

Ethology / Éthologie

Food transport in ants: Do *Lasius niger* foragers maximize their individual load?

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Abstract

The decision for a *Lasius niger* forager to lay a chemical trail and launch recruitment to a food source is governed by an internal individual threshold. The value of this threshold triggering chemical communication is not set by the maximal capacity of the crop. Actually, trail-laying ants are still able to drink additional food encountered on their homeward journey. The partial filling of the crop by trail-laying ants may be a means for the ants to shorten foraging trips and to speed up the information updating within the nest. Moreover, by partially filling their crop, foragers keep a potential for sampling resources and for tasting other encountered food sources. **To cite this article:** A.-C. Mailleux et al., *C. R. Biologies 332 (2009)*.

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Résumé

Transport de nourriture chez les fourmis : Les fourrageuses de *Lasius niger* maximisent-elles leur charge individuelle ?
Chez la fourmi *Lasius niger*, la décision de tracer une piste chimique et de lancer un recrutement vers une source de nourriture repose sur un seuil de réponse interne et propre à chaque individu. La valeur de ce seuil déclenchant la communication chimique n'est pas déterminée par la capacité maximale du jabot (estomac social) de la fourmi. En effet, les fourmis recruteuses déposant une piste chimique de recrutement sont encore capables de boire à une source découverte lors de leur retour vers le nid. Ce remplissage partiel du jabot des recruteuses leur permettrait de gagner du temps afin d'accélérer le transfert d'informations actualisées vers le nid. De plus, en se remplissant partiellement, les fourmis gardent la possibilité d'échantillonner d'autres sources nouvellement rencontrées qui pourraient s'avérer plus profitables. **Pour citer cet article :** A.-C. Mailleux et al., *C. R. Biologies 332 (2009)*.

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Mots-clés : Recrutement ; *Lasius niger* ; Seuil de réponse ; Chargement

1. Introduction

The whole organisation of insect societies relies on the variability of individuals in their propensity to carry out some tasks and to respond to internal and external stimuli. In ants, individuals are characterised by their

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own response threshold to a given stimulus [1–4], this response threshold being determined by several internal factors such as genetic predisposition [5,6], the age [7], the physiology [8], the caste belonging [9–11] or the individual experience [12,13]. In the case of foraging, such thresholds can also vary in relation to other factors such as demand for food [14–17], distance from nest to food patches [18], or presence of amino acids in honeydew [19].

In previous papers, we have shown that, in *Lasius niger*, an internal response threshold governs the decision of an ant forager to launch recruitment to a newly discovered food source [20–23]. Indeed, when a scout finds a sucrose solution droplet, the decision to inform nestmates by the laying of a recruitment trail is an all-or-nothing response, based on the ability of this scout to ingest a food volume acting as a threshold. If the scout cannot obtain this volume, it goes back to the nest without recruiting. Information about the food volume is thus conveyed to the society through the percentage of trail-laying individual among returning ants.

The threshold determining the trail-laying response of foragers is not a fixed value shared by all members of the colony, but varied from one individual to another. However, we do not know whether this critical response threshold is determined by physiological constraints such as the maximal capacity of the crop. Therefore, in the present article, we investigate through an experimental approach, and with the help of a model, whether the rule of thumb evidenced for a single food source remains valid when a scout has to collect two droplets to reach its threshold volume, the first droplet on the foraging area and the second one placed on their way back to the nest. To this end, we extend the one-source experiment initially developed by Mailleux [20, 21] to a double source set-up.

The present article raises the following questions: Are the foraging activities of ants modified as they encounter a new source on their way back to the nest? Do they retrieve this additional food load? Is the value of the threshold volume triggering chemical recruitment set by the maximal capacity of the crop? We studied the ingested volume, the intensity and frequency of the trail laying behaviour, and the time spent foraging before, between and after ants found the two sources.

2. Material and methods

2.1. The experiment

Experiments were carried out on the black garden ant, *Lasius niger*, a common Palearctic species, which

feeds on the honeydew of aphids like *Tuberolachnus salignus*, *Aphis fabae* or *Metopeurum fuscoviride* [24–31]. We dug colonies of 1000–2000 workers out of earth slopes in Brussels and reared them in the laboratory in plaster nests at a room temperature of $22 \pm 3^\circ\text{C}$. These colonies were queenless. Each nest ($20 \times 25 \times 0.5$ cm) was divided in four interconnected sections ($16 \times 4 \times 0.5$ cm) covered by a red glass plate. Nests were regularly moistened and were fed three times a week with brown sugar solution (0.6 M) and dead cockroaches (*Periplaneta americana*). We carried out assays on four colonies that were starved for four days.

