



## How food type and brood influence foraging decisions of *Lasius niger* scouts

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We investigated how the type of food (sucrose or protein) and the presence of brood influence foraging decisions of *Lasius niger* L. scouts. In particular, we studied whether and how these parameters alter the drinking behaviour of scouts and the allocation of workers to food retrieving and recruiting tasks. We analysed drinking and recruiting behaviour of single scouts from nests with or without brood that encountered a proteinaceous or sucrose droplet. A substantial fraction of scouts encountering a proteinaceous droplet did not ingest it and did not then return to the nest whereas nearly all drank at sugar droplets; brood presence did not influence this decision. Once an ant started drinking, it needed to drink a critical volume before returning to the nest; this critical volume did not depend on the type of food and the presence of brood. Scouts laid a trail only if they returned to the colony. Food type and brood presence altered the proportion of individuals that laid a trail but not the individual trail-laying intensity. We discuss the consequences of this decision system through simple individual assessments and decision rules, with regard to the self-organized foraging patterns of this species and the efficient collective exploitation of natural resources.

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Through the sharing of information between nestmates, ant societies achieve collective decisions and adjust foraging patterns to the diversity of resources available in their environment (reviewed in Hölldobler & Wilson 1990; Detrain et al. 1999). Additional factors that are not directly related to food characteristics can also contribute to the shaping of their foraging patterns, such as the physical environment (Detrain et al. 2001), the presence of competitors (Traniello 1987; Savolainen 1991; Traniello & Beshers 1991) or predators (Hunt 1983; Nonacs & Dill 1991; Detrain et al. 1999), the level of colony starvation (Cosens & Toussaint 1986; Nonacs & Dill 1991; Josens & Rocas 2000) and the social environment (e.g. the amount of brood, Sudd 1987; Herbers and Choinière 1996; Portha et al. 2002). Even within a species, ants can hence use a wide variety of foraging strategies ranging from solitary food collection to mass recruitment.

In this respect, aphid-tending ants such as *Lasius niger*, which feed on homopteran honeydew as well as on insect prey, are of particular interest to study how information about food type is processed and whether proteins or sugars influence the foraging decisions of individuals as well as the recruitment dynamics of the colony. Characteristics

of food resources known to alter the foraging patterns of aphid-tending formicines include their spatiotemporal availability (Traniello 1989; Traniello & Beshers 1991; Sundström 1993; Quinet & Pasteels 1996), food quality (Hangartner 1970; Nonacs & Dill 1991; Beckers et al. 1993; Josens et al. 1998), food quantity (Traniello 1987; Mercier & Lenoir 1999; Mailleux et al. 2000), food distance (Bonser et al. 1998; Devigne & Detrain 1999) and food type (Traniello et al. 1992; Sundström 1993; Portha et al. 2002).

Most of these studies have given functional interpretations of the foraging strategies observed at the colony level, within an evolutionary and optimal theory framework. However, it is less clear which feedback mechanisms are involved and how these patterns are achieved. Only a few studies (reviewed in Detrain et al. 1999) have tried to determine how ants assess food characteristics and colony needs, process information and interact during food exploitation. Portha et al. (2002) showed that *L. niger* is able to shape its collective foraging response according to the nature of the food and the presence of brood within the colony. Pheromone trails are critical for the transition from a solitary to a collective exploitation of the food source in this mass-recruiting species (Jaffé 1980; Deneubourg et al. 1986). However, little work has been done on how a scout decides to return to the nest and to lay a trail. Although it is recognized that scouts of *L. niger* initiate recruitment to sucrose sources only if they are able to fill

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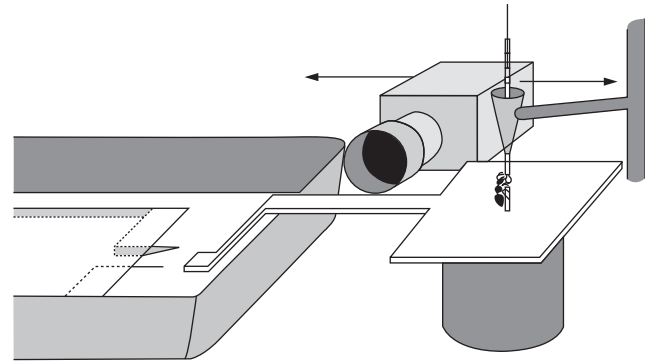
their crop up to a threshold volume (Mailleux et al. 2000), whether this rule can be generalized to other food types is unknown.

We investigated how the type of food and the presence of brood influence foraging decisions of scouts, in particular whether the threshold volume rule remains valid for proteinaceous food sources and various colony needs. We studied how food type and brood alter the drinking behaviour of scouts and influence the allocation of workers to food-retrieving and recruiting tasks.

