

Triggering and persistence of trail-laying in foragers of the ant *Lasius niger*

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Abstract

In the ant *Lasius niger*, the ability to ingest their own desired volume is the key criterion that rules the recruiting behaviour of scouts. This volume acts as a threshold triggering the trail-laying response of foragers. In this paper, we show that this desired volume is specific to each individual and is kept constant over successive trips to a food source. This individual specificity contrasts with the variability of all individual desired volumes within the colony. In this study, it is also shown that, among *L. niger* foragers, 14% never participate in the formation of the chemical pathway and never lay a trail over successive trips. Among the others foragers, interindividual differences in the persistence of trail-laying behaviour over successive trips are observed but do not rely on an individual specialisation, in which some ants would lay a trail more frequently and persistently than other scouts. We discuss how an individual in the foraging behaviour can play an essential role in the regulation of food retrieval dynamics.

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1. Introduction

In social insects, the specialisation of individuals in one set of tasks is known to be associated with age, size or morphology (for a review in ants see Oster and Wilson, 1978; Hölldobler and Wilson, 1990; Seeley, 1995). Research on the organisation of labour within ant colonies has also investigated how individuals of the same temporal or physical caste may vary in their “task profile”, i.e. their propensity and persistence in carrying out a task. In ants, individual specialisation has been reported in several social activities such as nest construction (Gordon, 1989), nest emigration (Abraham et al., 1984; Cerda and Reneta, 1992), brood retrieval (Verron, 1976; Lenoir, 1981) and foraging (Agbogba and Howse, 1992; de Biseau and Pasteels, 2000; Portha et al., 2004). Variability in task performance can be

explained by qualitative and quantitative variations in individual responsiveness (Robson and Traniello, 1998).

Several experiments support the idea that individuals are characterised by different response thresholds to a given stimulus (Beshers and Fewell, 2001). A variety of internal factors such as genetic predisposition, morphology, age or individual experience can determine the threshold of each individual (Robinson, 1992; Robinson and Page, 1995; Page et al., 1997; Fewell and Page, 1999, 2000; Weidenmüller, 2001; Weidenmüller et al., 2002). For instance, young honey bees treated with juvenile hormone show a lower response threshold to alarm (Robinson, 1992). In the polymorphic ant *Pheidole pallidula*, majors have higher threshold responses than minor workers to recruiting stimuli in at least two activities, foraging and defence (Detrain and Pasteels, 1991, 1992).

In a previous paper, Maillieux et al. (2000) compared the behaviour of scouts of the aphid tending ant *Lasius niger* at sucrose droplets of different volume. We have

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demonstrated that the key criterion for recruitment is the scout's ability to ingest its own desired volume of sucrose solution. If ants can ingest this desired volume, they lay down a trail and recruit nestmates but, if they cannot obtain this volume after a brief exploration of the foraging area, they go back to the nest without initiating recruitment. The desired volume acts as a response threshold that triggers the trail-laying response of foragers and the response is all-or-none. We have also observed that the intensity of chemical marking is independent of the ingested volume (Maillieux et al., 2000). The proportion of trail-laying individuals among returning ants convey information about the total food volume available to the colony. Collective regulation of foraging results from the interplay between the distribution of these desired volume thresholds among colony members and the food volume available.

Here we investigate whether a behavioural specialisation exists among *L. niger* foragers in their trail-laying activity. More precisely, we investigate whether some individuals are more frequently and persistently engaged in the laying of the recruitment trail than other foragers. Because the ability to ingest a desired volume acts as a response threshold ruling the decision of *L. niger* scouts to lay a trail (Maillieux et al., 2000), we focused on the individual specificity and constancy of this desired volume over successive trips to the food source.

