

Research article

## Spatial organization in ants' nests: does starvation modify the aggregative behaviour of *Lasius niger* species?

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**Abstract.** Ant colonies that undergo long starvation periods have to tune their exploratory and foraging responses to face their food needs. Although the number of foragers is known to increase with food deprivation in the ant *Lasius niger*, such enhanced food exploitation is not related to a more intense recruitment by successful scouts. We thus suggest that the colony's response to a food shortage could result from changes at the level of the ant recruits, in particular from changes in their spatial organization inside the nest. Since aggregation plays a key role in the social organization of ants, we assume that the colony's response to starvation could be due to changes in the aggregative behaviour of *L. niger* nestmates. We thus compared the aggregation dynamics of inner-nest workers and foragers having undergone either a short or a long-lasting starvation period. Whatever the ethological group (foragers or inner-nest workers), there was no significant influence of starvation on the aggregation dynamics nor on any feature of the observed clusters. This result shows that an increased foraging response to food shortage cannot be explained by changes in the tendency of nestmates to aggregate within the nest. Finally, we discuss other behavioural mechanisms, in particular changes in behavioural thresholds that could underlie the adaptive changes seen in colony foraging after long starvation periods.

**Keywords:** *Lasius niger*, Clustering, food shortage, mechanism, polyethism.

### Introduction

Starvation is well-known to influence the social organization of animals. Depending on food availability, there is an optimal group size that maximizes the balance between the costs (e.g. competition for a limited resource) and the benefits (e.g. increased efficiency of cooperative foraging) associated with group living (Krause and Ruxton, 2002). In many vertebrates i.e. primates (Hall, 1963 and Loy, 1970 in Wilson, 2000), cats (Crowell-Davis et al., 2004) and fish (Parrish and Edelman-Keshet, 1999; Barber et al., 1995; Hensor et al., 2003), the spatial proximity as well as the level of social interaction with conspecifics depend on the current nutritional state of group members. Food deprivation usually leads to a scattering of animals that individually search for food in order to maximize their own foraging efficiency. However, when cooperation is essential to survival, the cohesion of the group is not altered by starvation. In vampire bats, for instance, where 10% of adults fail to feed on a given night, living in resting aggregates allows hungry individuals to benefit from blood meals donated by successful partners (Wilkinson, 1984). Likewise, in social spiders, the cohesion of group members is not altered by food deprivation (Bodasing et al., 2002). Starvation can even increase the aggregation level, such as in cockroaches. Indeed, while well-fed cockroaches may emit a dispersal pheromone in crowded conditions, this is not observed for starved females (Tignor and Ross, 1987). Instead, after a prolonged food deprivation, cockroaches become more aggregated by staying longer in harbourages and by travelling smaller distances (Barcay and Bennett, 1991).

While in these latter cases, individuals have the option to leave or to not leave conspecifics following a food

shortage, some animal species such as social insects do not have such a choice and the whole life of a nestmate is dedicated to the colony efficiency and survival. Nevertheless, in those permanently group-living species, food deprivation also deeply influences the behaviour of foragers, the interactions between nestmates, as well as the group size of cooperating foragers (see e.g. Hölldobler, 1971; Traniello, 1977; Cosens and Toussaint, 1986; Roces and Hölldobler, 1996; Fourcassié et al., 2003; Mc Cabe et al., 2006). In both ants and honeybees, a long period of food deprivation stimulates the exploratory activity (Fourcassié and Deneubourg, 1994; Mailleux et al., 1999; Mailleux, 2002), enhances collective foraging by increasing the number of workers exploiting food sources and ultimately leads to higher quantities of food retrieved to the nest (Wallis, 1962, 1964; Howard and Tschinkel, 1980; Cosens and Toussaint, 1986; Josens and Roces, 2000; Schultz et al. 2002; Mailleux et al., 2006).

Several proximal mechanisms can explain the increased number of foragers (scouts and recruits) cooperating in colonies having undergone long periods of starvation. Over a long time scale, a hive or an ant colony may respond to frequent food shortages by modifying the distribution of workers over temporal castes, with more individuals shifting more quickly from the “inside nest” to the “forager” status (Schulz et al., 1998, 2002; Gordon et al., 2005; Toth et al., 2005). Various models have been put forward to explain such behavioural shifts from one ethological caste to another. These models put the stress either on the offer-demand balance for foraging tasks (see the foraging-for-work model: Tofts and Franks, 1992; Sendova-Franks and Franks, 1993; Franks and Tofts, 1994), on response thresholds of the workers (see Bonabeau et al., 1996; Beshers et al., 1999; Beshers and Fewell, 2001; Pankiw and Page, 2003) or on physiological regulatory processes (see e.g. the double repressor hypothesis, Amdam and Omholt, 2003).

