



How do ants assess food volume?

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By comparing the behaviour of *Lasius niger* scouts at sucrose droplets of different volumes, we empirically identified the criterion used by each scout to assess the amount of food available as well as the rules governing its decision to lay a recruitment trail. When scouts discovered food volumes exceeding the capacity of their crop (3 or 6 μ l), 90% immediately returned to the nest laying a recruitment trail. In contrast, when smaller food droplets (0.3, 0.7 or 1 μ l) were offered, several scouts stayed on the foraging area, presumably exploring it for additional food. If unsuccessful, they returned to the nest without laying a trail. The droplet volume determined the percentage of trail-laying ants but had no influence on the intensity of marking when this was initiated. The key criterion that regulated the recruiting behaviour of scouts was their ability to ingest their own desired volume. This volume acted as a threshold triggering the trail-laying response of foragers. Collective regulation of foraging according to food size resulted from the interplay between the distribution of these desired volume thresholds among colony members and the food volume available. We relate some aspects of the foraging ecology of aphid-tending ants to this decision-making process.

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The ecological success of ants depends on their ability to adjust their foraging strategies to both resources and environmental constraints (for a review see Hölldobler & Wilson 1990). In this respect, foraging patterns of ant species that feed on honeydew or nectar are related to both the nutritional demand of ants (Sudd & Sudd 1985) and the characteristics of the food resources. Among the food-related factors that influence the ants' behaviour are the quality of the honeydew or artificial nectar (Crawford & Rissing 1983; Sudd & Sudd 1985; Breed et al. 1987, 1996a; Cherix 1987; de Biseau et al. 1992; Bonser et al. 1998; Völkl et al. 1999), the density of homopterans (Addicott 1979; Itioka & Tamiji 1996), the spatial distribution of resources (Breed et al. 1987) and the distance to the food (Breed et al. 1996a; Bonser et al. 1998). The quantity of food resources also plays a key role in the level of aphid attendance by ants (Breed et al. 1987, 1996a, b). In aphids, such production is related to the colony size and to species-specific differences in the excretion rate per individual (Völkl et al. 1999).

Research has focused on the functional and evolutionary significance of the observed patterns of resource use while behavioural mechanisms and decision-making processes that underlie such foraging strategies are often

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disregarded. Indeed, few studies have investigated how information about food characteristics is assessed locally by the individual scout, communicated to nestmates through chemical trails and integrated into an adaptive collective response.

We investigated how the volume of a food droplet is measured at the individual level, and is subsequently communicated to nestmates via recruitment trails, in the aphid-tending ant *Lasius niger*. Since the first steps of recruitment affect the final foraging patterns, we observed the behaviours of scouts. Several morphological and behavioural parameters were measured and compared for ants faced with different food volumes. We asked the following questions. (1) Do ants assess food volume? How does a scout behave in relation to a food volume that is either greater or smaller than the loading capacity of its crop? (2) Does the ant assess the absolute volume of food or does it make a relative measurement of food quantity based on some individual criteria? In the latter case, are these criteria related to a physiological parameter (e.g. the crop volume) or to a temporal one (e.g. the time spent finding and/or ingesting food)? (3) How does a scout pass on its individual measurement of food volume to nestmates and how does it modulate its trail-laying behaviour? We discuss these questions in the context of ant–aphid mutualism and point out the ecological consequences of the decision-making process.

METHODS

The black garden ant, *L. niger*, is a common Palaearctic species, which feeds on the honeydew of aphids such as *Tuberolachnus salignus* (Mittler 1958), *Aphis fabae* (El-Ziady & Kennedy 1956; Klingauf 1987) or *Metopeurum fuscoviride* (Völkl et al. 1999). We collected colonies of 1000–2000 workers in Brussels and reared them in the laboratory in plaster nests. Each nest (20 × 25 × 0.5 cm) was subdivided into four interconnected sections (16 × 4 × 0.5 cm) covered by a glass plate. Nests were regularly moistened and the room temperature was kept at 22 ± 3°C. Ants were fed three times a week with brown sugar solution (0.6 M) and dead cockroaches, *Periplaneta americana*.

Distribution of Food Weights

We determined the distribution of food weights ingested by foragers under conditions of ad libitum feeding. After 4 days of food deprivation, 100 ants were weighed individually to within 0.1 mg before and after drinking at a sucrose solution (0.6 M, volume 1 ml). The concentration of the sucrose solution was close to the total concentration of sugars occurring in droplets emitted by *Lasius*-attended aphids (29–350 mg/ml; Mittler 1958; Auclair 1963; Völkl et al. 1999).

To weigh each ant, we trapped it in a paper envelope (5 mg, 1 cm²) to prevent it from running. Preliminary experiments showed that ants that were anaesthetized (by frost or by carbon dioxide) before being weighed were less willing to feed on the sugar solution. We used these individual weights to obtain the distribution of food weights ingested by *L. niger* foragers; we converted them to volumes by considering the density of the food solution (1.2 g/ml). This distribution allowed us to determine the range of food volumes to be tested in the following experiments.