In mass-recruiting ant species such as *Lasius niger*, the first scouts that lay a trail back to the nest play a key role in the triggering and the building-up of collective foraging patterns [21,32–34]. Consequently, we focused our observations on the foraging behaviour of these individuals. We choose to deliver a $0.7 \mu\text{l}$ droplet at each food source as this volume was comparable to the maximal amount of honeydew actually produced per aphid individual [24–26]. This volume was also lower than the average desired volume and it compelled most foragers to search for additional sources to reach their desired volume [20]. Drinking at the first droplet is then expected to satisfy only a small fraction of the ants that will lay a trail as they leave the area.

One hour before each experiment, the nest was connected by a bridge to a small foraging area. A scout was allowed to drink a first droplet of sucrose solution ($0.7 \mu\text{l}$, 0.6 M) at a single micropipette hanging in the centre of the square foraging area ($6 \text{ cm} \times 6 \text{ cm}$). The concentration of the sucrose solution was close to the total concentration of sugars occurring in droplets emitted by *Lasius*-attended aphids [24–26]. Once the scout had ingested the first droplet, the scout could either return to the nest or keep on searching for additional food droplets (see Fig. 1). On its homeward journey, a second droplet ($0.7 \mu\text{l}$, 0.6 M) was delivered by another micropipette hanging in the middle of the bridge, 9 cm from the first one. The second source was introduced after the first one. It was out of reach of the scout when it was walking on the bridge in the direction of the foraging area. More than 95% of the foragers found the second micropipette on their way back to the nest, and thus, had the opportunity to drink, or not, at this second food droplet. We analyzed only the behaviour of those foragers that had found the two food sources. Each of the 63 observed scouts was tested only once. After the passage of one scout, the bridge was renewed.

We studied the ingested volume, the intensity and frequency of the trail laying behaviour and, the foraging time of ants before, between and after that ants found

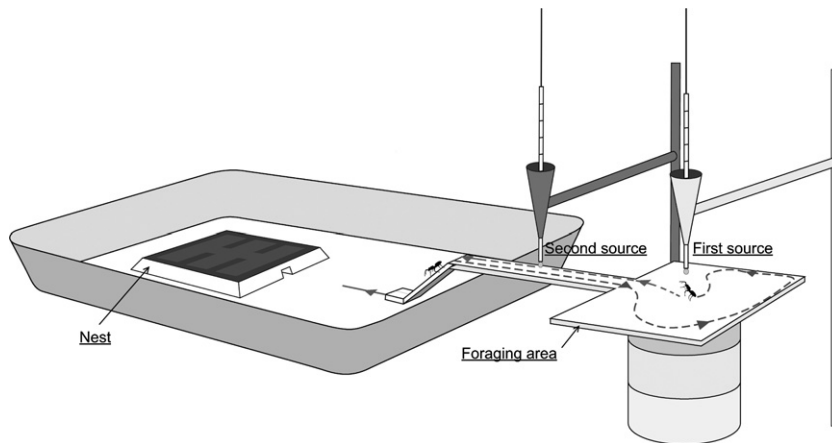


Fig. 1. Experimental set-up. Behavioural and morphological parameters measured are described in the text.

the two sources. During the experiment, a first camera was focused on the whole foraging area while another camera was focused on the bridge connecting the nest to the food source. The latter camera was travelling along the bridge and followed the ants' movements (magnification $\times 15$). On these magnified images, we measured the following first set of parameters (1-2-3) that aim at relating the trail-laying behaviour of scouts to the amount of food ingested and are measured before and after ants drank at the second micropipette: (1) The percentage of trail-laying scouts that have laid at least one trail mark over the bridge; (2) The individual trail intensity for each trail-laying ant. This intensity was assessed by the relative amount of time during which the ant was seen dragging its abdominal tip on a 3 cm section of the bridge, at the beginning of the bridge. This 3 cm distance was over the mean distance between two trail markings (around 2 cm). Indeed, previous studies have found out a good correlation between the intensity of the trail and the occurrence of gaster dragging over the substrate [32,33]; (3) The amount of sugar solution ingested by the ants was estimated by comparing the gaster size of each scout before and after it had drunk at the food droplet (for details of measurement methods see [20]). A second set of parameters (4-5-6) characterize the time allocation by scouts to each foraging step: (4) The time spent drinking at the first source; (5) The time spent between the two sources. It starts when ant stop to drink at the first source and ends when they drink at the second source; (6) The time spent drinking at the second source.