Over short time scales, a higher level of cooperation between starved foragers can be reached by increasing the intensity as well as the efficiency of recruitment towards new discovered food sources. In honeybees, nectar foragers alter their intensity of foraging and recruitment of nestmates based on a socially mediated assessment of colony stores and inflow (Seeley, 1995). Namely, the time it takes for returning foragers to be unloaded by food-store bees is an indicator of colony nectar inflow (Seeley, 1989). Foragers can also determine colony need for pollen via social interactions with nurse bees (Camazine, 1993) and/or direct assessment of pollen stores (Calderone, 1993; Dreller and Tarpy, 2000).

In ants, an increased foraging response of starved colonies may result from changes either in the behaviour of recruiting ants or in the behaviour of recruits within the nest. As regards the impact of starvation on recruiting ants, a food shortage enhances the trail laying behaviour of scouts having discovered food resources; as reported for *Solenopsis geminata* (Hangartner, 1969). However, this is not the rule for all ant species. In the case of *L. niger*,

the duration of starvation does not alter the percentage of trail-laying scouts nor the frequency of their trail deposits (Mailleux et al., 1999, 2006) towards liquid food sources. Since the intensity of recruitment signals released by successful scouts does not change with colony starvation, the enhanced foraging response of starved colonies should depend on changes in the behaviour of ants inside the nest. After a long period of starvation, ants are more likely to exit the nest either spontaneously, to explore the nest surroundings as scouts, or in response to a recruitment signal as a forager (Wallis, 1962, 1964; Howard and Tschinkel, 1980; Cosens and Toussaint, 1986; Mailleux et al., 1999; Mailleux, 2002).

In addition to a tuning of recruitment signals, starvation may induce changes in the spatial distribution of nestmates, such spatial changes being equally important to account for ant foraging dynamics. Indeed, since collective behaviour – such as foraging – is mainly based on amplifying phenomena, the aggregation level of nestmates may play a key role by determining how many individuals will interact with each other and will perceive recruitment signals. In fact, harsh conditions may induce a spatial reorganization of ants inside the nest: such conditions lead to an increase in the number of workers located near the entrance (Mailleux, 2002) and thereby in the pool of ants that will be the first to be recruited by scouts. This strongly suggests that starved workers behave differently inside the nest in terms of their spatial location and aggregative behaviour.

In a previous paper, we demonstrated that aggregation behaviour differs between ants present in the nest (so-called “inner-nest workers”) and ants foraging for food (so called “foragers”): the first group aggregates quickly in large clusters, while the foragers show a very low aggregation level (Depickère et al., 2004a). We formulated the hypothesis that a long period of food deprivation may increase the aggregation of the inner-nest ants that “wait” around the nest entrance, therefore increasing their probability to be recruited. Concurrently, food deprivation may decrease the aggregation of foragers; this favours their exit from the nest and increases their chance to discover new food sources.

To test this hypothesis, we compared the influence of starvation on the aggregation behaviour of inner-nest workers and of foragers of the black garden ant *Lasius niger*. Our main goal was to study how satiation influences the genuine tendency of nestmates to stay close to each other. Therefore, we aimed at eliminating any other factors known to influence aggregation, such as signals emitted by the queen and brood (Sempo et al., 2006b; Ortius and Heinze, 1999) or such as environmental heterogeneities (e.g. temperature, humidity or carbon dioxide gradients Ceuster, 1977; Potts et al., 1984; Cox and Blanchard 2000; Bollazzi and Roces, 2002; Tschinkel, 2004). This was done by conducting experiments outside of the nest, under red light conditions and by minimizing the ants’ disturbance in a homogeneous setup without brood and physical heterogeneities. We found it also

essential to analyze ‘pure’ groups (see Depickère et al., 2004b), composed exclusively of inner-nest workers or of foragers. Indeed, even though interactions between different behavioural castes contribute to the spatio-temporal organization of an insect society, a large part of the social interactions occurs between workers belonging to the same castes that are settled in the same area (Sendova-Franks and Franks, 1995).

