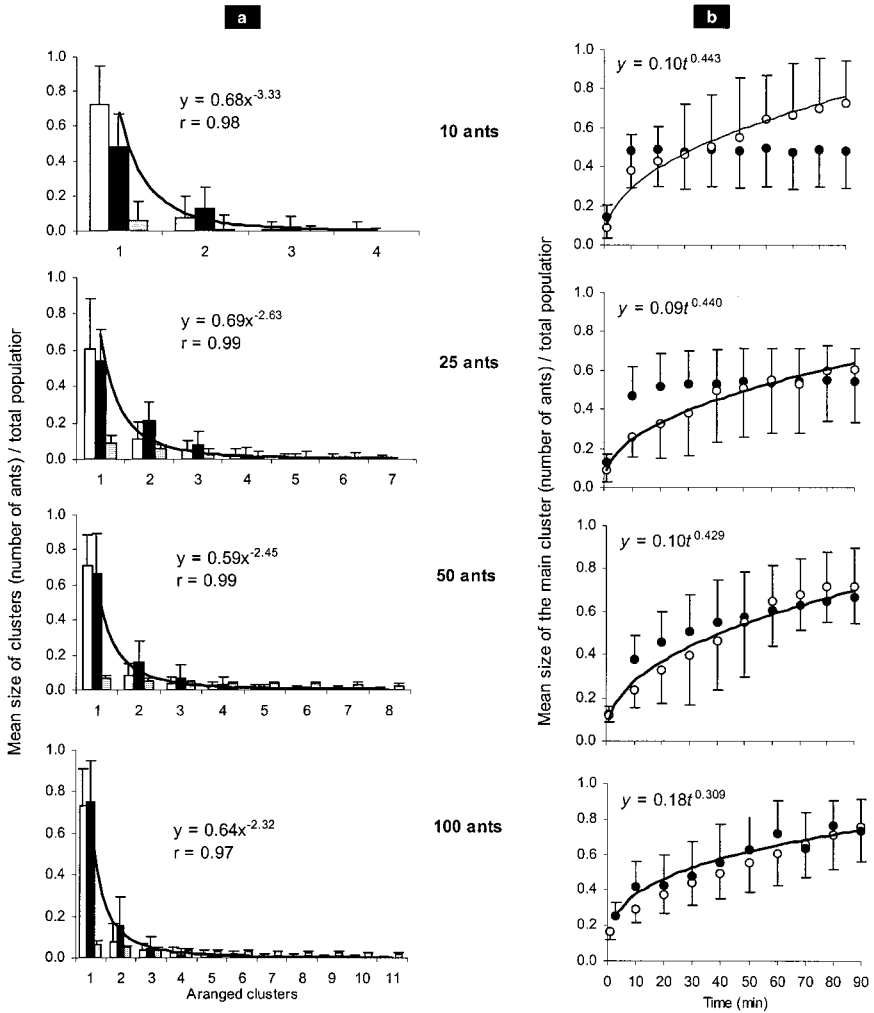


Fig. 4. Mean size of clusters. (a) Mean dimension at 90 min of each cluster (mean \pm SD) ranked in decreasing order, for each total population, for experiments (white), simulations (black), and uniform distribution of ants (gray). Experimental fittings: Pearson correlation coefficient—10 ants, $r = 0.98$, $N = 4$, $P < 0.05$; 25 ants, $r = 0.99$, $N = 7$, $P < 0.005$; 50 ants, $r = 0.99$, $N = 8$, $P < 0.005$; and 100 ants, $r = 0.97$, $N = 11$, $P < 0.005$. (b) Evolution of the mean size (mean \pm SD) of the main cluster (relative to the total population) for the four total populations in experiments (\circ) and in simulations (\bullet). Experimental fittings: Pearson correlation coefficient—10 ants, $r = 0.98$, $N = 10$, $P < 0.005$; 25 ants, $r = 0.99$, $N = 10$, $P < 0.005$; 50 ants, $r = 0.99$, $N = 10$, $P < 0.005$; and 100 ants, $r = 0.97$, $N = 10$, $P < 0.005$.

that aggregation was not influenced by external factors. The distribution of those centroids was not found to differ from a uniform distribution (chi-square test: $\chi_5^2 = 8.2$, $P = 0.15$). Second, the centroids were used in order to quantify the spatial stability of the clusters. The distance between the centroids of the main aggregates at two consecutive times decreases with time according to a decreasing exponential law (Fig. 5). The cluster therefore becomes more stable in space as time passes and the stabilization process is similar between the four conditions (Fig. 5). At the beginning, these distances are large (80 mm), showing the instability of the aggregates: they disappear and reappear at another place. With time, the size of the clusters increases and they become more stable: the intermain cluster distance decreases reaching 20 mm at the end of the experiments. When the distance is about 20–30 mm between two times, the cluster that fluctuates is the same cluster at the two points in time. Figure 5 represents the distance between the centroid of the main aggregate at 80 min and the centroid of the main aggregate at 90 min for all experiments as a function of the size (relative to the total population) of the aggregate at 90 min. The small aggregates show a low stability (i.e., large distance), while the large aggregates, gathering almost the entire population, are very stable.