2.2. The model

We used the model previously described in Maillieux et al. [20–22], and we applied it to this two-source

situation. The difference was that all ants leaving the foraging area in the direction of the nest still had the opportunity to ingest additional food on their way back to the nest, i.e. when the decision to recruit (lay a trail) is made. With this model, we simulated the behavioural sequence of a scout using parameter values drawn out from the single source experiment [20–22]. For each second spent at the food source, an ant is assumed to ingest a volume ΔV ($= 10^{-2} \mu\text{l}$ for *L. niger*). The probability of stopping ingesting food and leaving the source $S(V)$ grows with the volume already ingested (V) and follows a response threshold function: $S(V) = (\eta \Delta V) / (1 + e^{\eta(V - V_c)})$ where the constant η ($= 4.3$) measures the sensitivity of ants to the difference between the actually ingested volume V and the threshold V_c , V_c is defined as the threshold volume for which 50% of the ant population has reached their threshold volume and left the food droplet. η is drawn from the experimental threshold curve [20–22]. Among those ants that succeed in ingesting their threshold volume, a majority (90%), but not all individuals, engage in trail-laying behaviour. The remaining 10% do not lay a trail during their homeward trip while they behave as trail-laying foragers and ingest similar amounts of food.

Monte-Carlo simulations based on the behavioural rules described above were conducted for two small food droplets ($0.7 \mu\text{l}$), each of them being below the desired volume of 50% of foragers in these experimental conditions ($V_c = 1 \mu\text{l}$, see [20–22]). These Monte-Carlo simulations predicted the fraction of trail-laying ants that left the foraging area after having visited 1 or 2 micropipettes and the distribution of food volumes ingested by the ants. Therefore, the global distribution of food volumes ingested by all ants having discovered the food source was calculated and the global fraction of

Table 1

Three behavioural groups were defined. After drinking at the first micropipette, the TL1 laid trail on the first section of the bridge whilst nTL1 did not lay trail on this section. After drinking at the second micropipette, some of nTL1 started to lay a chemical trail on the second section of the bridge.

Behavioural groups	Experimental results				Theoretical results	
	At the 1 st source	At the 2 nd source	Total	<i>N</i>	Total	<i>N</i>
Fraction of trail-laying ants	38%	46%	84%	63	79%	500 000
Food volume ingested by all ants	0.47 ± 0.25	0.28 ± 0.20	0.75 ± 0.30	63	0.85 ± 0.30	500 000
Food volume ingested by TL1	0.49 ± 0.26 ^a	0.20 ± 0.14 ^b	0.69 ± 0.31	24	0.8 ± 0.30	190 000
Food volume ingested by TL2	0.43 ± 0.24 ^a	0.33 ± 0.20 ^c	0.76 ± 0.27	29	0.81 ± 0.29	294 570
Food volume ingested by nTL2	0.55 ± 0.22 ^a	0.31 ± 0.24 ^c	0.86 ± 0.26	10	1.10 ± 0.29	104 570

Fraction of trail-laying ants and food volume (µl) ingested at the first and second sources. Means are given ± S.D., *N* = number of scouts observed. The comparisons between the data of one column were made with Kruskal–Wallis tests and the post-hoc Dunn's multiple comparison tests were calculated when *p* was greater than 0.05. The comparisons between the data of two different columns were made with Friedman test. Data with the same letters were not statistically different (*p* = 0.05). Theoretical values and experimental data were not statistically different.

trail-laying ants was predicted. We then compared resulting theoretical values to experimental data from the two micropipettes set-up to test the validity of the behavioural rules implemented in our model.

3. Results

3.1. The experiment

3.1.1. Trail-laying and food volume ingested

On average, ants drank 0.47 ± 0.25 µl at the first food source ($X \pm S.D.$, Table 1). After drinking, when they return to the nest, 38% of them (called TL1) were observed laying trail on the first section of the bridge. Trail-laying ants (TL1) and nontrail-laying ants (nTL1) drank similar volumes at the first micropipette (volume ingested by TL1: 0.49 ± 0.26 µl; by nTL1: 0.46 ± 0.24 µl, Mann–Withney test, $U = 436.5$, NS). All ants (TL1 and nTL1) that found the second micropipette on their way back to the nest were observed plunging their mandibles into the droplet solution and drinking an additional food volume. On average, this additional volume corresponded to about 37% of the total food amount ingested by ants. TL1 ingested less food at the second source than nTL1 (volume ingested by TL1: 0.20 ± 0.14 µl; by nTL1: 0.33 ± 0.20 µl, Mann–Withney test, $U = 287$, $p < 0.03$, NS). TL1 continued to lay a trail after drinking at the second source. No significant correlation was observed between the food volume ingested at the first and second micropipette (Spearman rank correlation for TL1: $r_s = -0.17$, $N = 24$, NS; for nTL1: $r_s = -0.08$, $N = 39$, NS).