## Materials and methods

Colonies of 500–1000 workers of *L. niger* were collected in Brussels (Belgium). All experiments began two months after the collection of the ants. All colonies were reared under laboratory conditions at a temperature of  $24 \pm 2^\circ\text{C}$  and with a photoperiod of 12 hours. Ants were installed in tube nests (10 cm length, 1.5 cm in diameter) covered with red filter paper to mimic natural conditions of darkness (Wheeler, 1910). These tubes were placed together with food in a rearing box (50x30 cm) of which the edges were coated with Fluon to prevent ants escaping. Colonies were fed with a special diet (Bhatkar and Whitcomb, 1970) three times a week and with *Tenebrio molitor* larvae once a week. Water was always available.

All colonies were without brood to avoid disturbances due to changes in brood needs and to standardize as much as possible the starvation level of the colonies. Previous studies on the same ant species showed that broodless colonies were actually starved after only four days of food deprivation: when fed, they engaged in food recruitment behaviour, with the number of trail-laying ants similar to that of colonies containing brood (Portha et al., 2002, 2004).

### Setup

The experimental setup was an arena made up of a PVC ring of 2 cm height and 19.8 cm in diameter, placed on a black paper sheet. The inside edge was coated with Fluon. A dark cylinder surrounding the wall and a dark cover (30 cm above the arena) closed the setup to avoid any visual cues. In the cover, a central hole was used to illuminate the setup by a black chamber bulb (PF712E, 15W, see Depickère et al., 2004a,b for more details) and a second hole, not centred, allowed us to view the arena with a digital camera. Inner-nest workers were taken from inside the nest near to the brood to obtain a homogeneous group. Foragers were taken from outside the nest in the foraging area of the nest box. Tested ants stayed in their rearing box during the starvation period and left their colony only at the time of the aggregation experiment. Two periods of starvation were studied: 1 and 8 days, during which ants had access only to water (no sugar, no protein). For each experiment we studied the behaviour of twenty ants, which is representative of the number of ants actually interacting locally within the narrow tunnels and small chambers of an *L. niger* nest (see Rasse, 1999; Rasse and Deneubourg, 2001). These ants were first dropped in the centre of the arena and their spatial location was video recorded for 90 minutes. From the video recordings, we took snapshots every minute for the first 40 minutes and then every 5 minutes until 90 minutes. An additional snapshot was also made at 30 seconds (to give 51 snapshots in total). Twelve experiments for each ethological group and each starvation level were conducted.

### Aggregation Indexes

Since an ant measures 6 mm length (including antennae), a circle of 3 mm radius corresponds to the ‘physical area’ covered by an ant. However, the perception radius is larger since ants may detect each other from a distance, both visually and chemically. During preliminary tests, 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 considered 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 (Depickère et al., 2004a,c). Moreover, the index values, and therefore, our conclusions, are weekly sensitive to the value of the radius (Depickère, 2003).

A cluster involved two or more individuals. The Cartesian coordinates of the thorax of each ant were recorded and we calculated:

- the radial distribution of the ants in the arena. This was done by dividing the arena into five rings, each 2 cm in width, the outer edge of the external ring corresponding to the arena edge;
- the number of aggregated ants and so the fraction of aggregated ants among the 20 tested individuals;
- the number of clusters and their size (number of ants inside a cluster). For each experimental condition, all the clusters were ranked in decreasing size order. The median size of clusters was then calculated for each rank value;
- the spatial stabilization of the biggest cluster. For each experiment, we measured the distance between the centroid of the biggest cluster at time  $t$  and the centroid of the biggest cluster at time  $t+1$ . Then, for all tests carried out in the same experimental condition, the median distance was calculated for each time step;
- the total area of each cluster. At the end of the experiment (90 minutes), this area was calculated by drawing a circle around each ant. The area covered by all circles represented the total cluster surface (overlapping circle areas being counted only once). As an ant measures 5–6 mm in length (including its antennae), we used circles of 10 mm in radius (which could be considered as the perceptual field of one ant). This cluster area was calculated for inner-nest workers, the only group gathering in large clusters.

All results were expressed in terms of median, 1<sup>st</sup> and 3<sup>rd</sup> quartiles, due to the small samples size and their deviation from normality. Non-parametric tests were performed to compare results between the different starvation conditions.