## METHODS

We collected four *L. niger* 'mother' colonies that were parts of natural colonies from slopes of earth banks in Brussels, Belgium. In the laboratory, we reared ant societies in plaster nests (Janet type, 20 × 20 cm and 0.5 cm high) placed in arenas (50 × 38 cm) the borders of which were coated with fluon to prevent escapes. We covered the nest chamber with a red glass plate through which the ants could be observed. Each queenless nest contained 1500–2000 workers and brood. Nests were regularly moistened and kept at a room temperature of  $22 \pm 3^\circ\text{C}$ , 60% relative humidity with a constant photoperiod of 12 h of light per day. We supplied ants with water, sucrose solution (1 M), dead cockroaches, *Periplaneta americana*, and maggots, *Calliphora erythrocephala*, twice a week. One month after their collection, mother colonies were each divided into two experimental nests containing approximately half of the original worker population. To achieve this segregation, we chilled the mother nests for 20 min at  $4^\circ\text{C}$ , and then we removed the glass plate of the nest to allow a random collection of ants from all parts within the nest. Larvae from the mother colony were transferred to one of the experimental nests, the other one being deprived of any brood. Nests with brood contained similar numbers of larvae, which covered 15–20% of the nest area. After their settlement, we allowed nests to recover for at least 2 weeks before the tests.

After a food deprivation period of 4 days, we connected each experimental nest (five nests with brood and five without) by a cardboard bridge (length 22 cm, width 0.5 cm) to a small foraging area (6 × 6 cm). A microcapillary hanging above the middle of the foraging area delivered a food solution (Fig. 1). Each scout could feed ad libitum because the volume of the droplet (3  $\mu\text{l}$ ) exceeded the maximal capacity (about 1.8  $\mu\text{l}$ ) of the crop of *L. niger* workers (Mailleux et al. 2000). A drawbridge system controlled the access of ants to the foraging area by allowing only one scout at a time to climb on to the bridge. In between successive observations, we replaced the microcapillary as well as the whole bridge–foraging area set-up. By doing so, chemical marks possibly laid by a trail-laying ant were removed and the behaviour of the observed scout was not biased by the marking of previously tested ants. We followed three to five scouts per nest per day ( $N = 40$  days, one trial per day) with 1 h elapsing between the testing of successive scouts. This allowed nestmates to calm down after the return of the observed scout into the colony and trail marks possibly



**Figure 1.** Experimental set-up. The camera recorded the whole foraging sequence of ants on the bridge as well as on the foraging area. Behavioural and morphological parameters measured on the videorecording are described in the text.

laid around the nest entrance to evaporate (the trail lifetime being around 40 min, Beckers et al. 1993). Ants that did not find the droplet and returned to the nest or fell from the bridge or the foraging area were removed from the analysis.

A 3- $\mu\text{l}$  droplet of either sugary or proteinaceous solution was offered alternately to successive scouts each day. We alternated the type of solution with which we started. The sugary food droplet was a sucrose solution (1 M) and the proteinaceous solution consisted of 30 maggots, *C. erythrocephala*, killed by freezing, crushed in 5 ml of water and filtered. Food sources were the same size and differed only in whether they were composed of protein or sugar, which allowed us to assess the influence of the food type on the recruiting decisions of scouts. We compared the behaviour of scouts in four experimental conditions: (1) Sucrose/Brood condition (SB): scouts from a nest with brood presented with a sucrose droplet; (2) Sucrose/No Brood condition (SNB): scouts from a broodless nest presented with a sucrose droplet; (3) Protein/Brood condition (PB): scouts from a nest with brood presented with a proteinaceous droplet; (4) Protein/No Brood condition (PNB): scouts from a broodless nest presented with a proteinaceous droplet.

We videorecorded the behaviour of scouts, with a travelling camera (magnification  $\times 10$ ). We observed scouts from side on, starting from their entrance on to the bridge and ending when they left it to reach the nest arena. On these recordings, we quantified the following parameters.

(1) Ingested volume: we assessed this for each scout by measuring the maximal length and height of the abdomen to compare its abdomen size before and after it had drunk at the droplet. We measured the abdomen directly on the screen and rescaled it using a scaling ruler drawn on the section of the bridge. We assumed abdomen width to be equal to abdomen height and we approximated the abdomen volume by an ellipsoid (Mailleux et al. 2000). We observed that a minimum drinking time of 5 s was required to detect a difference in the size of the gaster before and after feeding, and consequently to determine the ingested volume. We then arbitrarily assumed that ants drinking for less than 5 s had not actually drunk at the food droplet. We did not omit them

from the analysis but assigned them an ingested volume of 0  $\mu$ l.

(2) The number of drinks was counted for each scout at the food source.