The surface area taken up by the main aggregate was calculated at different times (Fig. 3). The four conditions were pooled. The surface of the main cluster is related to its size by a power law with an exponent equal to 0.6: the density of a cluster increases with its size. This law does not depend on time. This result confirms our previous results, showing that the density increases within the peak of the angular distribution (Fig. 3).

To summarize—the global pattern of aggregation and aggregation dynamics are similar among the four total populations: one rapidly growing main cluster containing most of the workers (around 70%) is observed; its density and its stability grow with its size. The increase in the total population only weakly increases the rate of aggregation and the number of small satellite clusters.

Individual Level and Model. Data were obtained for the lowest density (10 ants). A unimodal velocity distribution is observed, with a mean of $\bar{X} \pm \text{SD} = 2.45 \pm 0.69$ cm/s; $N = 40$. The global probability of making a spontaneous stop or a spontaneous U-turn is 0.361 (Fig. 1; Pearson correlation coefficient, $r = 0.98$, $N = 13$, $P < 0.005$). The probability of stopping spontaneously (p_S) and the probability of making a spontaneous U-turn (p_U) are therefore 0.2354 and 0.1256 s^{-1} , respectively. The probability of leaving a stop p_L follows a power law (Fig. 1; Pearson correlation coefficient,

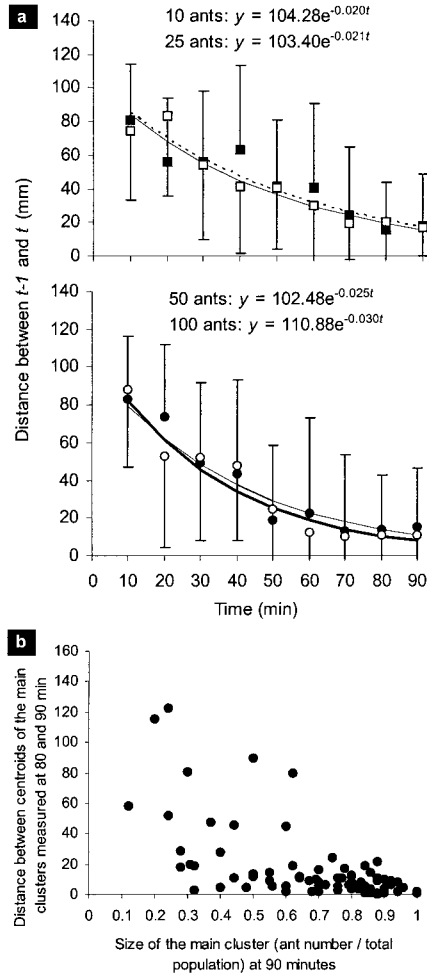


Fig. 5. Distances between the centroid of the main aggregate at $t-1$ and the centroid of the main aggregate at t . (a) Evolution of the distance (mean \pm SD) of the centroid of the main aggregate between $t-1$ and t (minutes). (■) 10 ants; (□) 25 ants; (●) 50 ants; (○) 100 ants. Fittings: Pearson correlation coefficient—10 ants (---), $r = 0.94$, $N = 10$, $p < 0.005$; 25 ants (—), $r = 0.98$, $N = 10$, $P < 0.005$; 50 ants (—), $r = 0.94$, $N = 10$, $P < 0.05$; 100 ants (—), $r = 0.95$, $N = 7$, $P < 0.005$. (b) Distribution of the distances between the centroid of the main cluster at 80 min and the centroid of the main cluster at 90 min as a function of the relative size of the cluster at 90 min.

$r = 0.94$, $N = 8$, $P < 0.005$):

$$P_L = a \cdot A^{-b} \quad A: \text{number of ants involved in the stop } (a = 0.35, b = 2.125) \quad (3)$$

In order to validate our hypothesis, which is that aggregation is based on these individual behavior patterns, results from simulations and from experiments are compared. The same evolution of the aggregated fraction is found (Fig. 2): a rise during the first 10 min and then a plateau. The value of this plateau is similar in the experiments and in the simulations. As in the experiments, a main aggregate is soon observed. The evolution of the main cluster size (Fig. 4) shows good agreement between simulations and experiments. Nevertheless, for the 10- and 25-ant cases, the aggregation in the simulations is faster. At 90 min, the same pattern is observed in simulations and experiments (Fig. 4): a main cluster and some satellites, the number of which depends on the total population, are found in the simulations. At 90 min, the sizes of the main clusters are very close, except for the 10-ant case, where the size is a little smaller in the simulations. The difference between simulations and experiments is discussed later (see Discussion).

