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Research article

How does colony growth influence communication in ants?

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Summary. As *Lasius niger* societies grow from incipient nests to mature colonies, their foraging strategies shift from the individual exploitation of food sources to mass recruitment. Colony size instead of age is the key factor that shapes the exploratory and foraging responses of *Lasius niger:* a drastic reduction (or increase) of the population elicits an activity profile similar to that observed in younger (or older) societies of the same size. As a colony grows, the proportion of patrollers significantly decreases while the proportion of conveyors remains rather constant. As regards the energetic return, it increases with incipient nest size due to the replacement of minims by ordinary workers of larger crop capacity. We also demonstrate that minims of incipient nests modulate their trail-laying behaviour according to the social context, in this case the colony size. During their ontogenesis, *L. niger* colonies exhibit a progressive integration of individual foragers into a network of communication, the adaptive significance of which is discussed.

Key words: Foraging, colony size, trail recruitment, incipient nest, *Lasius niger.*

Introduction

Lasius species, like other mass-recruiting ants, exhibit a continuum from solitary foraging to collective recruitment (Hölldobler and Wilson, 1990). They adjust their foraging tactics to the characteristics of resources (for a review see Detrain et al., 1999) such as spatio-temporal distribution of available food (e.g.; Hölldobler, 1976; Frank et al., 1991; Mailleux et al., 2001 submitted), food quality (e.g. Breed et al., 1987; de Biseau and Pasteels, 1994; Fewell et al., 1992; Hahn and Maschwitz, 1985; Pasteels et al., 1987) or size of the food sources (e.g. Breed et al., 1987; Traniello, 1983; Mercier and Lenoir, 1999; Mailleux et al., 2000). The intrinsic characteristics of ants' colonies also determine their foraging patterns. The nutritional demand of workers (Sudd and Sudd, 1985)

and brood (Lenoir, 1979, 1981; Portha et al., 2001) influences food preferences and levels of foraging activity. Besides, changes in colony size as it grows older, act upon its internal organisation (Howard and Tschinkel, 1980; Cassill and Tschinkel, 1999) and foraging strategy (Agbogba and Howse, 1992; Burkhardt, 1998; Gordon, 1995). In this respect, the efficiency of cooperative retrievals and recruitments are particularly sensitive to the number of workers involved.

Colonies of most mass-recruiting species are initially founded by one or few queens that first produce "minims" individuals distinctly smaller than the workers in mature colonies. The minim's size is partly trophogenic and can be modified by the rearing environment (Passera, 1977; Wood and Tschinkel, 1981). Minims are a widespread phenomenon in ants providing incipient colonies with the minimum number of workers needed to carry out vital tasks such as tending brood and foraging (for a review see Hölldobler and Wilson, 1990). As the colony grows older, its size increases exponentially (or logistically) from a few workers to thousands (e.g. Tschinkel, 1988; Wilson, 1971). Previous studies have examined how intraspecific changes in colony age and/or size influence patrolling behaviour (Gordon, 1986, 1989, 1992, 1995; Adams, 1990; Tschinkel et al., 1995) or the foraging strategy (Agbogba and Howse, 1992; Aron, 1986; Herbers and Choiniere, 1996). In this paper, we investigate how colony size and/or age influence the foraging strategies of a species. Collective and individual foraging behaviour is compared in incipient nests and mature colonies of *Lasius niger* in order to address the following questions:

(1) How do patrolling and foraging activities change as the colony grows older and larger?
(2) Which one of the age or size factors influences the foraging response?
(3) How does steep increase or drastic reduction of the workers' population affects foraging strategy?
(4) To what extent the observed changes in collective foraging strategy result from physiological / behavioral modifications of the individuals?

Material and methods

1. Laboratory rearing conditions

Mature colonies (n = 5) of *Lasius niger* of unknown age were collected from slopes of earth banks in Brussels. They were composed of around 1,100 workers (range: 800 to 1,400 workers) and were reared in plaster nests (20 × 20 × 0.5 cm) placed in plastic arenas (50 × 38 cm) of which borders were coated with fluon. They were reared at a temperature of 22 ± 3° with a 12h photoperiod and were fed three times a week with brown sugar solution (0.6 M), cockroaches (*Periplaneta americana*) and maggots (*Calliphora erythrocephala*).

As regards incipient nests, *L. niger* queens were collected in 1997, 1998, 1999 and 2000 in Brussels while they were walking on pavement after their nuptial flight occurring in July and August. Founding nests consisted of test tubes half filled with water retained by a cotton wool plug. The nest tubes were placed in plastic boxes (6 × 10 × 14 cm), the borders of which were coated with fluon to prevent escapes. They were reared under identical laboratory conditions than mature colonies excepting during the yearly hibernation period (from November to February), they were put in a refrigerator at 5 ± 2 °C, in the dark).