Responses to Different Food Volumes

We analysed the responses of ants to sucrose solution (0.6 M) for droplet volumes of 3 or 6 µl both of which exceeded the capacity of the crop. The experiment described above showed that 1.8 µl was the most that ants ingested when fed ad libitum. We also quantified behavioural responses of scouts to smaller droplets (0.3, 0.7 or 1 µl). These latter volumes were a similar size to honeydew droplets produced by aphids attended by *L. niger*. The average droplet size produced by *T. salignus* is 0.06 µl for first-instar larvae and at most 0.8 µl for apterous adults (Auclair 1963). We did not test volumes below 0.3 µl because of the relatively large loss of water by evaporation of such tiny droplets; the resulting increase in sucrose concentration could significantly alter the recruitment behaviour of scouts (Beckers et al. 1993).

We carried out assays on six nests that were deprived of food for 4 days. Within an experimental series, each volume tested was presented to a nest in independent assays at 1-week intervals. We randomly assigned the test

order of different volumes to each colony. One hour before each experiment, the nest was connected by a bridge (length 20 cm, width 0.5 cm) to a small foraging area (6 × 6 cm). At the beginning of this bridge, a drawbridge system (length 5 cm, width 0.5 cm) controlled the access of ants to the foraging area (Fig. 1). Ants could freely enter the area until one of them found the source. This scout had to climb on a metal stick before reaching the hanging droplet, the volume of which was controlled by a microcapillary. This narrow stick restricted access to the food droplet to only one ant at a time. As soon as this scout climbed on the stick, the droplet was renewed and we stopped the ants' flow to the area by raising the drawbridge. All other ants already present on the foraging area were removed. In between successive testing of scouts, the microcapillary was cleaned. Once the scout returned to the nest after having ingested the sugar solution, we gently removed it before it 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. Since chemical marks laid by the first recruiting ants could influence the behaviour of the following ones, we observed at most four ants in any one experiment. During the experiment, camera A was focused on the whole foraging area while camera B (magnification × 10) recorded ants as they walked in the middle of the bridge connecting the nest to the food source.

On these video recordings, we measured the amount of sugar solution ingested by the ants by comparing the abdomen size of each scout before and after it had drunk at the food droplet. The maximal length and maximal height of the abdomen were measured directly on video recordings from camera B that provided a magnified image of every ant walking on the bridge. Since the width of the abdomen could not be seen on these side-on images, we assessed it to be equal to the abdomen height. This approximation was supported by preliminary measurements on 40 ants fed ad libitum which showed that the average width:height ratio ± SD was 1.02 ± 0.10 and 1.01 ± 0.12 in ants with empty and filled gasters, respectively. We therefore approximated the abdomen to an ellipsoid to calculate the size of the abdomen of each scout before and after drinking and thus to assess the amount of food ingested.

We also measured the following time parameters. (1) The ant's walking velocity was measured in the middle of the bridge over a short portion (2.5 cm) on its way from and to the nest. (2) The searching time started when the scout crossed the middle of the bridge on its way to the foraging area and stopped when it found the droplet. (3) The drinking time lasted as long as the ant's mandibles were in contact with the sugar solution. (4) The giving-up time started when the ant stopped drinking until it was seen in the middle of the bridge on its way back to the nest. (5) The number of visits to the food source was the number of times that the ant was seen climbing on the metal stick to reach the droplet.

Trail-laying behaviour was assessed as follows. (6) The percentage of trail-laying scouts was the percentage of ants that had discovered the droplet that laid at least one trail mark over the whole length of the bridge. (7) The

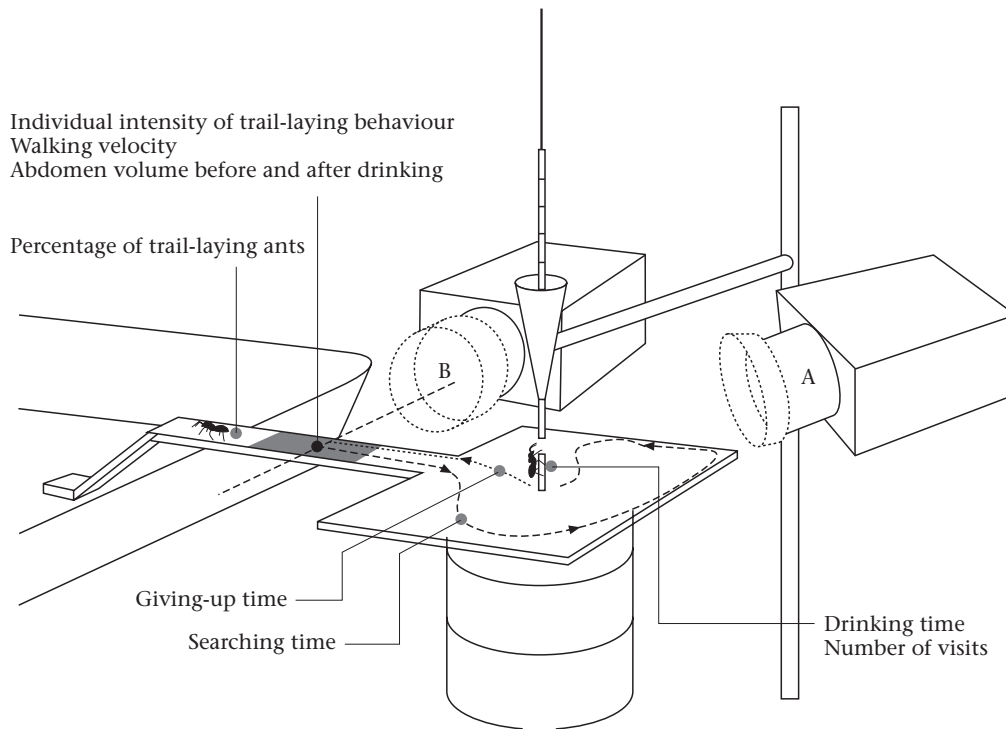


Figure 1. Experimental set-up. Camera A was focused on the whole foraging area while camera B recorded ants as they walked in the middle of the bridge (2.5-cm section). Behavioural and morphological parameters measured on the video recording are described in the text.

individual intensity of trail-laying behaviour for each trail-laying ant was assessed by the relative amount of time for which the ant was seen dragging its abdominal tip on the substrate. This behaviour was measured over a 2.5-cm section in the middle of the bridge. Preliminary experiments showed that observations limited to this 2.5-cm section provided a reliable estimate of the average marking over the whole length of the bridge.