Preliminary experiments without starvation (0 day of food deprivation,  $N=6$ ) were conducted with foragers and used as a control for verifying the possible influence of one day of starvation on ants’ aggregation behaviour. We found out no statistical difference in the aggregative response between non-starved and one-day starved colonies, neither in the fraction of aggregated ants at 90 minutes (Mann-Whitney U test:  $U=6$ ,  $N_1=N_2=6$ ,  $p=0.06$ ) nor in the size of the main cluster (Mann-Whitney U test:  $U=8$ ,  $N_1=N_2=6$ ,  $p=0.13$ ). This result shows that after one day of food deprivation, ants can be considered as unstarved. This is corroborated by the fact that *Lasius niger* foragers do not recruit after such a brief period of food shortage (Mailleux, 2002; Mailleux et al., 2006).

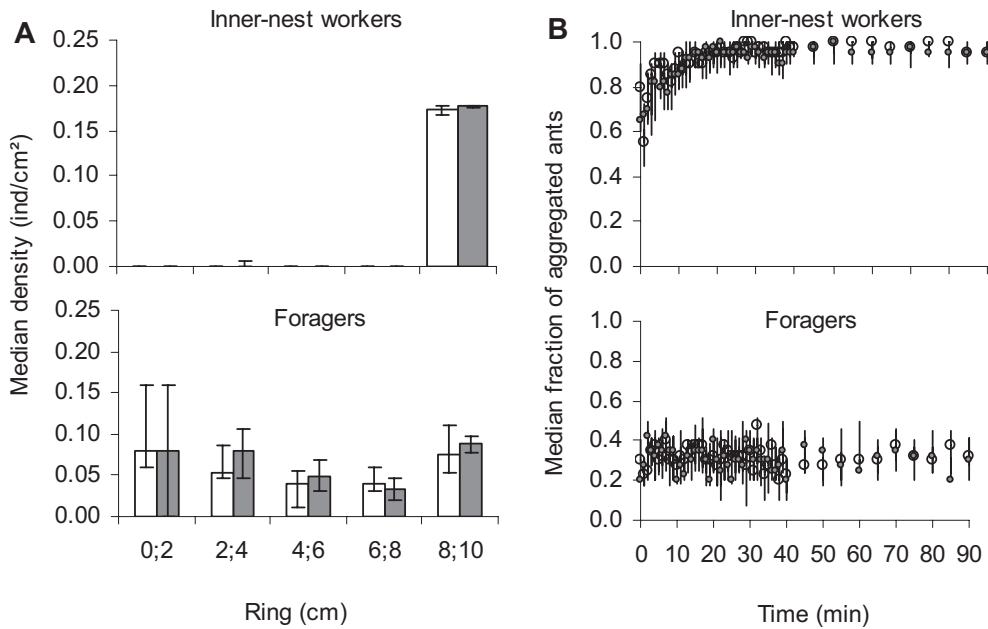
## Results

### Inner-nest workers

At the end of the experiment, the inner-nest workers (97%) were mainly distributed in the external ring close to the arena edge (Fig. 1A). There was no difference between one and eight days of starvation (comparison between the numbers of ants in the external ring at 90 minutes: Mann-Whitney U test:  $U=59.5$ ,  $N=12$ ,  $p=0.47$ ). Inner-nest workers thus showed a high level of thigmotaxis, their tendency to follow the setup edges not being influenced by their level of starvation. The fraction of aggregated ants steeply increased at the beginning of the experiment, with 90% of the inner-nest workers gathered together after only 15 minutes. This fraction then

**Table 1.** Statistical tests comparing the ants' response after 1 and 8 days of starvation for the following parameters: the median fraction (1<sup>st</sup>; 3<sup>rd</sup> quartiles) of aggregated ants and the median fraction of ants in the biggest cluster (1<sup>st</sup>; 3<sup>rd</sup> quartiles), both in % of the total population at 90 minutes.