(3) The percentage of trail-laying ants was the percentage of scouts that discovered the droplet and that laid at least one trail mark over the whole length of their return trip to the nest (either on the foraging area, the bridge or on the nest arena).

(4) The individual intensity of trail-laying behaviour was the number of marks laid per individual over the 11-cm-long horizontal part of the bridge. For this parameter, we ran 20 additional trials to get a sufficient number of trail-laying scouts in the four experimental conditions.

(5) The total time spent on the foraging area started when the scout reached the foraging area and stopped when the scout left it on its way back to the nest.

(6) The drinking time lasted as long as the ant's mandibles were in contact with the food droplet.

(7) The exploring time was the sum of the times that lasted between the successive drinks of the scout.

(8) The leaving time started when the ant stopped its last drink and finished when it left the foraging area to return to the nest arena.

## Data Analysis

To compare data for the behavioural parameters, we used nonparametric procedures because normality conditions (checked with Kolmogorov–Smirnov tests) were not always met. We used a Mann–Whitney  $U$  test for two-sample comparisons and a Kruskal–Wallis test followed by a post hoc Dunn test for multiple-sample comparisons. Samples with fewer than five individuals were not included in the statistical analysis (see Table 1 and text). Because these data were normal and homoscedastic (checked with a Bartlett test), pooled individual intensities of trail-laying behaviour were compared with an unpaired  $t$  test. Proportions of behavioural categories were compared with Fisher's exact tests and chi-square tests. Statistical tests were two tailed unless indicated otherwise.

**Table 1.** Behaviours ( $\bar{X} \pm$  SD) of the three groups of scouts in relation to experimental conditions

Behavioural parameters	Exploring ants	Nontrail-laying returning ants	Trail-laying returning ants	$P$
<b>Total time (s)</b>				
SB	162 $\pm$ 38 (2)	140 $\pm$ 86 (5)	122 $\pm$ 52 (24)	NS
SNB	101 $\pm$ 60 (3)	122 $\pm$ 54 (8)	103 $\pm$ 28 (17)	NS
PB	213 $\pm$ 158 (24)	122 $\pm$ 61 (14)	141 $\pm$ 63 (20)	NS
PNB	202 $\pm$ 221 (18)	143 $\pm$ 133 (15)	109 $\pm$ 66 (8)	NS
	NS	NS	NS	
<b>Drinking time (s)</b>				
SB	30 $\pm$ 35	85 $\pm$ 32	85 $\pm$ 27	NS
SNB	8 $\pm$ 10	74 $\pm$ 34	77 $\pm$ 25	NS
PB	14 $\pm$ 18 <sup>a</sup>	51 $\pm$ 22 <sup>b</sup>	73 $\pm$ 29 <sup>b</sup>	< 0.0001
PNB	8 $\pm$ 10 <sup>a</sup>	59 $\pm$ 32 <sup>b</sup>	62 $\pm$ 35 <sup>b</sup>	< 0.0001
	NS	NS	NS	
<b>Ingested volume (<math>\mu</math>l)</b>				
SB	0.31 $\pm$ 0.44	1.09 $\pm$ 0.28	1.13 $\pm$ 0.40	NS
SNB	0.17 $\pm$ 0.30	0.99 $\pm$ 0.44	0.95 $\pm$ 0.38	NS
PB	0.21 $\pm$ 0.33 <sup>a</sup>	0.75 $\pm$ 0.28 <sup>b</sup>	0.97 $\pm$ 0.49 <sup>b</sup>	< 0.0001
PNB	0.12 $\pm$ 0.24 <sup>a</sup>	0.89 $\pm$ 0.36 <sup>b</sup>	0.89 $\pm$ 0.55 <sup>b</sup>	< 0.0001
	NS	NS	NS	
<b>Leaving time (s)</b>				
SB	26 $\pm$ 29	8 $\pm$ 6	10 $\pm$ 9 <sup>x</sup>	NS
SNB	66 $\pm$ 62	17 $\pm$ 27	14 $\pm$ 9 <sup>x</sup>	NS
PB	113 $\pm$ 134 <sup>a</sup>	31 $\pm$ 40 <sup>b</sup>	34 $\pm$ 56 <sup>aby</sup>	< 0.03
PNB	102 $\pm$ 176	24 $\pm$ 37	9 $\pm$ 4 <sup>x</sup>	NS
	NS	NS	< 0.05	
<b>Drinks number</b>				
SB	2.5 $\pm$ 0.7	2.0 $\pm$ 0.7	2.0 $\pm$ 1.5	NS
SNB	1.7 $\pm$ 1.2	2.1 $\pm$ 1.3	2.2 $\pm$ 2.1	NS
PB	2.4 $\pm$ 1.7	2.0 $\pm$ 1.0	2.1 $\pm$ 1.7	NS
PNB	2.4 $\pm$ 1.4	2.0 $\pm$ 1.5	2.1 $\pm$ 1.4	NS
	NS	NS	NS	
<b>Exploring time (s)</b>				
SB	18 $\pm$ 19	43 $\pm$ 75	18 $\pm$ 35	NS
SNB	12 $\pm$ 21	30 $\pm$ 33	10 $\pm$ 18	NS
PB	57 $\pm$ 97	32 $\pm$ 48	21 $\pm$ 39	NS
PNB	75 $\pm$ 101	32 $\pm$ 62	34 $\pm$ 54	NS
	NS	NS	NS	