In each founding nest, we placed four queens as pleometrotic incipient nests are known to be more successful than haplometrotic ones (For *Lasius niger*, see Lenoir, 1979; Sommer and Hölldobler, 1995; for other species, see Hölldobler and Wilson, 1977, 1990; Tschinkel and Howard, 1983; Tschinkel, 1995). As previously observed by Lenoir (1979), these pleometric incipient nests evolved into single-queen ones, mostly before the hibernation period (85% of incipient nests turned to monogyny before the hibernation). As the number of queens may influence the activity of *L. niger* colonies, we waited for the natural elimination of supernumerary queens and we carried out experiments only on secondary monogyne incipient nests.

A total of 104 groups of four queens were placed in founding nests. Most incipient nests did not survive the precarious period during which the first, second and third brood was reared. Such failure was due either to the death of all co-founding queens, to the infertility of the surviving queen or to the decline of incipient nests with young workers unable to achieve all vital tasks. The mortality rate of incipient nests was 33% (n = 104), 47% (n = 70) and 29% (n = 28) before the first, second and third hibernation respectively. We collected data only from incipient nests containing a) a healthy queen: it survived at least three years and b) a healthy population: the worker number never seriously decline.

2. Foraging behaviour and population growth of "standard" colonies

We tested the foraging behaviours of so-called standard incipient nests that were allowed to grow without any manipulation of the colony demography. Four days before each experiment, an incipient nest was deprived of sugar solution but was still provided with proteinaceous food in order to avoid cannibalism of larvae or eggs (Lenoir, 1979). One hour before the experiment, minim scouts had free access, through a cardboard bridge (length 20 cm, width 0.5 cm), to a small foraging area (6 × 6 cm). A sucrose droplet (1.5 ml) large enough to avoid over-crowding of drinking ants was placed in front of the bridge on the foraging area. We measured on video recordings:

(1) The maximum number of patrollers (Pm) that was the highest number of ants simultaneously present on the foraging area during a period of one hour before the introduction of the food source.
(2) The maximum of foragers' flows (Fm) that was the highest numbers of ants entering the foraging area per five minutes window, recorded over a period of one hour starting with the introduction of the food source.

We choose to use maximum values instead of averages as our main focus is on the upper limit of the number of workers simultaneously engaged in each of these two tasks. In particular, this measure of maxima eliminates the possibility that different delays in the onset of exploration or foraging in different trials cause anomalous differences in the results.

As for patrolling activity, we considered it important, as the number of scouts simultaneously present on explored areas is a critical factor for the emergence of collective trail recruitment.

(3) The total number of conveyors (C) that was the numbers of foragers conveying the food solution to the nest during the one hour experiment. The total transported food volume (V) was the average volume ingested per individual (see below) multiplied by the total number of conveyors.

After each experiment, the population of workers (W) was counted in the tested incipient nests.

3. Individual behaviours of workers in "standard" colonies

The experimental set-up was the same as the one previously described except that the food droplet (3 µl) was delivered through a hanging micropipette (see Mailleux et al., 2000). Once the first scout discovered the food droplet and returned homewards, we gently removed it before the ant entered the nest. By doing so, we prevented the recruitment of nestmates and limited the scope of this study to the behaviours of scouts only. The experiment lasted at most 4 hours. As chemical marks laid by the first recruiting ants could influence the behaviour of the followers, we observed at most 4 ants per experiment. We video-taped individual behaviour of minims while they were on the bridge and on the foraging area. On a magnified image (X25), we measured two morphological parameters: the length of the alitrunk in profile (from the anterior edge of the pronotum to the posterior base of the propodeum), the maximal length and maximal height of the gaster before and after drinking. By approximating the gaster to an ellipsoid, the two latter measures allowed us to calculate the volume of sugar solution ingested by each ant (Mailleux et al., 2000). We also measured the following behavioural parameters:

(1) Walking velocity: the ant's speed averaged over the entire foraging trip (food-bound + nest-bound).
(2) Drinking time: length of the time interval during which the ant's mandibles were in contact with the sugar solution.
(3) Departure time: started when the ant stopped drinking and stopped when it reached the middle of the bridge on its way back to the nest.
(4) Number of visits to the food source: number of times that the same ant was seen drinking at the droplet.
(5) Percentage of trail-laying scouts: the percentage of ants that laid at least one trail mark over the whole length of the bridge.
(6) Individual intensity of trail-laying behaviour: the relative amount of time during which each trail-laying ant was seen dragging its gaster on a predefined section (12 cm) of the bridge.