2. Methods

L. niger is a common Palaearctic ant species feeding on honeydew from aphids, scale insects and nectaries (Mittler, 1958; Pontin, 1958; Auclair, 1963; Lawton and Heads, 1984; Sakata, 1994, 1995; Völkl et al., 1999; Offenberg, 2001). 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 ($20 \times 25 \times 0.5 \text{ cm}^3$) was divided in four interconnected sections ($16 \times 4 \times 0.5 \text{ cm}^3$) 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 studied how the foraging response of an ant changes over five successive visits to the food source using the same experimental procedure developed in Maillieux et al. (2000). The food source consisted of a droplet of sucrose solution (0.6 M). As the offered food volume ($3 \mu\text{l}$) exceeded the maximum capacity of a *L. niger* crop, each ant was able to ingest its desired volume and hence to lay a recruitment trail. The food droplet was renewed between successive visits of the scout. We carried out assays on five colonies that were starved for 4 days. At 1 h before each experiment, the nest was connected by a bridge to a small foraging area.

At the proximal end of this bridge, a drawbridge system controlled the access of ants to the area. Foragers were given free access until one of them found the source. The first ant drinking at the droplet was marked with a spot of paint applied to the abdomen, while the other scouts were removed from the foraging area. The drawbridge was used to allow the marked scout to do five successive trips to the food and to exclude all others foragers. Thus, we isolated the foraging behaviour of one scout by limiting the influence of congeners (e.g. by chemical marking or tactile interactions). We observed 35 ants and renewed the bridge between each experiment. Each scout was tested only one time, except those that never laid a trail over five trips; those were tested again 1 week later.

During the experiment, camera A was focused on the whole foraging area while camera B (magnification $\times 20$) 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 (for details of measurement methods see Maillieux et al., 2000). We also measured the following parameters for each of the five trips: (1) the ants' walking velocity averaged on their way to and from the nest; (2) the drinking time lasting as long as the ant's mandibles were in contact with the sugar solution; (3) the trip time taken by the ant to go to the food source, find it, return to the nest and unload itself through trophallaxis but did not include the drinking time; (4) the individual intensity of trail-laying behaviour for each trail-laying ant, 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 12-cm section in the middle of the bridge; (5) the percentage of trail-laying scouts that laid at least one trail mark over the bridge.

3. Results

3.1. Morphological and behavioural parameters of foragers on their first visit to the source

The ant's abdomen volumes before and after drinking as well as the volumes ingested were normally distributed (Kolmogorov–Smirnov test: before: $D = 0.15$, $N = 35$, NS; after: $D = 0.18$, $N = 35$, NS; ingested volumes: $D = 0.17$, $N = 35$, NS) on their first visit to the food source. Ants drank an average of $0.7 \mu\text{l}$ of sugar solution (Table 1). They drank at the food source for 78 s on average (Table 1) with drinking time values being normally distributed (Kolmogorov–Smirnov test: $D = 0.11$, $N = 35$, NS). Individual trip time showed an exponential distribution ($r^2 = 0.81$) indicating that the probability per unit time for each scout to find the

Table 1
Behaviours of 35 scouts over five trips to the food source

Number of the trip to the food source	1	2	3	4	5	Statistical tests
Abdomen volume before drinking (μl)	0.9 \pm 0.3	1.0 \pm 0.3	1.0 \pm 0.3	0.9 \pm 0.3	0.9 \pm 0.2	$F_{4,170} = 0.25$, NS
Ingested food volume (μl)	0.7 \pm 0.3	0.6 \pm 0.4	0.6 \pm 0.4	0.6 \pm 0.4	0.6 \pm 0.3	$F_{4,170} = 0.35$, NS
Drinking time (s)	78.1 \pm 34.9	66.0 \pm 28.7	70.1 \pm 36.1	78.8 \pm 45.1	73.7 \pm 34.6	$F_{4,170} = 0.27$, NS
Trip time (s)	441.7 \pm 195.3	275.9 \pm 117.2	227.5 \pm 89.3	211.3 \pm 95.6	NA	$F_{4,170} = 6.74$, $P < 0.001$
Velocity of ants (cm/s)	1.7 \pm 0.6	2.1 \pm 0.7	2.1 \pm 0.6	2.4 \pm 0.9	2.5 \pm 0.8	$F_{4,170} = 24.39$, $P < 0.001$
Trail laying intensity [\rightarrow S]	NA	0.05 \pm 0.05(16)	0.06 \pm 0.06(26)	0.05 \pm 0.06(24)	0.05 \pm 0.06(21)	$F_{4,170} = 0.16$, NS
Trail laying intensity [\rightarrow N]	0.10 \pm 0.06(30)	0.06 \pm 0.06(27)	0.07 \pm 0.08(24)	0.06 \pm 0.05(21)	0.06 \pm 0.06(15)	$F_{4,170} = 3.14$, $P = 0.02$
Percentage of trail-laying ants [\rightarrow S]	NA	46	74	69	60	
Percentage of trail-laying ants [\rightarrow N]	86	77	69	60	43	$Q = 48.00$, $P < 0.01^*$