Numbers in parentheses indicate sample size. See text for detailed statistical procedure; groups sharing the same letter were not statistically different under post hoc Dunn tests at 0.05 level of significance.

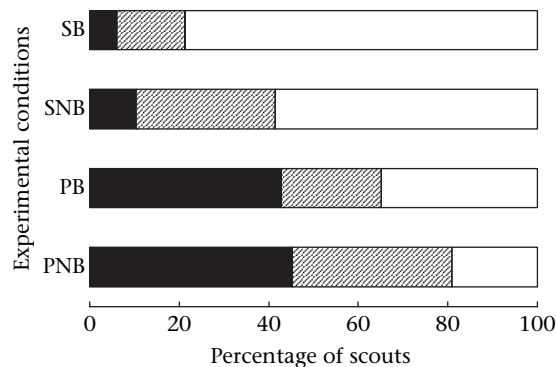
## RESULTS

Scouts could be divided into three groups. (1) Exploring ants: these ants came back to the nest tray but did not enter the nest chamber within 5 min after their return. None of these ants was ever seen laying a chemical trail at the food source, on the bridge or on the nest tray and they spent most of their time on the foraging area in searching behaviour (see below). (2) Returning ants: these ants came back to the nest tray and never explored it for more than 5 min. They usually entered the nest chamber within the first minute after their return. These ants contributed to the return of the food to the colony (see below). Among these returning ants, we could identify: (2a) nontrail-laying returning ants, which did not lay a chemical trail on their way back to the nest; and (2b) trail-laying returning ants, which laid at least one chemical mark on their way back from the food source to the nest.

### Trail Recruitment and Food Retrieval

The proportion of scouts in each of the three groups differed significantly between the four experimental conditions ( $\chi^2_6 = 37.849$ ,  $P < 0.0001$ ; Fig. 2). Few scouts became exploring ants at a droplet consisting of sucrose (6 and 10% for nests with brood and broodless nests, respectively) but many were observed at a proteinaceous droplet (43 and 45% for nests with brood and broodless nests, respectively;  $\chi^2$  comparing the proportion of exploring ants among scouts:  $\chi^2_3 = 23.681$ ,  $P < 0.0001$ ). There was no significant influence of brood presence on the proportion of exploring ants for a given food type (Fisher's exact test: SB versus SNB:  $P = 0.658$ ; PB versus PNB:  $P = 0.843$ ).

The proportion of trail-laying ants among returning ants also differed between experimental conditions ( $\chi^2_3 = 13.757$ ,  $P = 0.003$ ). Nearly all returning ants (84%) from nests with brood that found a sucrose droplet



**Figure 2.** Influence of experimental conditions on the behaviour of scouts. SB: scouts from a nest with brood presented with a sucrose droplet,  $N = 33$ ; SNB: scouts from a broodless nest presented with a sucrose droplet,  $N = 29$ ; PB: scouts from a nest with brood presented with a proteinaceous droplet,  $N = 63$ ; PNB: scouts from a broodless nest presented with a proteinaceous droplet,  $N = 42$ . ■: Exploring ants; ▨: nontrail-laying returning ants; □: trail-laying returning ants.

returned and laid a trail to the nest but only 65% did so in broodless nests. This proportion of trail-laying returning ants was lower for proteinaceous than for sucrose droplets (with brood: 61%; without brood 35%; one-tailed Fisher's exact test comparing proportion of trail-laying ants among returning ants: SB versus PB:  $P = 0.036$ ; SNB versus PNB:  $P = 0.032$ ). The presence of brood in the colonies tended to increase the proportion of trail-laying ants among returning ants for a given food source (one-tailed Fisher's exact test comparing proportion of trail-laying ants among returning ants: SB versus SNB:  $P = 0.096$ ; PB versus PNB:  $P = 0.044$ ). We used one-tailed tests because Portha et al. (2002) showed a stronger collective response for colonies containing brood and the direction of the variation was thus expected.