4. Manipulation of incipient nests' demography

We tried to identify the respective influence of colony age and size on the foraging behaviour of *L. niger* incipient nests. As population size increased when the incipient nest grew old, we dissociated colony size from age by comparing unmanipulated incipient nests and mature colonies to incipient nests of which the demography (number of workers or larvae) was artificially altered.

4.1 "Boosted" incipient nests

L. niger species easily adopt homospecific brood from another colony (Lenoir, 1979, 1981). Hence, we gently introduced brood from one colony (about 20 cocoons, larvae and eggs were not quantified) in front of the nest tube of the incipient nest to be "boosted" (number of "boosted" incipient nests = 5). Both purloined and "boosted" colonies were one year-old having survived the first hibernation. We boosted each incipient nest three times at monthly intervals by collecting brood from different colonies. The foraging behaviours of boosted colonies were

tested before each introduction of foreign brood. The time evolution of foraging behaviour of boosted colonies (n = 5) was compared to that of unmanipulated incipient nests of the same age (n = 11).

4.2 Reduced incipient nests

We artificially reduced the workers' population of one-year-old incipient nests (x ± SD = 45.0 ± 21.2) by removing randomly selected workers. Those reduced incipient nests were composed of one queen, around 20 workers (x ± SD = 19.9 ± 4.7 ants) and all the brood initially present in the colony. Similar abrupt variations of population can occasionally occur under natural circumstances such as predation and nest flooding. One month after stealing workers, we tested for the impact of this drastic reduction of the population on the foraging and trail-laying behaviours of ants.

Results

1. Foraging behaviour and population growth of "standard" colonies

Incipient nests' size was significantly correlated to age, though a high inter-colonial variability was observed (Spearman rank correlation: $rs = 0.54$, n = 37, z = 3.3, p < 0.001). The foraging dynamics changed as *L. niger* incipient nests grew larger and older (Fig. 1 a). The smallest incipient nests of less than 25 ants relied on few foragers to meet their food requirements. As incipient nests' size increased (up to 200 ants), the average flows of foragers grew more steeply to reach peak values before progressively decreasing in the course of foraging. Indeed, a significantly higher flow-rate increase (number of ants entering the area over the first 15 minutes) was found for colonies of more then 50 ants compared to colonies of less then 25 ants (Kruskall-Wallis test, $H_3 = 14.06$, p < 0.01 followed by post-hoc Dunn tests, colonies of (0−25) compared to colonies of (50−75): Q = 3.30, p < 0.01, colonies of (0−25) compared to colonies of (75−200): Q = 2.71, p < 0.05). Independently of colony size, the foragers' flow always peaked after about 20 minutes (Kruskall-Wallis test, $H_3 = 3.70$, NS).

The number of minims involved in exploration and foraging tasks increased with the size/age of incipient nests. Incipient nest size, maximum number of patrollers, maximum flow of foragers and total number of conveyors were jointly correlated (Kendall's coefficient of concordance test: $Wx = 0.91$, n = 26, p < 0.001). When looking at the proportion of workers involved in each of these tasks, it significantly decreased with increasing size of incipient colonies (Kruskall-Wallis tests, p < 0.001 for all variables).

When pooling data from incipient nests and mature colonies, the maximum number of patrollers (Pm) increased with colony size (W) following the best-fit relationship $Pm = 0.40 \, W^{0.62}$ (R = 0.89, n = 37, p < 0.001). The investment of *L. niger* colonies in patrolling grew at a lower rate than population size, as evidenced by the exponent (0.62) that was significantly lower than 1 (t-test: t = 7.43, p < 0.001). The maximum flows of foragers (Fm) and the total numbers of conveyors (C) grew at a closer to that of colony size (W) as shown by the following equations: maximum flow of for-
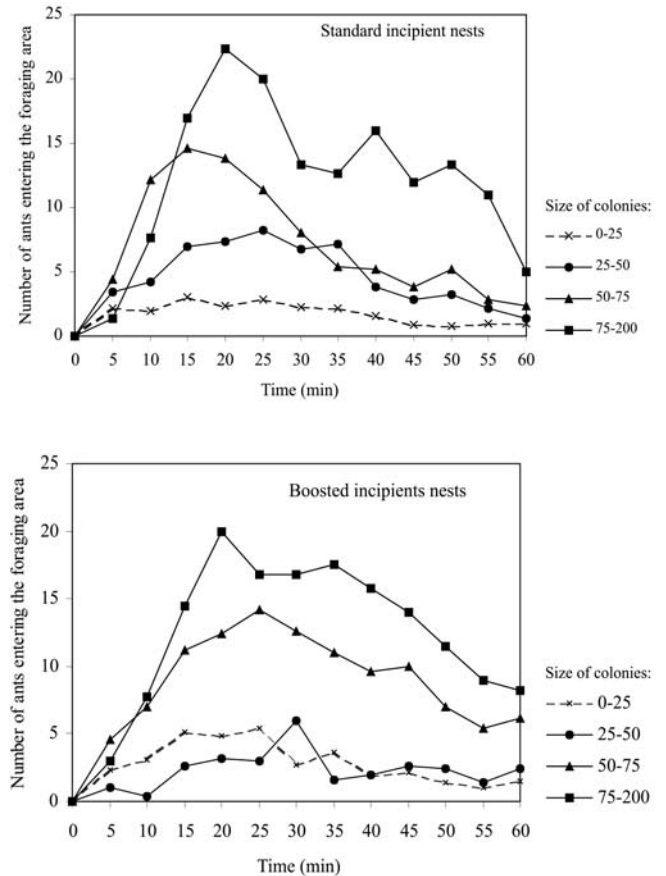