Means \pm SD are given for all parameters. For each trip, the trail-laying intensity and the percentage of trail-laying ants are measured on their way to the nest [\rightarrow N] and to the source [\rightarrow S] (the number of observed ants is given between brackets). The parameters were compared over the five trips by means of Anova tests (except * = Cochran test). P -values and results of the statistics for each parameter ($\alpha = 0.05$) are given in the last column. NA: data not available. NS: no statistically significant differences.

source was constant. There was no correlation between the trip and drinking times. Nor were these correlated with the abdomen sizes of the scouts (before and after drinking) or with the ingested food volumes. All these results were consistent with those observed by Maillieux et al. (2000, 2003).

3.2. Travelling and drinking behaviours compared over a series of five trips

The drinking behaviour of the observed individuals was independent of the number of their trip (Table 1). Indeed, when taking into account all these foragers and their abdomen volumes before and after drinking, their ingested food volume and their drinking times showed distributions and average values that were similar, whatever the number of the visit to the food source. The food volumes ingested by each scout over its successive trips to the food were related to one other (Fig. 1, Kendall's coefficient of concordance test: $W_x = 0.57$, $N = 35$, $P < 0.001$). Thus, there was an interindividual variability of the ingested volumes, but they were specific to each individual and rather constant over successive trips. Similarly, the drinking times of each scout were related to each other over the five visits to the source (Kendall's coefficient of concordance test: $W_x = 0.73$, $N = 35$, $P < 0.001$). There was no correlation between individual ingested volume and the abdomen size before drinking, nor between any time parameters (drinking times, trip times, walking velocity, no significant Spearman rank correlation between all parameters compared two by two). While the drinking behaviour of a forager did not change over successive trips, travel time decreased because scouts ran faster (Table 1, Page test, $z = 6.24$, $P < 0.001$) and spent shorter trip times (Page test, $z = 5.35$, $P < 0.001$). This last result showed that scouts found their way more easily and turned less around the source.

3.3. Trail-laying behaviours compared over a series of five trips

The majority of scouts that found the 3 μl droplet participated in the trail recruitment of nestmates: 86% of the observed ants—called trail-layers (TL)—dragged their abdominal tip at least once on the first passage back to the nest (Table 1). This percentage of scouts laying a trail was similar to that reported in previous studies (Maillieux et al., 2000; Portha et al., 2004). A minority of scouts (14%, $N = 35$) that found the droplet did not lay a trail either on their first return to the nest nor over the following successive trips between the source and the nest. Therefore, we called them persistent non trail-layers (PNTL) in the following sections of this paper.

Morphological and behavioural parameters of TL ($N = 30$) were not statistically different from those of PNTL ($N = 5$) (Table 2: Kolmogorov–Smirnov: no significant differences for all parameters except the drinking times of the second trip, $P = 0.01$). Over successive trips, TL as well as PNTL travelled in a more straightforward way with an increased velocity. This reduced the round trip time for TL (Page test: velocities, $z = 4.98$, $P < 0.001$; trip time, $z = 5.34$, $P < 0.001$) and for PNTL (Page test: walking velocities, $z = 2.59$, $P < 0.005$; trip time, $z = 3.54$, $P < 0.001$). For PNTL, these behavioural changes could not be due to any increase of the trail intensity over the successive trips; these ants may have progressively learned the way back to the nest.