Decision Criteria of Trail Recruitment

In the final experiments, we identified which food-size-related criteria determined when a scout stopped drinking and started recruiting nestmates. Two criteria could be measured by a scout: a temporal criterion such as the drinking time ('drinking time hypothesis') or a physiological criterion such as the food volume ingested ('ingested volume hypothesis').

Drinking time hypothesis

We quantified behaviours of 100 ants with the same experimental set-up and procedure as described above. Scouts were allowed to feed ad libitum but had to suck the droplet of sugar solution (0.6 M) through a cotton-wool cork inserted in the microcapillary, which artificially increased the drinking time. This design allowed us to dissociate the time spent drinking from the food volume ingested and thus to assess how the time spent at the food source may alter the behaviours of scouts.

Ingested volume hypothesis

Experiments with a freely delivered 3- μ l droplet allowed us to obtain the distribution of food ingested among ants that 'decided' to lay a trail. This volume distribution provided the experimental data from which we developed a theoretical model. This model assumed that the amount of food ingested determines when scouts leave the food source and recruit nestmates. We compared theoretical predictions of this model with experimental results obtained when small droplets of ca. 0.3, 0.7 or 1 μ l were presented to scouts. This comparative analysis allowed us to test the validity of the ingested volume hypothesis.

RESULTS

Distribution of Food Weights

Ant weights before drinking ($\bar{X} \pm SD = 2.0 \pm 0.4$ mg) and after drinking (2.9 ± 0.6 mg) were normally distributed (Fig. 2a; Kolmogorov-Smirnov test: ants with empty gaster: $D=0.07$, $N=100$, NS; ants that had drunk at the droplet: $D=0.08$, $N=100$, NS). The amounts of food individually ingested were also normally distributed (Fig. 2a; Kolmogorov-Smirnov test: $D=0.07$, $N=100$, NS). When allowed to drink ad libitum, ants drank a mean \pm SD of 0.9 ± 0.4 mg of sugar solution ($N=100$). However, a few ants (8%) did not feed at all or ingested quantities too small for us to detect.

No correlation was found between the weight of an ant before it reached the droplet and the amount of food