### Characterization of Behavioural Groups

#### Foraging behaviour of exploring ants

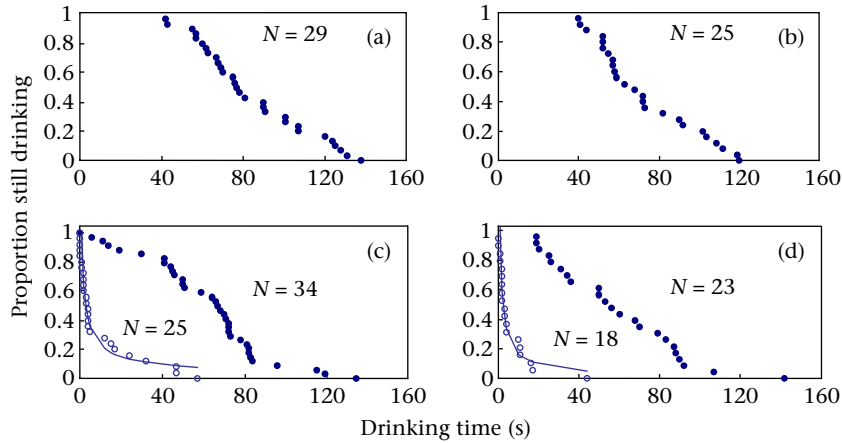
Because there were four exploring ants in the sucrose conditions (SB and SNB; Table 1), we analysed their behaviour only in the protein conditions (PB and PNB).

Exploring ants did not contribute to the transfer of information about food to the colony since they did not enter the nest after their foraging trip and were never seen laying a chemical trail. Most of the exploring ants were nondrinking individuals (PB: 17/24; PNB: 13/18; Fisher's exact test:  $P = 1.000$ ). Experimental conditions did not significantly influence the allocation of time in each step of the behavioural sequence of exploring ants (Mann-Whitney  $U$  test: drinking:  $U = 177.5$ ,  $P = 0.333$ ; number of drinks:  $U = 200.5$ ,  $P = 0.702$ ; exploring:  $U = 183$ ,  $P = 0.407$ ; leaving the arena:  $U = 172.5$ ,  $P = 0.275$ ;  $N_{PB} = 24$ ,  $N_{PNB} = 18$ , all NS). Exploring ants from the two conditions spent a similar amount of time on the foraging area (total time:  $U = 185$ ,  $N_{PB} = 24$ ,  $N_{PNB} = 18$ ,  $P = 0.438$ ). They devoted most of this time to exploring and leaving and individuals varied considerably in their persistence at searching as shown by the high standard deviations of exploring and leaving times (Table 1). Experimental conditions did not affect the ingested volume of food ( $U = 192.5$ ,  $N_{PB} = 24$ ,  $N_{PNB} = 18$ ,  $P = 0.551$ ), which appeared low compared to the crop capacity of worker ants.

We plotted the proportion of ants still drinking at the food source as a function of the time spent drinking (Fig. 3). Exploring ants of the two conditions were clearly distinct from returning ants with respect to their drinking behaviour (Fig. 3c, d). The proportion of exploring ants still drinking at the proteinaceous droplet ( $F(t)$ ) decreased exponentially with time and followed a law of the form:

$$F(t) = \theta t^{-\epsilon}$$

(if  $t > 1$  s, and with  $F(t) = 1$  if  $t < 1$  s).  $\theta$  is a constant reflecting the initial state; in this case at the beginning all ants were still drinking and then  $\theta$  was expected to equal 1;  $t$  is the time already spent drinking and  $\epsilon$  is a constant. The best fits of the experimental curves were obtained for the following parameter values: PB:  $\theta = 1.0064$  and  $\epsilon = 0.6353$  ( $R^2 = 0.91$ ); PNB:  $\theta = 1.0171$  and  $\epsilon = 0.7905$  ( $R^2 = 0.88$ ). This indicated that exploring ants had a high



**Figure 3.** Proportion of ants still drinking at the food source as a function of the time already spent drinking. (a) SB condition; (b) SNB condition; (c) PB condition; (d) PNB condition. See legend to Fig. 2 for details of conditions. ●: Returning ants; ○: exploring ants; line: best fit of experimental data using the model of decision for exploring ants (see text).

probability of stopping drinking per unit time, and that this probability was not constant but decreased over the time already spent drinking.

#### Foraging behaviour of returning ants

The behaviour of returning ants clearly differed from that of exploring ants. We compared exploring and returning ants only for the PB and PNB conditions, as there were too few in the SB and SNB conditions.