3.3.1. Persistent non trail-layers

We tested the persistence of non trail-laying on a longer time scale. The behaviour of PNTL was similar after 1 week (Kolmogorov–Smirnov: no significant differences for all parameters). If we assume that all ants had an equal probability of not laying a trail, this

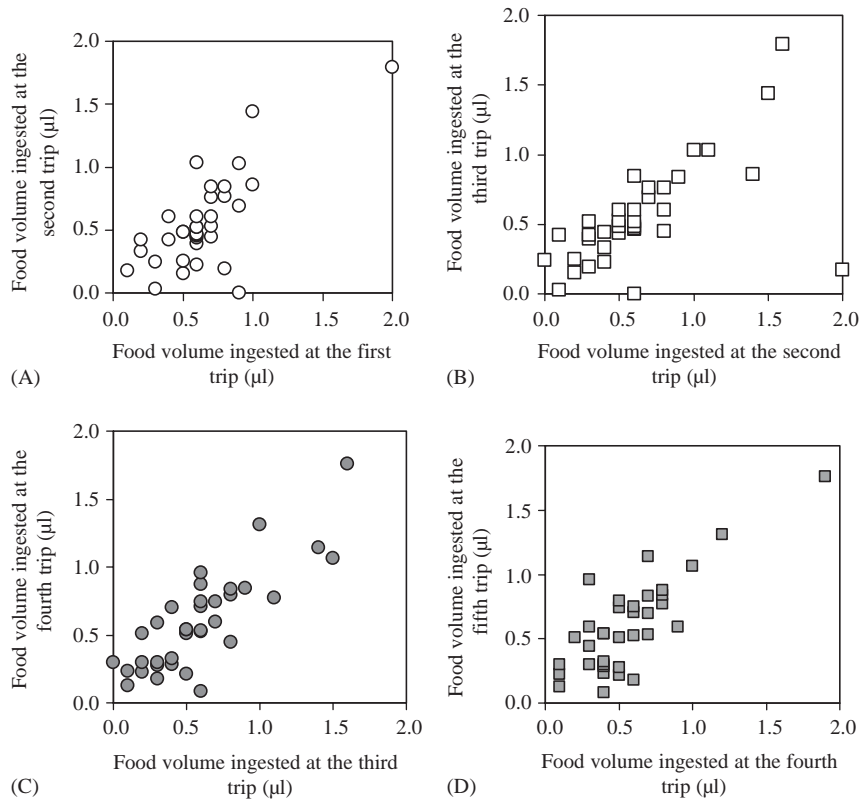


Fig. 1. Evolution of ingested food volumes over successive trips to the food source ($N = 35$). Relation between food volumes ingested at the first and at the second trip (Fig. 2a: ○), at the second and third trip (Fig. 2b: □), at the third and fourth trip (Fig. 2c: ●), at the fourth and fifth trips (Fig. 2d: ■).

Table 2
Behaviours of trail-layers and persistent non trail-layers over five successive trips to the food source