Group and condition		1 day	8days	U	P
Inner-nest workers (N=12)	Med. fraction	95 (5;5)	95 (0;5)	58	NS
	Med. fraction of ants in the biggest cluster	75 (26;10)	68 (18;8)	61.5	NS
Foragers (N=12)	Med. fraction	33 (13;9)	30 (3;11)	70	NS
	Med. fraction of ants in the biggest cluster	10 (0;10)	10 (0;1)	66	NS

**Figure 1.** Spatial distribution of ants and their level of aggregation for 1 day (white) and 8 days (grey) of starvation. A. Radial density of ants at 90 minutes in the five rings (median, 1<sup>st</sup> and 3<sup>rd</sup> quartiles); B. Median fraction (1<sup>st</sup> and 3<sup>rd</sup> quartiles) of aggregated ants as a function of time

remained constant until the end of the experiments (Fig. 1B). Ants rapidly gathered in one main cluster (Fig. 2A), which involved 75% of the total ant population at 90 minutes (Fig. 2B). The values of these two parameters did not change significantly with the duration of the starvation period (Table 1).

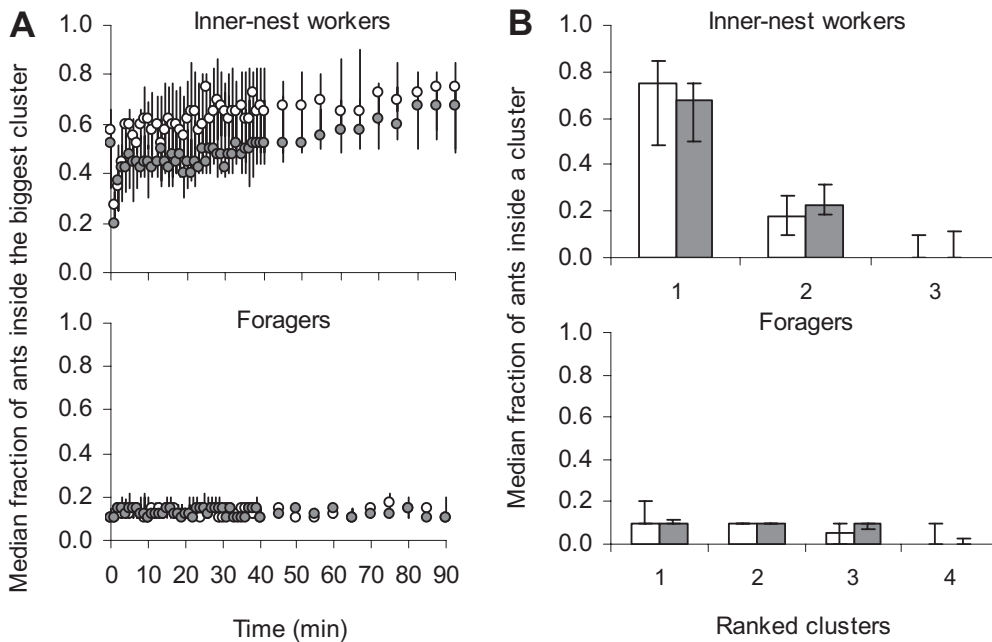
The main cluster becomes spatially stable over time. As shown by Figure 3, the median distance between centroids of the biggest cluster at time  $t$  and  $t+1$  decreased over time, from 8 cm at 30 seconds to 1–3 cm at 90 minutes. This progressive stabilization of the main cluster was similar for one and eight days of food deprivation.

If one considers all aggregates present at 90 minutes, the area of one cluster is related to its size (i.e. the number of aggregated individuals) by a power law (see fitting equations of  $\ln$  linearized data on Fig. 4.) This shows that the density of ants within a cluster tends to increase with its size. Such a power law did not differ between one and eight days of starvation (power of about 0.4 in both cases).