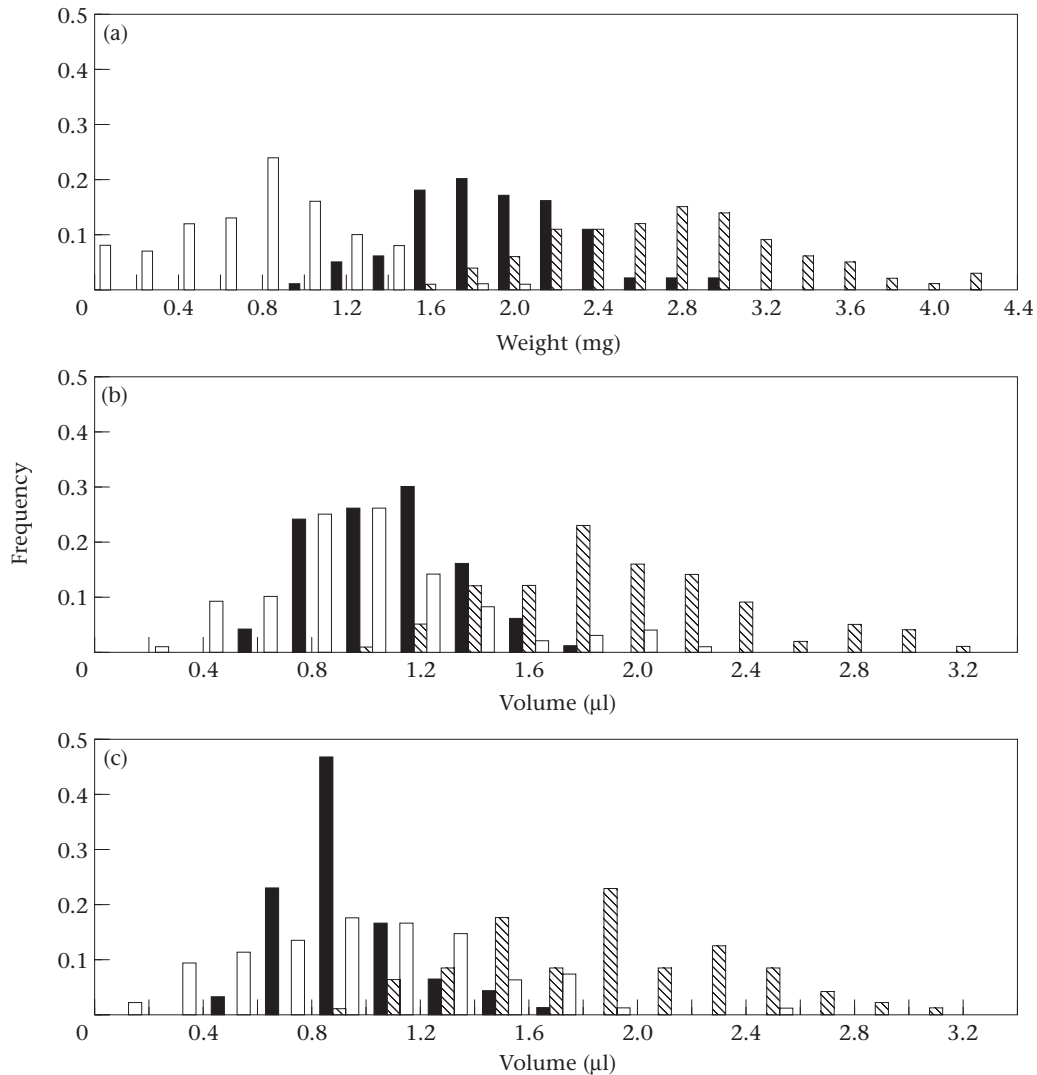


Figure 2. Distribution of ant weights or gaster volumes before (■) and after (▨) they drank a sugar solution and the distribution of ingested food amounts (□). (a) Sugar solution offered ad libitum ($N=100$ ants); (b) 3- μl droplet of sugar solution offered ($N=95$) and (c) sugar solution offered ad libitum through a cotton-wool cork ($N=97$).

ingested (Spearman rank correlation: $r_s=0.01$, $N=100$, NS). Therefore, the weight of a forager did not influence the amount of food it would ingest. An individual could drink large volumes of food solution, ingesting as much as its own weight. The largest weight gain observed was 2.2 mg, accounting for an ingested volume of ca. 1.8 μl .

Responses to Food Volumes

Droplets exceeding crop capacity

Since 1.8 μl was the maximum volume ingested, each scout that discovered a 3- μl droplet could fill its gaster to repletion. The abdomen volumes before and after drinking as well as the volumes ingested were normally distributed (Fig. 2b; Kolmogorov–Smirnov test: before: $D=0.08$, $N=95$, NS; after: $D=0.07$, $N=95$, NS; ingested volumes: $D=0.09$, $N=95$, NS). Ants drank on average 0.9 μl of sugar solution (Table 1). No correlation was found between the abdomen volume of an ant before drinking and the

volume of food ingested (Spearman rank correlation: $r_s=0.11$, $N=95$, NS).

Given the density of the food solution, the distribution of ingested food volumes observed at a 3- μl droplet (Fig. 2b) matched that of ingested weights observed in colonies fed ad libitum (Fig. 2a; Kolmogorov–Smirnov test: $D=0.11$, $N_1=95$, $N_2=100$, NS). This agreement between weight and volume data validated our method of assessing ingested volumes by direct measurement of abdomen size on video recordings and approximation of abdomen volume by an ellipsoid.

Scouts found the 3- μl droplet on average within 1 min at their arrival on the foraging area (Table 1). Individual searching time showed an exponential distribution ($R^2=0.90$) indicating that the probability per unit time for each scout to find the source was constant. Ants drank at the food source for 1.5 min on average (Table 1) with drinking time values being normally distributed (Kolmogorov–Smirnov test: $D=0.08$, $N=95$, NS). The bulk

Table 1. Behaviour of scouts at different volumes of sugar solution

	Droplet volume (μl)					CW*
	0.3	0.7	1	3	6	
Ingested food volume (μl)	0.2 \pm 0.1	0.5 \pm 0.2	0.7 \pm 0.3	0.9 \pm 0.4	1.0 \pm 0.5	0.9 \pm 0.4
No. of scouts observed	24	15	36	95	18	97
Velocity before drinking (cm/s)	1.8 \pm 0.8	1.5 \pm 0.6	2.1 \pm 1.1	1.8 \pm 0.9	1.6 \pm 0.7	NA
Velocity after drinking (cm/s)	1.9 \pm 0.7	1.9 \pm 1.1	1.5 \pm 0.7	1.6 \pm 0.6	1.8 \pm 0.5	NA
No. of scouts observed	24	15	36	93	17	103
Searching time (s)	70 \pm 73	64 \pm 48	68 \pm 61	57 \pm 71	56 \pm 46	67 \pm 68
Drinking time (s)	51 \pm 18	61 \pm 16	77 \pm 21	89 \pm 24	76 \pm 21	305 \pm 232
Giving-up time (s)	113 \pm 129	56 \pm 35	42 \pm 56	28 \pm 29	23 \pm 30	32 \pm 22
Number of visits at the food source	2.4 \pm 2.7	1.7 \pm 2.0	1.3 \pm 2.0	1.1 \pm 1.2	1.0 \pm 1.0	1.1 \pm 1.2
No. of scouts observed	26	15	39	95	18	97
Percentage of trail-laying ants	14	17	70	91	97	86
No. of scouts observed	42	29	60	112	36	111
Trail laying intensity (%)	14 \pm 6	4 \pm 9	12 \pm 9	14 \pm 11	10 \pm 11	10 \pm 9
No. of trail-laying ants	6	5	42	102	35	95

Means are given \pm SD. NA: Data not available.

*Sugar solution offered ad libitum through a cotton-wool cork.