Number of the trip		1	2	3	4	5	Friedman tests
Abdomen volume before drinking (μl)	PNTL	1.0 ± 0.2	1.1 ± 0.2	1.0 ± 0.2	1.0 ± 0.2	1.0 ± 0.2	$Fr = 3.40$, NS
	TL	0.9 ± 0.3	0.9 ± 0.3	0.9 ± 0.3	0.9 ± 0.3	0.9 ± 0.3	$Fr = 1.83$, NS
	K-S test	$D = 0.36$, NS	$D = 0.33$, NS	$D = 0.30$, NS	$D = 0.43$, NS	$D = 0.50$, NS	
Ingested food volume (μl)	PNTL	0.5 ± 0.2	0.4 ± 0.1	0.4 ± 0.2	0.4 ± 0.2	0.5 ± 0.1	$Fr = 2.84$, NS
	TL	0.7 ± 0.3	0.6 ± 0.4	0.6 ± 0.4	0.6 ± 0.4	0.6 ± 0.4	$Fr = 6.05$, NS
	K-S test	$D = 0.40$, NS	$D = 0.27$, NS	$D = 0.43$, NS	$D = 0.43$, NS	$D = 0.30$, NS	
Drinking time (s)	PNTL	47.5 ± 14.0	44.1 ± 16.3	50.2 ± 14.1	48.6 ± 28.0	65.2 ± 36.2	$Fr = 7.69$, NS
	TL	83.2 ± 34.8	69.6 ± 28.8	73.5 ± 37.7	83.8 ± 46.4	75.1 ± 34.8	$Fr = 2.79$, NS
	K-S test	$D = 0.57$, NS	$D = 0.73$, $P = 0.01$	$D = 0.37$, NS	$D = 0.50$, NS	$D = 0.30$, NS	
Trip time (s)	PNTL	435.8 ± 55.1	271.1 ± 44.5	231.6 ± 128.2	163.8 ± 30.7	NA	$Fr = 22.32$, $P < 0.01$
	TL	442.7 ± 210.5	276.7 ± 125.8	226.8 ± 84.1	219.3 ± 100.7		$Fr = 37.44$, $P < 0.01$
	K-S test	$D = 0.31$, NS	$D = 0.44$, NS	$D = 0.35$, NS	$D = 0.45$, NS		
Velocity of ants (cm/s)	PNTL	1.5 ± 0.4	2.4 ± 0.6	2.1 ± 0.6	2.4 ± 1.0	2.8 ± 0.6	$Fr = 10.4$, $P < 0.01$
	TL	1.7 ± 0.6	2.0 ± 0.7	2.1 ± 0.7	2.4 ± 0.9	2.4 ± 0.9	$Fr = 26.19$, $P < 0.01$
	K-S test	$D = 0.20$, NS	$D = 0.50$, NS	$D = 0.23$, NS	$D = 0.27$, NS	$D = 0.33$, NS	

Means ± SD are given for all parameters. Persistent non trail-layers (PNTL, $N = 5$) were compared to trail-layers (TL, $N = 30$) by one-sample Kolmogorov–Smirnov tests (K–S test, $\alpha = 0.05$). Parameters characterising the two groups were compared over the five trips by Friedman tests ($\alpha = 0.05$). NA: data not available. NS: no statistically significant differences.

probability P_n to be a PNTL can be drawn from the percentage of non trail-laying ants observed during the first experiment: $P_n = 5/35 = 0.14$. In this case, the probability of those five ants to remain PNTL when

tested again after 1 week should be very low and should be equal to: $P_{nn} = 0.14^5 = 5 \times 10^{-5}$. Our observations did not support this assumption; the five PNTL observed during the first experiment remained non

trail-layers after the one-week interval. This result suggests that these PNTL came from a subpopulation of scouts that never lays trails, at least within this experimental time scale and conditions.

3.3.2. Trail-layers

Scouts never laid a trail on their first outward journey to the foraging area (passage 1), but most of them started laying a trail after having discovered the food source. All these TL laid chemical trails on their first return back to the nest (passage no. 2). When returning to the source for the first time (passage no. 3), only 46% of scouts laid a chemical trail. As they went back to the nest for the second time (passage no. 4), the percentage of trail-laying scouts increased to 76% before declining gradually at each passage. At the fifth come back to the nest (passage no. 10), only 43% of the ants still laid a trail.

Half of the ants laying a trail at the first return to the nest (passage 2) continued on their next passage and then showed a constant or a slightly lower probability of continuing to lay a trail until their last trip (around 0.8; Fig. 2). On the other hand, ants that stopped laying a trail could restart marking on a latter trip, but the associated probability was low and decreased with the number of passages (Fig. 2). As a result, only 30% of TL kept on laying a trail over their five successive trips.