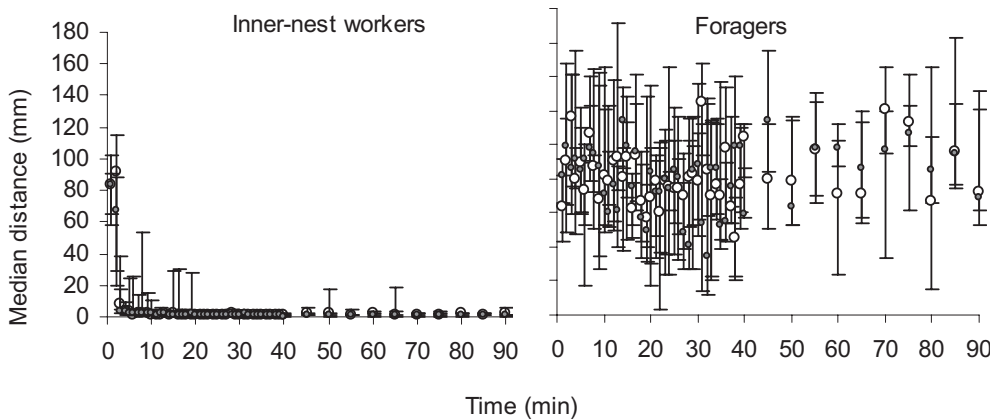
### Foragers

Foragers were located over the entire arena at 90 minutes, with the majority of ants staying in the external ring (Fig. 1A). The thigmotaxis of foragers was, however, lower than that of inner-nest workers. In fact, at 90 minutes, only 48% of foragers were in the external ring, compared to 97% or to 90% of inner-nest workers for one-day and eight days of starvation respectively (Mann-Whitney U test (N=12): one day:  $U=3.5$ ,  $p=0.0001$ ; eight days:  $U=12$ ,  $p=0.0002$ ). There was no difference in the radial distribution of foragers between one and eight days of starvation (Comparison between 1 and 8 days of starvation, of the number of ants in each ring: Mann-Whitney U test (N=12): ring 0;2 cm:  $U=66.5$ ,  $p=0.74$ ; 2;4 cm:  $U=64.5$ ,  $p=0.66$ ; 4;6 cm:  $U=58$ ,  $p=0.41$ ; 6;8 cm:  $U=54.5$ ,  $p=0.30$ ; 8;10 cm:  $U=60.5$ ,  $p=0.51$ ).

The fraction of aggregated foragers remained low during the whole experimental time period (Fig. 1B). Foragers usually gathered in a few small clusters. The biggest cluster involved at most 10% of the total population for both the 1 day and 8 days starvation times (Fig. 2B, Table 1) and its size remained constant during the whole experiment (Fig. 2A). There was no spatial stabilization of the largest cluster, since the



**Figure 2.** Fraction of ants inside the clusters (white: 1 day, grey: 8 days of starvation). A. Median fraction of ants (1<sup>st</sup> and 3<sup>rd</sup> quartiles) aggregated in the biggest cluster as a function of time; B. Median fraction of ants (1<sup>st</sup> and 3<sup>rd</sup> quartiles) aggregated at 90 minutes in clusters ranked in a decreasing size order



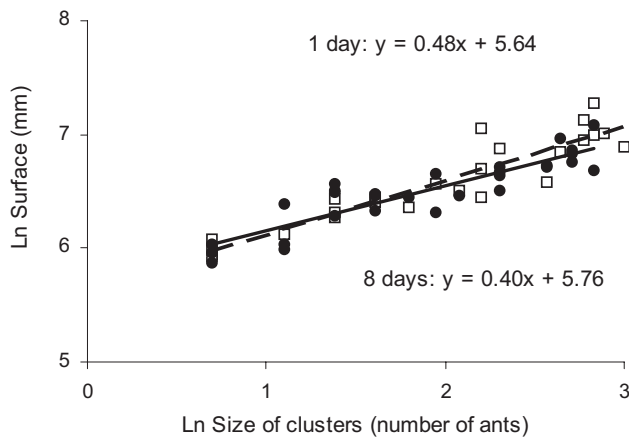
**Figure 3.** Spatial stability of the biggest cluster over time. This is given by the median distance (1<sup>st</sup> and 3<sup>rd</sup> quartiles) between the centroid of the biggest cluster at time  $t$  and the centroid of the biggest cluster at time  $t+1$  (white: 1 day, grey: 8 days of starvation)

distance between centroid at time  $t$  and  $t+1$  always remained high (Fig. 3). This suggests that clusters frequently disappeared to be reformed in another part of the arena.