DISCUSSION

Our results show how aggregation emerges in a homogeneous environment: without environmental cues, we have active aggregation (clusters are only due to the attraction between ants). Aggregation is fast and robust. In the reference situation (10 ants, 0.1 ants/cm^2), the aggregated ant fraction approaches the final value (80% of the total population) after 10 min. At the end, about 70% of the population is aggregated in a single main cluster. An increase in population density (to 1 ant/cm^2) does not change these characteristics, and similar patterns are observed: neither the aggregated fraction nor the relative sizes of the main clusters change. Only the rate weakly increases, as does the number of small satellite aggregates (from 3 for 10 ants to 10 for 100 ants).

The spatial stability of the main cluster and its density (following an allometric law) increase with its size. This suggests a reorganization of the cluster and greater difficulties for one ant to come into contact with another ant in the cluster as the cluster grows. In fact, as ants are closed up, movements become more difficult and therefore contacts with ants besides those of immediate vicinity and contacts with ants arriving in the clusters are reduced. In *L. niger*, the formation of clusters is known, in particular, near the entrance of the nest where the surface is limited. This high cluster density

provides the opportunity for many ants to gather together in a zone where they can wait for interaction with nestmates, for recruitment for instance.

Study of individual behavior and the calculation of probabilities show exponential distributions where the exponent β represents the probability. This probability is constant in time, showing the absence of any memory effect. Exponential distributions have been demonstrated for different behavior in arthropods (for a detailed discussion, see, e.g., Pasteels *et al.*, 1987; Calenbuhr and Deneubourg, 1992; Calenbuhr *et al.*, 1992; Saffre *et al.*, 1999, Jeanson *et al.*, 2003). The model, based on rules obtained by analysis of individual behavior in the lowest density case, predicts similar results to those obtained by experiment for the three other densities. This agreement suggests that density does not change the rules governing individual behavior and that chance encounters and the modulation of the resting time in the cluster are sufficient to predict aggregation similar to that observed in experimental situations.

The main disagreements between model and experiment concern the main cluster, which has an underestimated size for the smallest density (10 ants) and an overestimated growth for 10 and 25 ants in the simulations. These quantitative disagreements may result from marking: some experiments show that *L. niger* uses ground marking, probably passive marking by cuticular hydrocarbons (Yamaoka and Akino, 1994). This marking affects the place of aggregation (Depickère *et al.*, 2004a) and so may stabilize the clusters, particularly for small populations, and affect the speed and behavior of the ants. This contribution was not estimated experimentally.

For all densities, the same fraction of ants (10–15%) at the end of the experiments remains unaggregated. This suggests that some individuals have a lower probability of being in a cluster. Some individuals could specialize in moving between groups. Moreover, experiments show that patterns of aggregation depend on the caste or specialization (Depickère *et al.*, 2004b).

Other insects show similar patterns of individual behaviors and aggregation (Dambach and Goehlen, 1999; Rivault *et al.*, 1998; Jeanson *et al.*, 2001). This convergence suggests that these phenomena must be widespread and that these generic rules and mechanisms are robust. However, these patterns of aggregation are not observed for all ant species. Under similar conditions, high or low aggregation levels (e.g., one main cluster, many small ones, or no cluster) may be observed even in the same genus (e.g., *Myrmica* spp. [Leroux and Leroux, pers. Comm.]). It is important to understand the origins of these differences. Are these different responses due to the genetic diversity of the colony (e.g., mono- or polygynous) or to other social or ecological characteristics? Is the same basic behavior present for different species, but with different parameter values? This idea is supported by the fact that our model

shows that the same mechanisms, but with different values of parameters (probability of leaving, etc.), do not result in aggregation.

Aggregation is a good example of a Turing-like structure where peaks in density (aggregates), more or less regularly distributed, emerge in a homogeneous environment (Glandsdorff and Prigogine, 1971; Murray, 1993). These structures are characterized by different collective regulations such as the correlation between the number of aggregates and the diameter of the setup. Our clustering phenomena fall within the family of local activation/long range inhibition (LALI) processes originally suggested by Gierer and Meinhardt (1972). The pattern results from competition between amplification mechanisms (“positive feedbacks”), governed by the cluster size and the probability of leaving and inhibition mechanisms (“negative feedbacks”), which arise automatically as a result of the depletion of the number of ants moving freely. Social insects (and social animals) might actually use these types of mechanisms to produce a wide variety of spatiotemporal structures (Deneubourg, 1977; Hammerstein and Leimar, 2002; Theraulaz *et al.*, 2002).

In our experimental setup, no heterogeneity is introduced. In natural situations, the patterns emerge from interactions among individuals and between individuals and the environment (interattraction and response to heterogeneities). It will be important to analyze how these heterogeneities may affect aggregation and individual behavior. Indeed, some experimental results show an interesting sensitivity of the aggregation patterns to heterogeneity, based on interattraction (Chrétien, 1996; Camazine *et al.*, 2001). Similar results have also been demonstrated for subsocial insects, like cockroaches (Amé *et al.*, 2004), which aggregate with mechanisms similar to ants'. This fact shows the wide spread of this phenomenon and of its mechanisms.

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