The interindividual heterogeneity of trail-laying behaviours suggested that TL could differ by their trail-laying persistence. To test this hypothesis, we established, for each trail-layer, the sequence of the behaviours (trail-laying or not) during its successive passages ($N = 30$). We used these 30 behavioural

sequences to calculate a probability transition matrix. This matrix was constructed with the assumption that there was no scout laying a trail more persistently than the others. We thus predicted the distribution of the number of passages over which a trail should be laid in a homogeneous population of scouts. We found that this theoretical distribution of the number of passages with trail-laying behaviours was not statistically different from its experimental counterpart (Fig. 3, one-sample Kolmogorov–Smirnov test, $D = 0.14$, NS). Hence, at least for these experiments, there was no need to invoke an individual specialisation to account for the variability in the persistence of trail-laying behaviour among *L. niger* foragers that do lay trails.

The number of marks laid per trail-laying ant was specific to each individual, since the individual intensities of trail laying were highly related over successive trips (Kendall's coefficient of concordance test: $W_x = 0.39$, $N = 19$, $P < 0.001$). On average, this individual trail intensity did not differ over the five successive trips on the way to the source (Table 1). Similar values of trail intensities were observed on the homeward passages excepting for the nearly twice higher number of marks laid by scouts on their first return to the nest.

The individual intensities of trail laying were not correlated with any of the other behavioural or physiological parameters (Kendall's coefficient of concordance test: NS for all parameters).

4. Discussion

Previous experiments (Maillieux et al., 2000) showed that a rule based on individual thresholds exists in the food recruitment of *L. niger*. Only scouts that succeed in

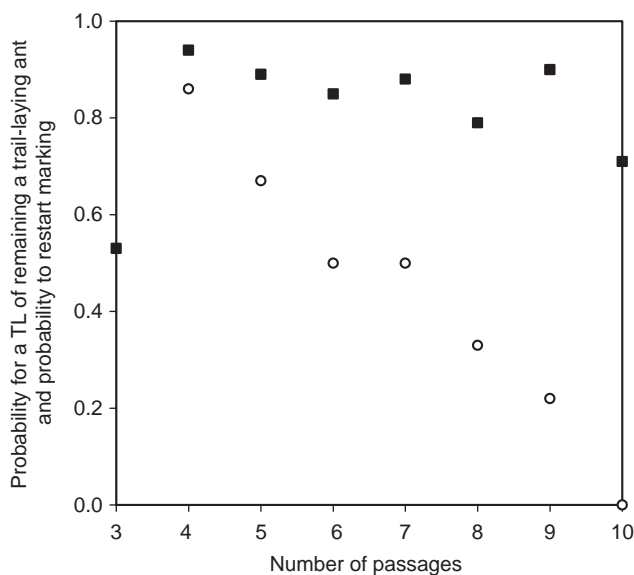


Fig. 2. Probability of remaining a trail-laying ant (■) and probability to restart marking (○) as a function of the number of passages ($N = 30$).

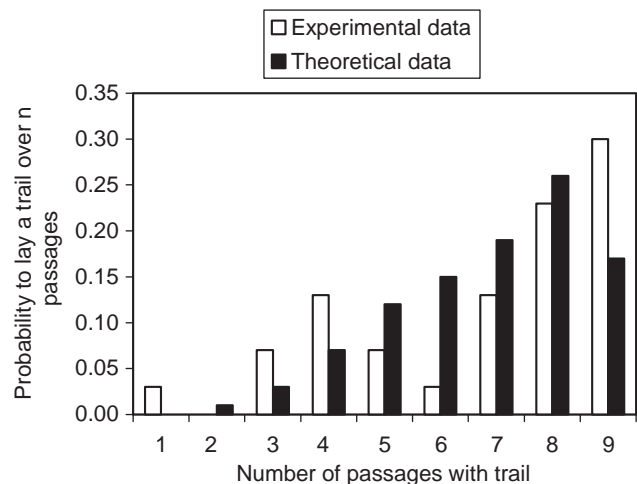


Fig. 3. Probability to lay a trail over n passages. Blank bars represent relative numbers of passages over which a trail-laying behaviour is observed. Black bars gives the expected number of passages with trail-laying behaviours resulting from 2000 simulations in which no specialisation was assumed (see text for more details).