**Discussion**

The influence of starvation on ant colonies is usually studied in terms of behavioural changes at the level of scouts by paying attention to their modulation of recruitment signals as well as to their food intake (Hangartner, 1969; Josens and Roces, 2000; Mailleux, 2002; Mailleux et al., 2006). Nevertheless, food deprivation also acts upon the behaviour of ants inside the nest. Indeed, starvation elicits a spatial redistribution of workers who tend to aggregate themselves near the nest entrance. By doing so, they gain access to social information and increase their

probability to respond to recruiting stimuli released by successful foragers. Since it shapes many aspects of ants' social organization, the aggregative phenomenon is expected to change with the satiation level of colony members. However, our experiments failed to demonstrate any influence of starvation on the aggregative behaviour of either inner-nest workers or foragers. Whatever the ethological caste, neither the aggregation dynamics nor any feature of clusters (cluster size, number, area, etc.) changed after one or eight days of food deprivation. In order to investigate any possible changes in social interactions, we observed ants in a homogeneous setup that was previously used to successfully demonstrate aggregation differences between brood tenders and foragers (see Depickère et al., 2004a). By keeping the environment as simple as possible, we need however to be cautious: further studies should investigate whether any nest related cues (i.e. the sense of a ceiling by the ants'



**Figure 4.** Surface of the clusters at 90 minutes as a function of their size (in number of ants) for inner-nest workers for 1 day (white square) and 8 days (black circle) of starvation, linearized by a ln-ln transformation, suggesting a power law relation. Fittings (correlation coefficient): 1 day (solid line):  $r=0.94$ ,  $N=27$ ,  $p<0.005$ ; 8 days (dotted line):  $r=0.90$ ,  $N=29$ ,  $p<0.005$

antennae) may have some effect on ant spatial distribution.

In ants, aggregation does not appear as a key parameter to explain the spatial reorganization of ants inside the nest, or the higher number of recruited foragers observed after a long food deprivation. We have thus to figure out other explanations that do not imply changes in ant aggregation behaviour. One may assume that the increased number of ants staying near the nest entrance after a long starvation period could result from changes in the sensitivity of highly starved ants to heterogeneities and gradients inside the nest. For instance, the ants' response threshold to luminosity or temperature could decrease with their nutritional state. This has been demonstrated in collembolans, where the phototactic behaviour increased with starvation (Dromph, 2003). Spatial reorganization is not the only factor improving recruitment efficiency in starved colonies. Indeed, ants that are located near the nest entrance are likely to be individuals with lower response thresholds to the tactile and / or chemical signals emitted by recruiting ants (De Biseau and Pasteels, 2000; Maillieux, 2002). Their higher responsiveness may speed up their exit to the foraging area and hence may increase the efficiency of highly starved colonies to exploit new food opportunities.

Although our study showed no effect of food shortage on aggregation pattern, it has confirmed that the two ethological castes differ in their aggregative behaviour (Depickère et al., 2004a). Indeed foragers were distributed among several small and unstable aggregates, while nest workers gathered in one large and stable cluster. The lack of influence of starvation on aggregation may be adaptive, as it ensures a cohesion between nestmates and hence the maintenance of a structure of the nest population whatever the colony's nutritional state (see also Backen et al., 2000). The workers' clusters show a

spatial stability that can be reinforced by chemical marking (Depickère et al., 2004d; Sempo et al., 2006a). By grouping themselves while resting in the nest, workers most probably benefit from reduced stress, reduced energy consumption (Galle, 1978 but see also Lighton and Bartholomew, 1988), decreased water loss (Walters and Mackay, 2003), enhanced dormancy (starvation induced dormancy, Lighton, 1989) and therefore increased survival (Kaspari and Vargo, 1995).

This study is a first step towards a better understanding of the aggregation phenomenon, which is a basic trait of many collective activities such as defence, nest building or food exploitation (Camazine, 1991; Sendova-Franks and Franks, 1999; Deneubourg et al., 2002; Theraulaz et al., 2003). This seemingly simple behaviour is more complex than expected and more natural situations should be investigated in the future. For instance, we could use mixed groups of inner-nest workers and foragers and study whether their aggregation is coupled to a spatial sorting of the ethological castes within the nest (Potts et al., 1984; Depickère et al., 2004a; Sempo et al., 2006a). It is well demonstrated that gregarious behaviour contributes to the amplification of individual response to gradients, heterogeneities or signals. (Camazine et al., 2001; Lioni and Deneubourg, 2004; Challet et al., 2005; Detrain and Deneubourg, 2006). This raises the question as to whether the grouping of ants within a cluster makes them more sensitive than isolated individuals to physical gradients or any other stimuli such as brood demand for food (Cassill and Tschinkel, 1995). Within this perspective, a better knowledge of aggregation opens the way to an improved understanding of the mechanisms underlying division of labour in ants.

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