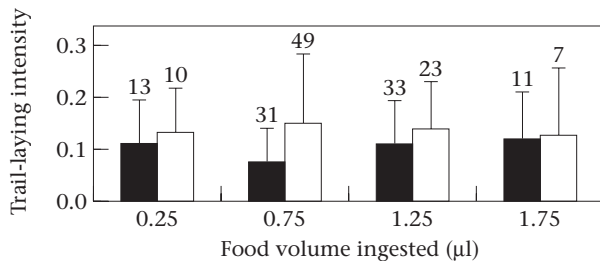


Figure 3. Intensity of individual trail-laying behaviour (proportion of time that the ant was seen dragging its abdominal tip on the substrate) as a function of food volume ingested by the scout. □: Ants that drank a 3- μl sugar solution; ■: ants that fed ad libitum through a cotton-wool cork. The number of scouts observed is given above each bar. Lines above bars indicate SD.

of the droplet was ingested at once as shown by the average number of visits to the food source (Table 1). No significant correlation was found between an ant's drinking time and the food volume it had ingested (Spearman rank correlation: $r_s=0.13$, $N=95$, NS). After having drunk at the droplet, ants left the foraging area quickly, within 28 s on average, and returned straight to the nest (Table 1). These giving-up times were also exponentially distributed ($R^2=0.94$) indicating that the probability per unit time to return to the nest was constant.

There were no correlations between these time parameters (walking velocity, searching, drinking and giving-up times). Nor were they correlated with the abdomen sizes of the scouts (before and after drinking) or with the food volumes they had ingested.

The majority of ants that found the 3- μl droplet participated in the trail recruitment of nestmates: 91% of the observed ants dragged their abdominal tip at least once on their way back to the nest (Table 1). The intensity of the individual trail-laying behaviour did not differ with the food volume ingested by the ants (Fig. 3; Kruskal-Wallis test with data separated in four categories of 0.50 μl : $H_3=7.2$, $N=89$, NS).

No significant change was observed when the droplet was 6 μl (Table 1). The ingested volumes (Table 1) were not statistically different for a 3- or 6- μl food source (Mann-Whitney test: $Z=1.1$, $N_1=18$, $N_2=95$, NS). Similar time values (velocity, searching, drinking and giving-up times) were observed for both droplet volumes (Mann-Whitney test: velocity before drinking: $Z=-0.1$, $N_1=17$, $N_2=93$, NS; velocity after drinking: $Z=1.6$, $N_1=17$, $N_2=93$, NS; searching time: $Z=0.3$, $N_1=18$, $N_2=95$, NS; drinking time: $Z=-0.3$, $N_1=18$, $N_2=95$, NS; giving-up time: $Z=-0.3$, $N_1=18$, $N_2=95$, NS). Moreover, the same percentage of trail-laying ants (chi-square test: $\chi^2_1=1.1$, NS) and the same individual intensity of chemical marking (Mann-Whitney test: $Z=1.6$, $N_1=35$, $N_2=102$, NS) were observed as for a 3- μl droplet.

Therefore, behaviours of scouts tested with different volumes were similar as long as the food offered exceeded the crop capacity of an ant.

Droplets below crop capacity

We investigated how scouts behaved when they found smaller volumes of food droplets that were below the capacity of their crop. The abdomen volumes before drinking were similar in the different experiments (0.3–6 μl ; Kruskal-Wallis test: $H_4=8.2$, NS) but the average volume ingested increased significantly with the amount of food delivered (Table 1; Kruskal-Wallis test: $H_4=70.4$, $P<0.001$). For all volumes tested, no correlation was found between the abdomen volume of an ant before it reached the food source and the volume of sugar solution ingested (Spearman rank correlation: 0.3 μl : $r_s=-0.22$, $N=24$, NS; 0.7 μl : $r_s=-0.01$, $N=15$, NS; 1 μl : $r_s=0.22$, $N=36$, NS).

Ants' velocities (either to or from the nest) were similar for the different droplet volumes (Table 1; Kruskal-Wallis test from 0.3 to 6 μl : from the nest: $H_4=7.1$, NS; to the nest: $H_4=8.9$, NS). Whatever the size of the droplet, it took about 1 min for a scout to find the food source (Table 1; Kruskal-Wallis test: $H_4=6.6$, NS). This suggested

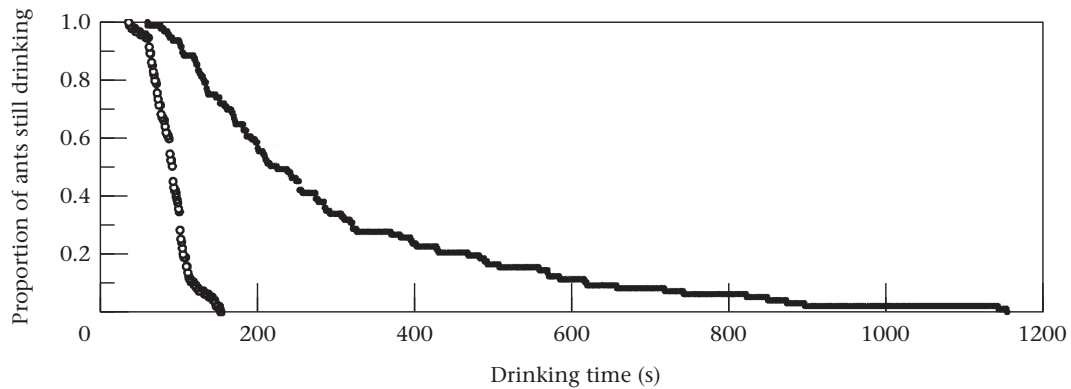


Figure 4. Proportion of ants still drinking at the food source as a function of drinking times. The food volume offered was delivered either freely (○; 3 μ l, $N=95$) or ad libitum through a cotton-wool cork (●; $N=97$).