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 specific to each individual and rather constant, at least on a short time scale over successive visits to the food source.

The ability to reach the “desired volume” is not the only parameter determining the trail-laying response of foragers, since 14% of the population of scouts never lay a trail. These PNTL persist in their lack of marking behaviour during foraging, and keep their non trail-layers “status” for at least 1 week. Further studies are needed to determine if this results from a long-term specialisation or from a lack of physiological maturation, as was suggested by Cammaerts-Tricot and Verhaeghe (1974) for *Myrmica rubra*.

It is worth noting that the moment at which foragers start laying a trail after food discovery is highly variable between species (Hahn and Maschwitz, 1985, Mercier and Lenoir, 1999). For instance, in *Messor rufitarsis* (Hahn and Maschwitz, 1985) and *Polyrhachis laboriosa* (Mercier and Lenoir, 1999), ants start marking only after several successful visits to the food whereas in *L. niger* the first successful visit of a scout to a sucrose source is enough to trigger the trail-laying behaviour. As individual decisions to lay trail directly influence the efficiency of the recruiting and orienting trails, one may expect that differences in the ecological niche parameters such as habitat, diet or competition level should play a central role in the interspecific variability of the trail-laying onset. For instance, as regards the recruiting function of the trail, ant species exploiting and monopolizing large food sources could be more prone to trigger a trail recruitment out of their first visits to the food patches. Similarly, in respect to the trail orienting function, the higher complexity of spatial orientation in a three-dimensional arboreal space could also have favoured the quick trail-laying onset compared to ground-foraging species. Such adaptive issues equally concern the persistence of the trail-laying once initiated. Over their successive foraging trips, *L. niger* scouts progressively stop to lay a trail (see also Beckers et al., 1992) as reported for other ant species like *Camponotus rufipes* (Geissler and Roces, 2001). The individual persistence of trail-laying behaviour is highly variable among workers: some individuals stop after their first return to the source while others keep on laying a trail even at their fifth visit to the food source. However, our results show that this variability does not rely on behavioural specialisation in which some ants lay more frequently and persistently than other scouts.

The triggering and persistence of trail-laying as a function of the number of visits to the food source is essential in the regulation of foraging activities by enabling adjustment of the number of foragers to the food source's characteristics. The interplay between the

distribution of the individual desired volumes within the colony and the food resources abundance determines the fraction of trail-laying individuals and hence governs the colony recruitment response. Besides, the decrease of the fraction of TL over successive trips reduces the rate of recruitment while at the same time foragers may learn their route, making orientation trails unnecessary. Indeed, several species are known to become familiar with the visual landmarks while following chemicals trails (Hölldobler and Wilson, 1990; Aron et al., 1993; Quinet and Pasteels, 1996) and foragers can specialise on a particular foraging zone. Thus, decision rules governing trail recruitment appear as trade-offs between collective processes such as trails and individual ones such as individual spatial memory. Similar trade-offs between interindividual amplification processes and individual sampling capabilities, learning or reinforcement could regulate other activities (Deneubourg et al., 1987). Indeed, defence (Hölldobler, 1981; Lumsden and Hölldobler, 1983), nest moving (Franks et al., 2002) or exploration (Devigne and Detrain, 2002) are largely based on trail recruitment and other amplification mechanisms. Sendova-Franks and Franks (1994) suggested that reinforcement learning plays a role in the ability of *Leptothorax* ant colonies to quickly re-assemble after dissociation. Jaisson (1980) shows how learning affects the choice of a new nest. Similarly, simple reinforcement and individual experience leading to learning have been demonstrated in many other activities such as building behaviour (Jeanne, 1999) or aggregation (Vienne et al., 1990; Depickère et al., 2004a, b; Depickère et al., in press). Testing how learning is associated with a decrease of interindividual processes could be the next step to draw a coherent picture of the regulating patterns involved in these complex activities.

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