Figure 1. Changes in the flows of foragers entering the foraging area as a function of the time after the introduction of the food source, for the different sizes of incipient standard (fig. 1 A) and boosted nests (fig. 1 B). The curves represents the mean of entering ants/5 min (n = 5, except in the [75–200] class: n = 4). Each standard colony was tested just one time. The five boosted colonies were tested before the first supply of brood and one month after each supply (each colony was tested four times)

agers: $Fm = 0.47 \, W^{0.82}$ (R = 0.90, n = 37, p < 0.001); number of conveyors: $C = 1.56 \, W^{0.87}$ (R = 0.88, n = 37, p < 0.001). But only the exponent 0.87 did not statistically different from 1 (maximum flow of foragers: t-test: t = 5.20, p < 0.001; number of conveyors: t-test: t = 1.99, NS). As for the efficiency in food retrieval, the best-fit relationship between the total volume of transported food (V) and the workers' number $V = 0.97 \, W^{1.25}$ (R = 0.98, n = 37, p < 0.001) showed that it increased at a higher rate than colony size (t-test: t = 6.89, p < 0.001). This trend mainly resulted from the larger body sizes and hence larger food volumes ingested per conveyors that lived in mature colonies in comparison with minims from incipient nests.

2. Individual behaviours of workers in "standard" colonies

The alitrunk lengths of minims (0.8 ± 0.2 mm for all minims observed in incipient colonies, n = 98) were significantly correlated with their abdomen volumes before drinking (0.4 ± 0.1 mm³) (Spearman rank correlation: $rs = 0.61$, n = 98,

z = 5.91, p < 0.001). Lengths of alitrunk and abdomen volumes before drinking did not significantly changed with the size of incipient colonies (Table 1). We should however notice that in the largest incipient nests (75–200 ants) the abdomen volumes of some minims (15%, n = 34) were larger than the maximum abdomen volume (0.6 mm^3) of minims from smaller incipient nests. As these larger individuals drank more sugar solution, ingested food volumes were significantly higher in the largest incipient nest (75–200 ants) than in less populous ones (Table 1). Ants showed similar drinking times (around 50 s) whatever the size of their incipient nests. As for the number of visits to the food source and its correlated departure time (rs = 0.69, n = 109, z = 7.00, p < 0.001), both decreased as the population size grew: scouts from smaller incipient nests circled around the food source and came back several times to the droplet whereas ants from the largest incipient nests (75–200 ants) ingested food at once and returned immediately to the nest. In small-sized incipient nests, the bulk of sugar solution was ingested at the first visit. Additional visits did not appear to aim to acquire additional food quantities as mandibles were in contact with the solution for two seconds at most. Ants' velocities were similar whatever the populations' sizes. We found no significant correlation between all time variables (walking velocities, drinking and departure times).