After having drunk at the second micropipette, when they returned to the nest, 74% of nTL1 started to lay a chemical trail on the second section of the bridge and were so-called TL2 (see Table 1). However, 26% of the nTL1 that found out additional food were still unsat-

isfied and did not lay a trail and were so-called nTL2. These nTL2 probably belong to a group of workers that never lay trails whatever the volume of the discovered food source offered. They were called persistent nontrail-layers and account for 10 to 20% of the scouts' population as shown in previous studies [19].

The trail intensity varied from one individual to another. It was not correlated to the gaster size. For TL1, the mean number of trail marks laid per cm were not statistically different before (0.16 ± 0.07) and after (0.11 ± 0.08) having drunk at the second micropipette (Wilcoxon matched-pairs signed-ranks test $T^+ = 729$, NS) and were not correlated ($r_s = -0.04$, $N = 24$, NS). This result suggested that the variability in the trail-laying intensity does not rely on behavioural specialisation in which some ants recruit more intensively than other scouts. Likewise, for TL2, the trail intensity of TL2 (0.11 ± 0.09) was not statistically different from the trail intensity laid by TL1 individuals before (Mann–Whitney test: $U = 236.5$, NS) or after drinking at the second micropipette (Mann–Whitney: $U = 258.5$, NS).

3.1.2. Time parameters

On average, ants spent about 51 ± 12 sec drinking at the first food source. These drinking times at the first micropipette were similar for trail-laying ants (TL1) and nontrail-laying ants (nTL1) (for TL1: 52 ± 13 sec; for nTL1: 50 ± 11 sec, unpaired *t*-test, $t = 0.65$, $DF = 61$, NS). The time spent walking between the two sources was significantly shorter for the ants that reached their desired volume at the first micropipette (TL1) than for unsatisfied ants (for TL1: 58 ± 33 sec; for nTL1: 134 ± 87 sec, Mann–Whitney test, $U = 175$, $p < 0.0001$). The longer time elapsed between the two sources reflected the exploratory behaviour of unsatisfied scouts, which circled around the first source and kept on searching for additional food [19]. All behavioural groups

Table 2

Time allocation to each foraging steps for all the observed behavioural groups.

Behavioural groups	Experimental results					Theoretical results	
	Drinking time at the 1 st source (s)	Time spent between the two sources (s)	Drinking time at the 2 nd source (s)	Total time (s)	<i>N</i>	Total time (s)	<i>N</i>
All ants	51 ± 12	105 ± 80	23 ± 11	178 ± 83	63	176 ± 85	500 000
TL1	52 ± 13 ^a	58 ± 33 ^b	20 ± 13 ^f	130 ± 39 ^f	24	120 ± 39	190 000
TL2	51 ± 40 ^a	141 ± 89 ^c	25 ± 10 ^f	212 ± 92 ^g	29	219 ± 119	294 570
nTL2	46 ± 12 ^a	114 ± 83 ^c	20 ± 12 ^f	180 ± 81	10	186 ± 96	104 570

Means are given ± S.D., *N* = number of scouts observed. The comparisons between the data of one column were made with Kruskal–Wallis tests and the post-hoc Dunn's multiple comparison tests were calculated when *p* was greater than 0.05. The comparisons between the data of two different columns were made with Friedman test. Data with the same letters are not statistically different (*p* = 0.05). Theoretical values and experimental data were not statistically different.

(TL1, TL2, nTL2, Table 2) spent similar times drinking at the second micropipette.

The food volume ingested are linearly related to the drinking times at the first micropipette ($r_s = 0.22$, $N = 63$, $p < 0.05$). A similar linear regression was observed between the food volume ingested and the drinking times at the second micropipette ($r_s = 0.31$, $N = 63$, $p < 0.05$). The slopes and intercepts of the two linear regressions were not statistically different (*F* tests comparing linear regressions; slopes: $F(1, 122) = 0.01$, NS; intercepts: $F(1, 122) = 0.26$, NS). The food volume ingested = $0.006 * \text{time to drink} + 0.15$ ($r_s = 0.46$, $N = 126$, $p < 0.05$). This result showed that ants drank at the first and second micropipettes with similar intake rates (food volume ingested/time to drink) on average. The intake rates at the first source ($r_s = 0.12$, $N = 63$, NS) and at the second source ($r_s = 0.09$, $N = 63$, NS) were not affected by ant gaster size before drinking. This suggested that the physiological ability in fluid ingestion (intake rate) was an individual characteristic but inter-individual differences were not linked to their crop size.