that there was no perception of the sugar solution at a distance by ants and that increasing the size of the droplet did not make it easier to find. As for the volumes ingested, the average drinking time increased significantly with the volume of the droplet offered (Table 1; Kruskal–Wallis test: $H_4=57.1$, $P<0.001$). The giving-up time of ants and their number of visits to the food source decreased significantly with increasing droplet sizes (Table 1; Kruskal–Wallis test: giving-up time: $H_4=32.7$, $P<0.001$; number of visits: $H_4=21.4$, $P<0.001$). Longer giving-up times at smaller droplets reflected the behaviour of some scouts which circled the source and kept on searching for additional food.

The percentage of trail-laying ants at small droplets was always lower than that observed at a 3- or 6- μ l droplet (Table 1). This percentage increased significantly as a function of the droplet size (chi-square test from 0.3 to 6 μ l: $\chi_4^2=28.8$, $P<0.001$). Among those ants that laid a trail, the individual intensity of marking did not vary with the volume of the droplet offered (Kruskal–Wallis test from 0.3 to 6 μ l: $H_4=7.0$, NS). On average, trail-laying ants were seen dragging their abdominal tip over the substrate during 4–14% of the time spent on their way back to the nest. The volume offered thus influenced significantly the percentage of trail-laying ants but did not alter the individual intensity of their marking.

Decision Criteria of Trail Recruitment

Drinking time hypothesis

The distribution of volumes ingested by ants that had sucked the sugar solution through a cotton-wool cork was not different from that observed when food was freely delivered (see Fig. 2c; Kolmogorov–Smirnov test: $D=0.12$, $N_1=95$, $N_2=97$, NS). In contrast, drinking times increased dramatically (Fig. 4) and lasted more than three times as long on average as at a 3- or 6- μ l droplet (Table 1; Kruskal–Wallis test: $H_2=11.9$, $P<0.001$).

The searching and giving-up times were not influenced by the difficulty of ingesting food since they did not differ from those measured when a 3- or 6- μ l droplet was freely delivered (Kruskal–Wallis test: searching time: $H_2=4.9$, NS; giving-up time: $H_2=5.2$, NS).

Despite their difficulty in ingesting food through the cotton-wool cork, the majority of ants laid a trail (86%) when returning from feeding. Neither the percentage of trail-laying ants nor their average intensity of marking was different from those observed when the food (3 or 6 μ l) was freely delivered (chi-square test: percentage of trail-laying ants: $\chi_2^2=2.6$, NS; Kruskal–Wallis test: intensity of marking: $H_2=5.0$, NS). The latter results showed that the time spent drinking at the food source did not influence the probability of an ant laying a recruitment trail. This suggested that the drinking time was not the criterion that determined recruitment by *L. niger* scouts.

Ingested volume hypothesis

The alternative ingested volume hypothesis assumes that the ability of a scout to ingest a desired volume V determines whether it lays a recruitment trail. Each ant has a desired volume of its own which is not necessarily equal to the maximal capacity of its crop. The distribution of desired volumes in the population of foragers is given by the food volumes ingested by trail-laying ants when allowed to feed to repletion (as in the experiment carried out with a droplet of 3 μ l). This experimental distribution can be fitted by a model that assumes that the probability of a scout stopping to drink and starting to lay a recruitment trail is not constant but increases close to a critical volume V_c . According to this hypothesis, the relative number of ants (Fr) having ingested at least a volume V before laying a trail is:

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

where the constant η indicates the sensitivity of ants to differences between V and V_c .

For the 3- μ l experiment, the best fit to the experimental data (Fig. 5) was obtained for the following parameter values: $V_c=0.9$ μ l and $\eta=4.3$ ($R^2=0.97$). For a larger droplet of 6 μ l, a good fit was obtained for similar values of $V_c=1.0$ and $\eta=3.5$ ($R^2=0.96$). This model remained valid when the ants' ingestion was slowed down by a cotton-wool cork with values of $V_c=1.0$ and $\eta=4.1$ ($R^2=0.98$; see Fig. 5).