The percentage of trail-laying scouts increased significantly with the size of incipient nests (chi-square test: $\chi^2_3 = 38.0$, P < 0.001) but, among those ants, the individual trail-laying intensity did not differ (Table 1 and Fig. 2). Trail-laying scouts were not morphologically nor behaviourally different from non trail-laying ones. The only exception was trail-laying ants of small-sized incipient nests (0–25 ants) that drank larger volumes (0.22 ± 0.1 μl, n = 34) than non trail-layers (0.15 ± 0.1 μl, n = 16) (Kolmogorov-Smirnov test: D = 0.43, p < 0.05).
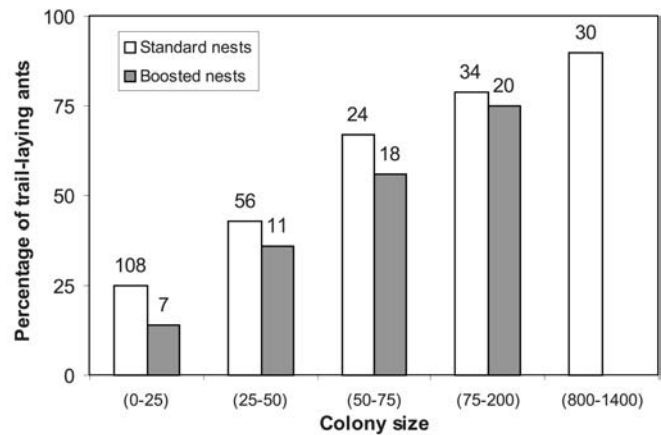

Figure 2. Changes in the size of control incipient nests (□) and boosted incipient nests (■) as a function of time. Bars = means ± standard deviation. n = 7 for the control nests, n = 5 for the boosted nests

Scouts from mature colonies differed morphologically from those of the largest size incipient nests (75–200 ants) showing larger abdomen volumes (D = 0.82, p < 0.001) and longer alitrunks (D = 0.84, p < 0.001). As a corollary, behavioural variables related to ants' body size were significantly different between mature and largest incipient nests: ingested food volume (D = 0.72, p < 0.001), drinking time (D = 0.58, p < 0.001) and ants' velocity (D = 0.87, p < 0.001). Other behavioural variables were similar in mature colonies and largest incipient nests: number of visits to the source (D = 0.09, NS), departure time (D = 0.31, NS), percentage of trail-laying ants as well as their individual intensity of marking (D = 0.22, NS). Conclusion therefore is that, with the exception of variables immediately related to body-size, minims of large incipient nests (about 100 workers) behave similarly to workers of mature colonies.

Table 1. Individual behaviours of standard incipient nests differing by their age and size. Means ± SD are given for all parameters. The number of observed scouts is given between brackets. Standard incipient nests of different sizes (excluding mature colonies) were compared by means of Kruskall-Wallis tests. Values of p and results of the statistic test ($\alpha = 0.05$, NS = non statistical difference) are given in the last column for each parameter

Colony size [number of ants] Age (months)	Incipient nests [0–25] Age: 10.8 ± 4.0	Incipient nests [25–50] Age: 11.3 ± 2.1	Incipient nests [50–75] Age: 11.9 ± 0.4	Incipient nests [75–200] Age: 23.7 ± 1.2	Mature colonies [800–1400] Unknown age	Kruskall-Wallis tests
Length of the alitrunk (mm)	(35) 0.7 .2	(18) 0.8 ± 0.2	(11) 0.8 ± 0.2	(34) 0.8 ± 0.3	(30) 1.2 ± 0.2	KW = 0.52 NS
Abdomen volume before drinking (μl)	(35) 0.4 ± 0.1	(18) 0.4 ± 0.1	(11) 0.3 ± 0.1	(34) 0.4 ± 0.2	(30) 0.9 ± 0.3	KW = 0.98 NS
Ingested food volume (μl)	(35) 0.2 ± 0.1	(18) 0.2 ± 0.1	(11) 0.3 ± 0.1	(34) 0.3 ± 0.2	(30) 0.7 ± 0.3	KW = 10.20 NS
Drinking time (s)	(58) 47.7 ± 22.2	(28) 45.3 ± 22.3	(12) 51.3 ± 11.5	(34) 52.3 ± 14.5	(30) 81.7 ± 35.4	KW = 2.81 NS
Number of visits	(57) 2.4 ± 2.9	(24) 2.1 ± 2.6	(12) 1.8 ± 1.3	(34) 1.2 ± 1.5	(30) 1.3 ± 0.6	KW = 15.76 p < 0.005
Departure time (s)	(45) 42.6 ± 43.1	(18) 26.4 ± 21.6	(12) 22.4 ± 20.1	(34) 17.7 ± 10.3	(30) 16.0 ± 11.8	KW = 10.95 p < 0.05
Velocity (cm/s)	(31) 1.0 ± 0.3	(18) 0.9 ± 0.3	(10) 1.0 ± 0.2	(34) 0.8 ± 0.3	(30) 1.8 ± 0.5	KW = 7.8 p = 0.05
Trail laying intensity	(14) 0.08 ± 0.07	(13) 0.12 ± 0.11	(9) 0.07 ± 0.06	(24) 0.10 ± 0.07	(27) 0.10 ± 0.6	KW = 2.03 NS