Returning ants did not differ from exploring ones in the total time they spent on the foraging area (Kruskal–Wallis test: PB:  $H_2 = 2.729$ ,  $P = 0.256$ ; PNB:  $H_2 = 1.844$ ,  $P = 0.398$ ) or in exploring time (PB:  $H_2 = 1.264$ ,  $P = 0.531$ ; PNB:  $H_2 = 1.726$ ,  $P = 0.422$ ) or number of drinks (PB:  $H_2 = 0.709$ ,  $P = 0.701$ ; PNB:  $H_2 = 1.009$ ,  $P = 0.604$ ). However, returning ants differed in the time spent drinking and in the ingested volume. Post hoc Dunn test comparisons (Table 1) revealed that differences arose from the returning ants drinking more than exploring ants in both PB (drinking:  $H_2 = 34.323$ ,  $P < 0.0001$ ; ingested volume:  $H_2 = 29.596$ ,  $P < 0.0001$ ) and PNB (drinking:  $H_2 = 27.452$ ,  $P < 0.0001$ ; ingested volume:  $H_2 = 24.974$ ,  $P < 0.0001$ ) conditions (Fig. 3c, d). Returning ants left the foraging area sooner than exploring ants even though the highly variable behaviour of exploring ants blurred statistical comparisons (PB:  $H_2 = 7.434$ ,  $P = 0.024$ ; PNB:  $H_2 = 3.447$ ,  $P = 0.128$ ; Table 1).

#### Trail-laying versus nontrail-laying ants

Trail-laying and nontrail-laying ants drank the same volume of food and spent the same time drinking, exploring and leaving the foraging area (Table 1) within each experimental condition. In addition, the time spent on each step of the foraging sequence did not differ significantly for trail-laying ants (Kruskal–Wallis test: total time:  $H_3 = 5.574$ ,  $P = 0.126$ ; drinking:  $H_3 = 3.140$ ,  $P = 0.325$ ; ingested volume:  $H_3 = 3.527$ ,  $P = 0.279$ ; exploring,  $H_3 = 0.673$ ,  $P = 0.885$ ; number of drinks:  $H_3 = 0.211$ ,  $P = 0.978$ ) or for nontrail-laying ants (total time:  $H_3 = 0.413$ ,  $P = 0.935$ ; drinking:  $H_3 = 5.134$ ,  $P = 0.131$ ; ingested volume:  $H_3 = 4.180$ ,  $P = 0.238$ ; exploring:  $H_3 = 0.119$ ,

$P = 0.989$ ; leaving time:  $H_3 = 2.845$ ,  $P = 0.468$ ; number of drinks:  $H_3 = 0.485$ ,  $P = 0.212$ ). Leaving time was higher for the trail-laying ants in the PB condition ( $H_3 = 7.998$ ,  $P = 0.046$ ), because four ants stopped to groom themselves after their last drink, to clean their antennae accidentally soiled by the liquid. When we removed these ants from the analysis, the leaving times of trail-laying ants no longer differed between the four conditions (corrected  $\bar{X} \pm SD$  without soiled ants =  $14 \pm 11$  s,  $N = 16$ ; Kruskal–Wallis test:  $H_3 = 0.918$ ,  $P = 0.776$ ).

The average individual trail-laying intensity did not differ significantly between the trail-laying returning scouts of the four conditions (SB:  $\bar{X} \pm SD = 1.05 \pm 0.62$  spots/cm,  $N = 29$ ; SNB:  $0.92 \pm 0.45$  spots/cm,  $N = 24$ ; PB:  $0.79 \pm 0.61$  spots/cm,  $N = 25$ ; PNB:  $0.79 \pm 0.32$  spots/cm,  $N = 21$ ; Kruskal–Wallis test:  $H_3 = 6.084$ ,  $P = 0.112$ ). However, the data suggested a trend for a stronger trail-laying behaviour for sucrose sources than for proteinaceous ones. This trend was even more conspicuous when we pooled data regardless of the presence of brood within the colony. The average individual trail-laying intensity  $\pm SD$  was  $1.00 \pm 0.55$  spots/cm ( $N = 53$ ) for sucrose sources and  $0.79 \pm 0.49$  spots/cm ( $N = 46$ ) for proteinaceous ones, even though there was still no statistical significance (unpaired  $t$  test:  $t_{97} = 1.956$ ,  $P = 0.053$ ).

## Individual Decisions

#### Drinking behaviour

As drinking times and ingested volumes did not differ between ants that did and did not lay a trail on their homeward trip, we pooled them in the following analysis. Both parameters were highly correlated and linearly related for returning ants in the four conditions (SB:  $Y = 0.0098X + 0.2784$ , Pearson correlation:  $r_{27} = 0.71$ ,  $P < 0.0001$ ; SNB:  $Y = 0.0111X + 0.1343$ ,  $r_{23} = 0.70$ ,  $P < 0.0001$ ; PB:  $Y = 0.0101X + 0.2403$ ,  $r_{32} = 0.68$ ,  $P < 0.0001$ ; PNB:  $Y = 0.0074X + 0.4429$ ,  $r_{21} = 0.56$ ,  $P < 0.005$ ). Both drinking time and ingested volume can thus be used to quantify the drinking behaviour of scouts to a food source that is a freely delivered solution. The four linear regressions had similar

slopes ( $F_{3,103} = 0.525$ , NS) and elevations ( $F_{3,106} = 0.24$ , NS), indicating that returning ants ingested food at a similar and constant rate in all conditions.