3.2. The model

The theoretical results are shown in Table 1. From the model, the percentage of satisfied ants that decide to lay a trail after having ingested a volume (*V*) at the two micropipettes was 79%. It is similar to its experimental counterparts. Likewise, the theoretical distributions of the two behavioural parameters, i.e. the food volumes ingested by ants and their exploitation times- were not statistically different from the experimental ones. In conclusion, the general quantitative agreement between theoretical and empirical data validates the behavioural algorithms used in the model.

4. Discussion

Previous experiments [20–22] showed that a rule based on individual thresholds exists in the food recruitment of *Lasius niger*. Only scouts that succeed in ingesting a volume of sugar solution (the stimulus) exceeding their desired volume (the threshold) return to the nest and lay a recruitment trail. Here, we show that this desired volume threshold is not set by a physiological constraint such as the maximal capacity of the crop. Indeed, trail-laying ants are still able to drink additional food encountered on their homeward journey.

One may wonder why trail-laying ants do not drink the entire of the bulk at the first source (partial loading) and why “satisfied” individuals seem to “waste” time by drinking an additional volume corresponding to about 37% of the total amount of ingested food.

Three explanations for the partial loading can be given: (A) *a minimization of transport costs*: in honeybees, the partial loading of crop food carrying costs that can be very high for flying insects [35–37]. With ants, this explanation cannot account for partial crop loading since, unlike flying insects, walking ants that carry food internally within the crop are characterized by very low energy costs of food transport [38,39]. (B) *A prevention of overcrowding at foraging sites*: Burd hypothesized that in leaf-cutting ants, the cutting of smaller leaf fragments may reduce exploitation times and thus congestion at foraging sites [40,41]. In our experiments, congestion of foraging sites cannot explain why food load in the crop is not maximized, only one ant was allowed to access to the foraging area and to the food droplet. (C) *A quicker information transfer*: Our results strongly suggest that foragers reduce feeding time to return early from food sources and to recruit nestmates more rapidly. As the recruitment process follows snowball dynamics, a forager might decide to partially load its crop and

thus to reduce its own individual energy intake in order to speed up information transfer to nestmates. This strategy favours cooperation at foraging sites and will result in greater food gain in the long term [35,36,42–46]. Such behaviour, that seems suboptimal for solitary foragers, may in fact maximise colony-level efficiency in mass-recruiting ants [40–42,47].

However, the rapid transfer of information is not the only drive for partial food loading since all foragers decide to delay their return back to the nest when they meet and drink at the food droplet. This additional food intake is not surprising for nontrail laying ants since it allows them to reach their desired volume. Conversely, one may wonder why trail-laying ants, that are assumed to be satisfied, “waste” time by drinking at this new resource. Therefore, one should evoke a complementary hypothesis for this “wasted time” that is the improvement of information. We hypothesize that, by not filling up their crop, *Lasius niger* ants keep the potential for tasting other possibly more valuable resources. This allows scouts to increase the accuracy of their assessment of environmental resources and may possibly lead to a readjustment of the intensity/duration of recruiting signals. In the field, honeydew quantities and qualities vary widely between aphids depend on their species, plant host, age or spatial location [24,26,27]. In the face of such variability, ants draw advantages in tasting several food sources to update information and to get a reliable assessment of the resources profitability. Through sampling, ants may adjust more accurately the intensity of trail marks to food source characteristics. Afterwards, the best food sources are then selected by the whole colony simply by competition between recruitment signals differing in intensity and/or duration. Therefore ants may possibly redirect foraging routes toward the most profitable food sites. In the future, one should test the foraging behaviour of ants faced with two food sources differing by their composition (sugar or amino acid concentration...) using the same experimental procedure.

Our previous study [20,21] provided a direct support to the rule of thumb used by foragers to assess the volume of a single food source. The key criterion that triggers the trail-laying behaviour of foragers is their ability to ingest their own desired volume. Information about the total volume of a food source is thus conveyed to the society by the percentage of trail-layers among returning ants. The good agreement between theory and experiments in a set-up where foraging ants are faced to a new additional food source on their way back to the nest confirms the robustness of the behavioural rule that we evidenced in *L. niger*. In this article, we show

that this “rule of thumb” described before remains valid when foragers have to update their informations about the food source on the return to the nest.

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