3. Foraging behaviour in size-manipulated incipient nests

3.1. Boosted incipient nests

The boosting procedure (introduction of foreign brood) did not affect the survival of the five incipient nests as no mortality occurred after the next hibernation period. Before the first addition of brood, a similar number of ants was present in "boosted" incipient nests and unmanipulated ones (Kolmogorov-Smirnov test: $D = 0.48$, NS). As a consequence of monthly brood supplies, the number of ants in "boosted" incipient nests increased exponentially over time (Fig. 3, $W = 11.30 \ e^{0.61 \times}$, $R = 0.99$). Control nests grew linearly ($W = 13 + 3.6 \ x$, $R = 0.98$). The high rate of increase of the exponential growth of boosted nests confirmed the adequacy of our "boosting" procedure: workers seemed to readily adopt and to efficiently take care of newly introduced brood. From the first addition of brood, the number of workers in boosted colonies became significantly higher than in unmanipulated ones (Kolmogorov-Smirnov test after the first brood addition: $D = 0.86$, $p < 0.05$; after the second addition: $D = 1$, $p < 0.001$; after the third addition: $D = 1$, $p < 0.001$).

The recruitment dynamics (Fig. 1 b) of "boosted" incipient nests increased with the workers' population and were comparable to those observed in standard unmanipulated colonies of the same size (Fig. 1 b, Kolmogorov-Smirnov tests for colonies of $[0-25]$ ants: $D = 0.42$, NS; $[25-50]$ ants: $D = 0.51$, NS; $[50-75]$ ants: $D = 0.46$, NS; $[75-200]$ ants: $D = 0.26$, NS). Maximum number of patrollers (Pm), maximum flow of foragers (Fm), total number of conveyors (C) increased with size (W) of boosted incipient nests following the equations: $Pm = 0.21 \ W^{0.62}$ ($R = 0.6$, $n = 20$, $p < 0.005$); $Fm = 0.44 \ W^{0.80}$ ($R = 0.75$, $n = 20$, $p < 0.001$) and $C = 1.18 \ W^{0.99}$ ($R = 0.72$, $n = 20$, $p < 0.001$). As a corollary, total volume of food transported to the nest (V) also increased with colony size and could be fitted by the equation $V = 0.93 \ W^{1.1}$ ($R = 0.75$, $n = 20$, $p < 0.001$). Moreover the regressions of data from boosted colonies have exponent that are statistically similar to that of same-sized standard nests (t-tests: $t = 1.09$; $t = 1.63$; $t = 0.11$; $t = 0.22$ for patrollers, foragers, conveyors
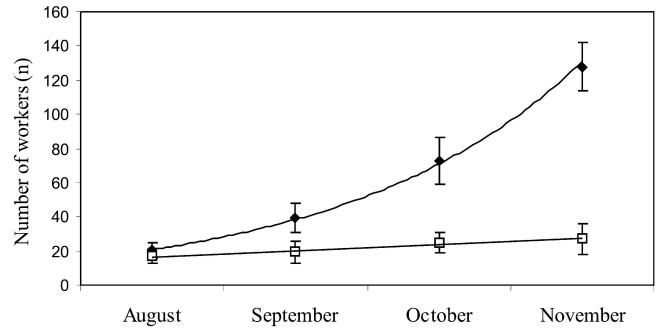

Figure 3. Percentage of trail-laying behaviour as a function of the size of the standards (□) and boosted (◆) nests. The number of scouts observed is given above each bar

and transported volumes respectively, all p values > 0.05). Hence, patrolling, foraging and food conveying activities were related to nest size in the same quantitative way for boosted and standard colonies, despite their difference in the age profile of the worker population.

All morphological and behavioural individual variables of "boosted" incipient nests were similar to those from standard populations of equivalent size (Table 2, Kolmogorov-Smirnov tests: NS for all parameters). The percentage of trail-laying scouts increased significantly with the size of boosted nests, this increase is statistically similar to that of same-sized standards nests (Table 2 and Fig. 2, chi-square tests compare standards and boosted colonies of $[25-50]$ ants: $\chi^2 = 0,19$, NS; $[50-75]$ ants: $\chi^2 = 0,53$, NS; $[75-200]$ ants: $\chi^2 = 0,12$, NS). This strongly suggests that size rather than age of incipient nests is the key factor determining both the collective foraging strategy of *L. niger* and the individual behavioural profile of minims.