### Decision to return to the nest

To see whether foragers drink a critical volume before leaving the food source, we pooled data from trail-laying and nontrail-laying returning ants that were similar with respect to any other parameter. Figure 4 shows the proportion of returning ants still drinking at the food source as a function of ingested volume for the four conditions. The probability of a scout stopping drinking and returning to the nest was not constant but increased close to a critical volume  $V_c$ . Thus, the relative number of ants  $F(V)$  having drunk at least a volume  $V$  before returning to the nest fits the following equation:

$$F(V) = \frac{1}{1 + e^{\eta(V-V_c)}}$$

where the constant  $\eta$  indicates the sensitivity of ants to differences between  $V$  and  $V_c$ . The best fit to experimental data (Fig. 4) was found for the following values: SB:  $V_c = 1.10 \mu\text{l}$  and  $\eta = 4.35$  ( $R^2 = 0.96$ ); SNB:  $V_c = 0.91 \mu\text{l}$  and  $\eta = 4.30$  ( $R^2 = 0.87$ ); PB:  $V_c = 0.84 \mu\text{l}$  and  $\eta = 4.35$  ( $R^2 = 0.97$ ); PNB:  $V_c = 0.84 \mu\text{l}$  and  $\eta = 4.23$  ( $R^2 = 0.98$ ). The average ingested volumes and the critical volumes tended to decrease when ants fed on protein and when the colonies were deprived of brood, but this trend was not statistically significant (see above and Table 1). For  $V = V_c$ ,  $F(V) = 0.5$ ; in other words  $V_c$  corresponds to the volume drunk when half of the ants left the source. We could have used a Hill function (Goldbeter 1996) to fit the data with a similar agreement. In this case,  $F(V) = 1 - [V^s / (V^s + V_c^s)]$  where  $s$  is the parameter related to the sensitivity of ants to differences between  $V$  and  $V_c$ .

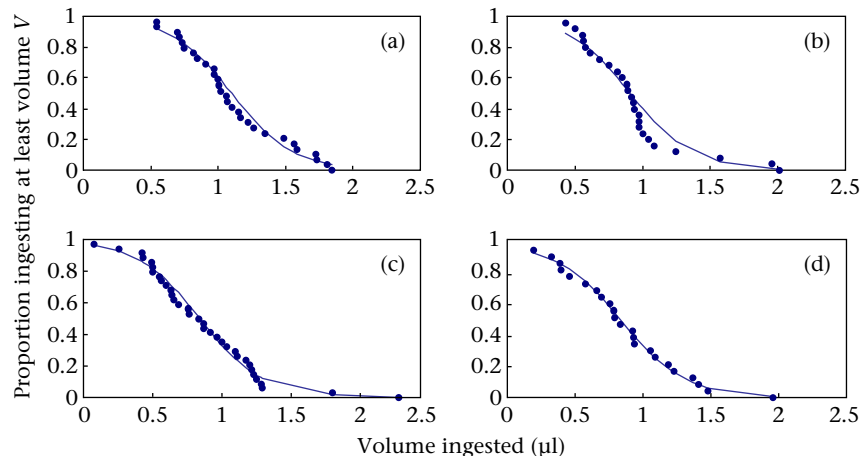
## DISCUSSION

The relative number of individuals involved in exploration, food retrieval or trail laying directly influences the

investment of the whole colony either in the exploration of areas or in the exploitation of the already discovered food source. Eventually this exploitation may be either more individual based or collective, depending on the proportion of trail-laying ants and then the trail recruitment strength. We have previously pointed out the variability in the collective exploitation of sugary or proteinaceous resources by *L. niger*, as well as the influence of brood on the self-organized foraging patterns of this species (Portha et al. 2002). Here, we have shown that *L. niger* can achieve this diversity at the collective level through changes in the occurrence of retrieving and trail-laying ants, without necessarily requiring quantitative changes at the individual level. The membership of an individual to a behavioural group depends on three key decisions influenced by food type and brood presence: drink at the food source, go back to the nest and lay a chemical trail.