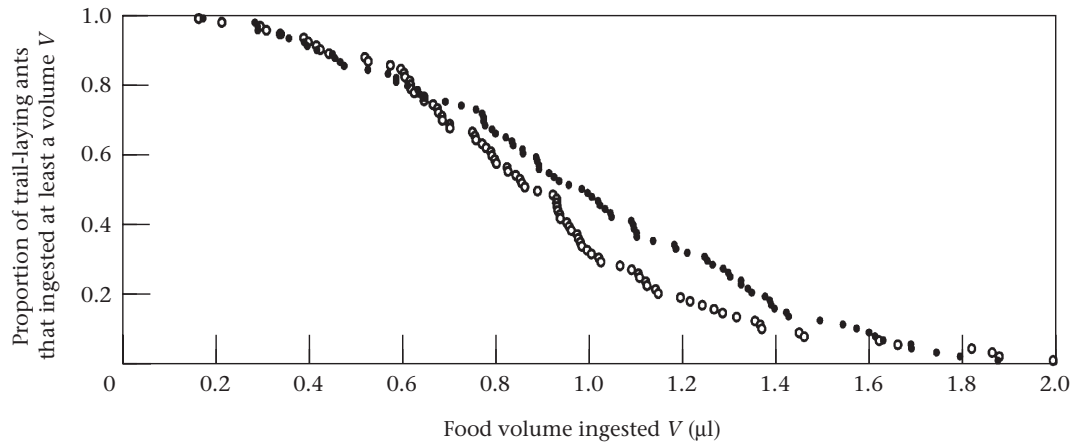


Figure 5. Proportion of trail-laying ants that ingested at least a volume V as a function of the volume ingested when the droplet was delivered freely (\circ ; 3- μl droplet, $N=89$) or through a cotton-wool cork (\bullet ; ad libitum, $N=88$).

Table 2. Percentage of trail-laying ants that had ingested a volume of at most 0.3, 0.7, 1 or 3 μl as a function of the droplet volume

Droplet volume (μl)	Volume ingested (μl)			
	0.3	0.7	1	3
0.3	14			
0.7	5	21		
1	10	31	57	
3	5	32	67	91
6	5	35	50	97

According to the model, the percentages of satisfied ants that decide to lay a trail after having ingested a volume (V) should be similar whatever the droplet volume (D), even under conditions of limited food availability (0.3, 0.7, 1 μl). This seemed to be the case (Table 2). The percentages of trail-laying ants that had ingested volumes of at most 0.3 μl did not vary with the droplet size (range 5–14%; chi-square test: $\chi^2_4=9.1$, NS). Similarly,

the percentages of ants that laid a trail after having ingested at most 0.7 or 1 μl were independent of the droplet volume (chi-square test: 0.7 μl : $\chi^2_3=1.5$, NS; 1 μl : $\chi^2_2=2.8$, NS).

The assumption that trail-laying ants were satisfied individuals that had ingested their desired volumes was confirmed by the following behavioural observations. Trail-laying and nontrail-laying ants behaved similarly when searching for food and spent similar times before discovering the droplet (Mann–Whitney test: 0.3 μl : $U=50$, $N_1=4$, $N_2=22$, NS; 0.7 μl : $U=17$, $N_1=3$, $N_2=12$, NS; 1 μl : $U=172$, $N_1=12$, $N_2=27$, NS). But they differed in their giving-up times since trail-laying ants always left the foraging area more quickly than nontrail-laying ones (Table 3; Mann–Whitney test: 0.3 μl : $U=80.5$, $N_1=4$, $N_2=22$, $P<0.05$; 0.7 μl : $U=36.0$, $N_1=3$, $N_2=12$, $P<0.05$; 1 μl : $U=250.0$, $N_1=12$, $N_2=27$, $P<0.05$). Whatever the droplet volume D , trail-laying ants returned straight to the nest with a short giving-up time of ca. 30 s (Kruskal–Wallis test from 0.3 to 6 μl : $H_4=8.7$, NS). In contrast, nontrail-laying ants circled the food supply and repeatedly climbed on to the stick. They also visited the food

Table 3. Behaviours ($\bar{X}\pm\text{SD}$) of trail-laying and nontrail-laying ants presented with droplets of different volumes

	Droplet volume (μl)				
	0.3	0.7	1	3	6
Searching time (s)					
Trail-laying ants	82±104	73±86	70±62	55±68	56±46
Nontrail-laying ants	68±69	63±46	58±55	86±112	NA
Giving-up time (s)					
Trail-laying ants	28±12	24±13	31±34	27±30	23±30
Nontrail-laying ants	128±135	63±35	74±94	38±20	NA
Number of visits					
Trail-laying ants	1.0±0.0	1.3±0.6	1.1±0.4	1.0±0.2	1.0±1.0
Nontrail-laying ants	2.6±1.7	1.9±1.1	2.1±1.7	1.0±0.0	NA
Number of trail-laying ants	4	3	27	89	18
Number of nontrail-laying ants	22	12	12	6	1

NA: Data not available.

source more (Table 3; Mann–Whitney test: 0.3 μ l: $U=74.0$, $N_1=4$, $N_2=22$, $P<0.05$; 0.7 μ l: $U=33.0$, $N_1=3$, $N_2=12$, $P<0.05$; 1 μ l: $U=230.0$, $N_1=12$, $N_2=27$, $P<0.05$). This confirmed that nontrail-laying ants were unsatisfied individuals that searched for additional food to reach their desired volumes before returning to the nest. The level of dissatisfaction of these nontrail-laying ants seemed to depend on the filling of their gaster as suggested by the decrease in giving-up time and number of visits for larger droplet volumes (Kruskal–Wallis test from 0.3 to 3 μ l: giving-up time: $H_2=8.7$, $P<0.02$; number of visits: $H_2=8.1$, $P<0.02$). When the volume offered was not limiting (3- μ l droplet), ca. 10% of individuals returned to the nest without laying a trail (Table 1). In every respect, these ants behaved as trail-laying individuals since they drank similar volumes (Mann–Whitney test: $Z=1.5$, $N_1=6$, $N_2=89$, NS), did not revisit the source (Table 3; Mann–Whitney test: $Z=0.98$, $N_1=6$, $N_2=89$, NS) and left the foraging area with similar giving-up times (Table 3; Mann–Whitney test: $Z=1.6$, $N_1=6$, $N_2=89$, NS).