3.2 Reduced incipient nests

The reduction of the workers' population did not affect the survival of incipient nests: 100% still survived till the second

Table 2. Individual behaviours of boosted incipient nests differing by their size. Means ± SD are given for all parameters. NA = not available. The number of observed scouts is given between brackets. The standard incipient nests (see Table 1 a) and boosted incipient nests of equivalent size were compared by means of one-sample Kolmogorov-Smirnov tests. Values of p and results of the statistic test ($\alpha = 0.05$, NS = non statistical difference) are given in the three last columns for each parameter

Size of boosted incipient nests	Initial population [0−25]	First addition of brood [25−50]	Second addition of brood [50−75]	Third addition of brood [75−200]	Kolmogorov-Smirnov tests [25−50]	[50−75]	[75−200]
Length of the alitrunk (mm)	(11) 0.8 ± 0.2	NA	(18) 0.8 ± 0.2	(19) 0.8 ± 0.2	NA	D = 0.20 NS	D = 0.31 NS
Abdomen volume before) drinking (µl)	(11) 0.3 ± 0.1	NA	(18) 0.3 ± 0.1	(19) 0.3 ± 0.1	NA	D = 0.22 NS	D = 0.30 NS
Ingested food volume (µl)	(11) 0.2 ± 0.2	NA	(18) 0.2 ± 0.2	(19) 0.2 ± 0.1	NA	D = 0.34 NS	D = 0.21 NS
Drinking time (s)	(11) 57.1 ± 15.1	NA	(18) 44.4 ± 30.1	(19) 57.9 ± 25.8	NA	D = 0.39 NS	D = 0.28 NS
Number of visits	(11) 2.1 ± 2.0	NA	(18) 2.1 ± 2.3	(17) 1.5 ± 1.7	NA	D = 0.25 NS	D = 0.32 NS
Departure time (s)	(6) 48.6 ± 52.5	NA	(17) 26.3 ± 21.9	(14) 24.4 ± 15.8	NA	D = 0.48 NS	D = 0.37 NS
Velocity (cm/s)	(5) 1.1 ± 0.3	NA	(18) 0.9 ± 0.2	(19) 0.9 ± 0.4	NA	D = 0.31 NS	D = 0.32 NS
Trail laying intensity	(5) 0. 6 ± 0.07	NA	(11) 0.11 ± 0.06	(14)) 0.10 ± 0.08	NA	D = 0.37 NS	D = 0.20 NS

Table 3. Behaviours of ants before and after reduction of the incipient nest size. Means ± SD are given for all parameters. The number of observations is given between brackets (Number of observed colonies in italic, Number of observed scouts in regular font style). The reduced incipient nests were compared before and after the reduction with the standard incipient nest of equivalent size by means of one-sample Kolmogorov-Smirnov tests (except * = chi-square test). Values of p and results of the statistic test ($\alpha = 0.05$, NS = non statistical difference) are given in the last column for each parameter

Size of nests	Reduced nests before reduction [25–75]	Standard incipient nests [25–75]	Statistical test	Reduced nests after reduction [0–25]	Standard incipient nests [0–25]	Statistical test
Number of patrollers	(7) 5.1 ± 2.8	(20) 5.1 ± 3.0	D = 0.99 NS	(7) 1.6 ± 1.1	(17) 2.1 ± 0.9	D = 0.39 p = NS
Maximal flow (n ants/5 min)	(7) 10.6 ± 4.0	(20) 14.9 ± 9.1	D = 0.35 NS	(7) 4.7 ± 1.3	(17) 4.0 ± 3.0	D = 0.41 p = NS
Number of conveyors	(7) 42.4 ± 17.5	(20) 50.7 ± 24.0	D = 0.36 NS	(7) 19.0 ± 4.5	(17) 23.3 ± 17.6	D = 0.45 p = NS
Percentage of trail-laying ants	(37) 41	(80) 50	χ^2 = 00.82* NS	(18) 22	(108) 25	χ^2 = 0.13* NS

hibernation period. A significant decline of the exploration force and of the foraging activity followed the reduction of incipient nest size (Wilcoxon sign ranks test: the maximum number of patrollers, $T^+ = 27$, $p < 0.05$, $n = 7$; the maximum flow of foragers, $T^+ = 28$, $p < 0.05$, $n = 7$; the total number of conveyors, $T^+ = 28$, $p < 0.05$, $n = 7$). Though not significantly different ($\chi^2 = 1.93$, NS), the percentage of trail-laying ants was clearly lowered in reduced incipient nests (Table 3). For all tested variables, the behaviour of ants from reduced incipient nests was found to be similar to that from standard populations of equivalent size (see statistical results on Table 3). This confirmed the strong influence of population size on exploratory, foraging and recruitment efforts of ant colonies.