### Decision to Drink

The decision to drink or not at the food droplet appeared to depend only on the nature of the food with no evidence of brood influence. A substantial fraction of the individuals did not ingest proteins, whereas nearly all ants drank at sugar droplets. It remains to be seen whether this reflects a stable specialization on a given food type (here sugars), as evidenced in other ant species (reviewed in Hölldobler & Wilson 1990). Exploring ants that drink little or none of the proteinaceous droplets reduce the flow of such foods to the nest. This may suggest that the proportion of proteins that foragers need to retrieve from food sources is low. Indeed, formicine ants such as *L. niger* could have a more carbohydrate-biased diet than previously thought (Tobin 1994), and may derive the bulk of their protein supply from aphid colonies, which provide them with amino acids through honeydew and with proteins through direct predation of aphids (Way 1963).



**Figure 4.** Proportion of returning ants still drinking as a function of the volume  $V$  of food already ingested. (a) SB condition,  $N = 29$ ; (b) SNB condition,  $N = 25$ ; (c) PB condition,  $N = 34$ ; (d) PNB condition,  $N = 23$ . See legend to Fig. 2 for details of conditions. ●: Experimental data; line: best fit of experimental data according to the model of Maillieux et al. (2000; see text).

## Decision to Return to the Nest

We have shown here that once an ant drinks, its decision to return to the nest relies on a single internal rule, the critical volume rule (Mailleux et al. 2000), whatever the type of food and the presence of brood in the colony. A scout needs to drink up to its critical volume of food before returning to the nest and this critical volume did not vary with the type of food and the presence of brood. This is noteworthy since, for instance, concentration (Bonser et al. 1998; Josens et al. 1998), viscosity (Josens et al. 1998), distance (Bonser et al. 1998) of the food and starvation level (Josens & Roces 2000) are known to influence the volume of food ingested.

## Decision to Lay a Chemical Trail

Our results show that the critical volume rule applies only to the decision to go back to the nest but not directly to that to lay a chemical trail, since trail-laying and nontrail-laying ants had similar ingested volumes. Being a returning ant was a prerequisite for the expression of trail-laying behaviour by the scouts but the decision to lay a trail depended on the type of food and the presence of brood. We failed to demonstrate any variation in individual trail-laying intensity, although our results suggest that trail-laying intensity may be stronger for ants feeding on sucrose than for ants feeding on protein. Mailleux et al. (2000) showed that *L. niger* determine the volume of a sugar solution at the colony level by the number of trail-laying ants rather than by the intensity of marking. How ants transfer information about the type of food needs further study.

An individual ant thus follows three consecutive steps of decision making using simple rules of thumb influenced by the nature of the food source and the presence of brood, allowing it to decide either to resume exploration, or to exploit the source and possibly lay a chemical trail. Determination of the relevant parameters of the food occurs mainly at the collective level by a modulation of the proportion of returning and trail-laying ants, resulting in the building of the appropriate foraging pattern through the self-organized process of mass recruitment. Indeed, the global proportions of trail-laying ants observed here fit perfectly with the increasing asymmetry of *L. niger* foraging patterns in identical conditions (Portha et al. 2002).

The natural context of foraging is that a number of potential food sources of greatly different characteristics are available for discovery and exploitation. Therefore, foraging efficiency should not be thought of only in terms of the optimal exploitation of a single food source through the balancing of food ingestion and information transfer to the nest (Roces 1990; Roces & Nùñez 1993). Another important issue is the balance between exploiting discovered sources and maintaining an efficient level of exploration of the foraging area, eventually leading to new discoveries. We have shown here that most of the foragers initiate recruitment to sucrose, leading to the strong collective exploitation of this highly rewarding and stable food in natural conditions (e.g. aphid colonies).

Conversely, protein food sources elicit weak feeding and recruitment responses that delay the recruitment and weaken the accuracy of trail following to these foods (Pasteels et al. 1987). This is in accordance with the opportunistic retrieval of prey, which are usually ephemeral and scattered small items, by individuals or small groups of foragers. Furthermore, foragers neglecting protein remain available for the discovery of additional or more profitable sources such as aphid colonies (Deneubourg et al. 1983). In addition, the increase in the proportion of trail-laying ants induced by the presence of brood can increase the exploitation of sugary foods and prey retrieval when the need for nutrients is high.

This combination of the individual assessment of simple cues from the food and the collective integration of the information provides a plastic and functional means to shape efficiently the foraging effort of the colony. *Lasius niger* has now proved to be able to integrate in its foraging decisions food-related parameters such as food type (this study), volume (Mailleux et al. 2000), quality (Beckers et al. 1993) and productivity (Mailleux et al. 2003), as well as nonfood-related factors such as brood presence (this study), physical environment (Detrain et al. 2001) and home range marking (Devigne & Detrain 2002). However, essential insights for the understanding of the recruitment process are still lacking (Jaffé 1980): we need more information about food and information processing within the nest to draw a coherent picture of the foraging system of this species.

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