DISCUSSION

The impact of food characteristics on the recruiting behaviour of individuals has been extensively reported in the literature (e.g. Hantgartner 1969; Bonser et al. 1998; Völkl et al. 1999; for a review see Detrain et al. 1999). Our study provides the first direct evidence of the criterion used by *L. niger* scouts to assess the amount of liquid food available, and that governs their decision to lay a recruitment trail. This criterion was internal and based on the ability of the ant to ingest a desired volume. This volume was not a fixed value shared by all members of the colony but varied from one individual to another. It was not related to any morphological parameter of scouts such as their abdomen size before drinking. Whether this desired volume is constant over the life span of the ant is still unknown. It might also fluctuate in relation to several internal or external factors such as the ant's demand for food (Sudd & Sudd 1985), the distance from the nest to food patches (Breed et al. 1996b), the sucrose concentration (Josens et al. 1998) or the presence of amino acids in the carbohydrate solution (Lanza et al. 1992).

Regulation of recruitment according to food volume follows a scenario based on a rule of thumb. When a scout discovered a food source larger than its own desired volume, it drank, returned to the nest and laid a recruitment trail. When a food droplet smaller than its desired volume was found, the scout stayed longer on the foraging area searching for additional food sources. If unsuccessful, it returned to the nest without laying a trail. The desired volume acts as a threshold which determines the response of foragers (Page et al. 1997; Huang & Robinson 1999). The interplay between the colony distribution of thresholds and the volume of the food droplet sets the proportion of scouts that will lay a recruitment trail. Together with a decrease in giving-up time, this explains why the global recruitment rate increases with the size of liquid food sources as reported in several species (e.g. *Paraponera clavata*: Breed et al. 1987, 1996a, b; *Myrmica sabuleti*: de Biseau & Pasteels 1994). A few ants did not lay

a trail even when a large amount of food was available (e.g. in the 3- μ l experiment). In all respects, these individuals behaved similarly to trail-laying scouts and ingested similar amounts of food. This suggests that, regardless of the amount of food available, a subgroup of scouts might never lay a trail or only after several successful trips to the food source.

Numerous studies have investigated how the chemical composition of food sources influences individual trail-laying behaviour (Verhaeghe 1982; Beckers et al. 1993; de Biseau & Pasteels 1994). In *L. niger*, scouts modulate the intensity of their marking according to the sucrose concentration (Beckers et al. 1993) but not according to food volume (this study). In addition, since their giving-up times were independent of the droplet size, each trail-laying ant conveyed information to nestmates at a similar rate, however large the food source. This suggests that the coding of quantitative information such as the food volume occurs at the colony level, not at the individual level, by a regulation of the proportion of trail-laying ants. The prey size, another quantitative parameter, is also assessed collectively but involves an individual decision rule based on the ability of each scout to retrieve the prey (Detrain & Deneubourg 1997).

The decision-making process shown here provides a framework to interpret some aspects of the foraging ecology of aphid-tending ants. In addition to their preferences for some sugars and amino acids (Lanza et al. 1992), ants are known to select aphid populations that produce large amounts of honeydew, especially when food resources are limited (Addicott 1978). The amount of honeydew available to the ants is directly related to the size and renewal rate of droplets emitted per individual as well as to the size, the number and density of aphids in the colony. Scouts may be limited in their ability to assess and integrate all these features of feeding sites in order to modulate their recruitment behaviour and to select the most rewarding aphid colony. The recruitment decision we have shown might appear to be crude. Nevertheless, it allows the ant colony to adjust the number of tending ants to the productivity of aphid colonies. If aphids are numerous and/or have a high production rate per individual, the likelihood of foragers ingesting their desired volumes and laying a trail will be high. This increase in the percentage of trail-laying ants with available honeydew will result in a preferential allocation of foragers to the most productive site. In contrast, if aphids are scarce or have not yet renewed their droplets when recruited ants reach the feeding site, several ants will not reach their desired volume and will start searching for additional food sources. These ants may then discover a neighbouring aphid population and refocus the foraging activity of the colony. The inability of foragers to ingest their desired volume might also explain the reported shift from mutualistic to predation behaviour on aphid colonies that produce little honeydew (Sakata 1994, 1995).

The foraging dynamics of the colony are also shaped by the aphid number and/or density, the size of honeydew droplets and their rate of renewal. All these parameters can alter the time spent by the foragers to reach their desired volume. Since most scouts have to stimulate

several aphids, for similar total amounts of honeydew produced by aphid populations, *L. niger* will preferentially exploit large and/or high-density colonies in which ants encounter aphids more quickly. Similarly, populations of aphids that excrete large droplets per individual and thus allow ants to be replete after one or two visits (e.g. *T. salignus* in Mittler 1958) may be preferred to larger colonies emitting small droplets per individual. The ants may also neglect aphid species that take longer to replace droplets after being tended since the temporary exhaustion of honeydew may induce these ants to visit a colony with a higher rate of honeydew renewal.

Ant foraging patterns can therefore be regarded as the interplay between individual recruitment decisions, which are governed by simple functional criteria, and environmental parameters that alter the frequency of recruitment cycles. The behavioural complexity observed at the colony level is thus reduced to the behavioural simplicity of individuals with limited cognitive abilities. Instead of assessing all parameters related to a food source, foragers can track environmental changes and generate adaptive decisions at the collective level by measuring a few relevant cues.

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