Discussion

Foraging by growing incipient nests and mature colonies progressively shifts from the exploitation of food sources by one or a few individuals to a trail recruitment of nestmates, with all intermediate stages. The extent to which scouts cooperate to retrieve food increases with colony size: while a minority of scouts from small incipient nests laid trail marks on their homeward trip, nearly all the ants from large incipient nests or mature colonies were involved in trail recruitment. *L. niger* colonies adjust their activity profile to the demography of the society: a drastic reduction (or increase) of the population elicits a foraging activity similar to that observed in younger (or older) societies of the same size. This demonstrates that colony size instead of age is the key factor that shapes the exploratory and foraging response of *L. niger*. The number of patrollers increases at a lower rate than total worker population. This confirms the prediction that the proportion of scouts maximising food retrieval decreases with increasing colony size (Jaffe and Deneubourg, 1992). As a colony grows, the proportion of conveyors remains rather constant while the energetic return (total food volume retrieved per time unit) increases due to the progressive replacement of minims by "normal size" workers of larger crop capacity. Hence, the prior investment of incipient colonies consists in the production of an optimum number of nanitics foragers, instead of a

smaller group of ordinary size workers. In the field, this optimum number can be reached more quickly by peaceful raiding between incipient colonies (Balas and Adams, 1996; Adams and Tschinkel, 1995). Though less efficient in food retrieval on an individual basis, nanitics can be collectively more efficient than a smaller group of workers of equal combined weight to perform co-operative tasks (as shown by Porter and Tschinkel, 1986 for brood care in *Solenopsis invicta*). In *L. niger*, cooperativity in foraging increases with the number of minims: the percentage of trail-laying ants increases to reach that of mature colonies above a threshold incipient nest size of 75–200 ants. When this cooperativity level is reached, the colony starts producing ordinary workers that are more efficient at retrieving food per foraging trip.

Several ants' species are flexible and able to adjust their social activity profile to changes in the composition of the society due to experimental sociotomies (see e.g. Fowler, 1984; Lachaud and Fresneau, 1987; Lenoir, 1979; Wilson, 1984; Sempo and Detrain, 2002; Gordon, 1986) or to natural sociotomies (Herbers and Choiniere, 1996). Our manipulations of incipient nests' size show that the trail-laying behaviour of *L. niger* does not depend only on age-related physiological maturation of ants (Cammaerts and Verhaeghe, 1974) but also of the social context. The flexible and reversible mechanisms that regulate the percentage of trail-laying ants according to group size could be either chemical or tactile. In the latter case, the interactions patterns could influence the probability that a scout will lay recruitment trail (Gordon et al., 1993). The modulation of individual behaviour in relation to group size is clearly adaptive as colony size is crucial to colony organisation and determines its needs and capacities (Bourke, 1999; Anderson and Mc Shea, 2001; Tschinkel, 1999). The scarcity of trail-laying behaviour in incipient colonies fits their discrete foraging strategy in which timid minims patrol at short distances (personal observation), preferentially in the darkness (unpublished data). As the loss of several workers is costly or even fatal to small incipient nests, individual foraging allows incipient societies to stay unlocated by predators or raiding conspecifics of mature colonies (Czechowski, 1984; Adams and Tschinkel, 2001). On the other hand, trail recruitment supports a strategy that can be implemented only by large sized-incipient nests and mature colonies able to mo-

nopolise and actively defend food sources against competitors (Adams and Tschinkel, 2001).

The evolution of recruitment behaviour is assumed to recapitulate at least to some extent the ant phylogeny (see e.g. Hölldobler and Wilson, 1990; Jaffe, 1984; Wilson, 1971; Maschwitz, 1975). The idea is that "primitive" ants are unable to recruit or recruit only a few individuals whereas more advanced species have developed the anatomical and physiological features enabling them to forage cooperatively and massively recruit nestmates. However, recruitment behaviours have also been selected in a convergent way among different species as an adaptation to colony features and environmental constraints (see e.g. Oster and Wilson, 1978; Hölldobler and Traniello, 1980; Hölldobler and Wilson, 1990; Baroni Urbani, 1993; Deneubourg et al., 1986; Pasteels et al., 1987). Beckers et al. (1989) provided direct evidence of interspecific convergence related to colony features: by correlating the foraging strategy of 98 species to their mature colony size, the authors found a crescendo of the integration of individual foragers into a network of communication. The present paper goes a step further by demonstrating 1°) that colonies of one species exhibit, during their ontogeny, the same increase in cooperativity level and 2°) that these changes in communication and foraging behaviour are straightforward responses to the colony size. By inducing the choice of one foraging pattern rather than the other, the social context acts as an efficient mechanism to initiate fast and efficient transition between foraging strategies in ant societies.

Acknowledgements

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