

Julien Le Breton · V. Fourcassié

Information transfer during recruitment in the ant *Lasius niger* L. (Hymenoptera: Formicidae)

Received: 28 February 2003 / Revised: 10 September 2003 / Accepted: 8 October 2003 / Published online: 5 November 2003
© Springer-Verlag 2003

Abstract In this paper, we used the food-correlated search behavior observed in foraging ants returning to a previously rewarding site to study information transfer during recruitment in the ant *Lasius niger*. We hypothesized that, if information about the characteristics of the food is conveyed during recruitment, food-correlated search tactics should also be observed in recruited workers. Our results show that the characteristics of the trajectories of recruited workers are comparable to those of scout ants returning to a site or prior food find and depend more on the type (prey/sugar) than on the quality (sugar concentration) of the food discovered by the scouts. Independent of sugar concentration, workers recruited to a source of sugar search with a greater sinuosity than workers recruited to a prey. Experimental manipulation of the recruitment signals (chemical trail and contact between ants) shows that the trail pheromone laid down by recruiting ants does not play a role in the modification of trajectory sinuosity. This change appears to be most likely triggered by a direct perception of the residue of sugar smeared on the body of the recruiting workers coming back to the nest.

Keywords Formicidae · *Lasius niger* · Recruitment · Communication · Exploration

Introduction

The foraging success of social insects is partly due to the sophisticated means of communication they have developed through evolution (Wilson 1971). Communication during recruitment in particular allows a colony to rapidly assemble a worker force in order to pre-empt newly discovered food sources, ensure their defense against competitors, as well as retrieve them quickly to the nest. Information about newly discovered food sources can be conveyed through a variety of stimuli involving all the sensory channels available in arthropods. Visual, tactile, vibrational, auditory, as well as gustatory and olfactory stimuli, have been shown to be involved in the recruitment processes of social insects (see reviews by Hölldobler 1999 in ants; Michelsen 1993; Seeley 1998 in honeybees; Nieh 1998 in stingless bees).

In ants, studies on the semantics of recruitment signals have generally focused on scout ants and have proceeded by trying to relate their behavior to the characteristics of the food they have found. A positive relationship has been found between the type (Cammaerts and Cammaerts 1980; Detrain and Pasteels 1991), quality (Hangartner 1969, 1970; Cammaerts 1977; Breed et al. 1987; Beckers et al. 1993), and quantity (Breed et al. 1987; Detrain and Deneubourg 1997; Robson and Traniello 1998; Mercier and Lenoir 1999; Mailleux et al. 2000) of food discovered (see review by Detrain et al. 1999) and the propensity to lay trails or the frequency of trail-laying in recruiter ants. Other signals such as those displayed by scout ants inside the nest have also been shown to depend on the type (Detrain and Pasteels 1991; De Biseau and Pasteels 1994) and quality (Cammaerts 1977; De Biseau and Pasteels 1994; Cassill 2003) of the food source encountered. Communication, however, is a two-party process involving a sender and a recipient. Therefore, for a stimulus to acquire a semantic value, it is not enough to show that its production by an animal is correlated with specific events. One should also verify that it is perceived and that the information it conveys is understood by the recipient animal. For example, the correlations mentioned above

Communicated by J. Heinze

V. Fourcassié (✉)
Centre de Recherches sur la Cognition Animale, CNRS UMR 5169,
Université Paul Sabatier, 118 Route de Narbonne,
Bât IVR3, 31062 Toulouse Cedex 4, France
e-mail: fourcass@cict.fr
Tel.: +33-5-61558871
Fax: +33-5-61556154

Present address:

J. Le Breton, Laboratoire de Zoologie Appliquée,
Centre IRD de Nouvelle-Calédonie,
BP A5 Nouméa, 98 848 Nouméa Cedex, New Caledonia

between food characteristics and scout-ant behavior do not imply that the latter can be considered as true signals (Seeley 1998), conveying specific information to other ants. As pointed out by Roces (1993, 2002), to verify the nature of the information transmitted by recruiter ants, one should also investigate in which way the behavior of recruited workers is modified following the perception of a recruitment stimulus. In ants, nevertheless, most authors have assessed the information content of recruitment signals indirectly, by simply measuring the number of workers departing from the nest or arriving at a food source (Crawford and Rissing 1983; Breed et al. 1987; De Biseau and Pasteels 1994). This crude measure provides little information on whether or not recruitment signals convey specific information to recruited ants about one or several characteristics of the food retrieved to the nest by scout ants.

In this paper, we study the informational value of the recruitment signals used by the ant *Lasius niger*, by analyzing the search response of recruited workers following the return to the nest of a successful forager. We checked whether, as in the species *Cataglyphis bicolor* (Schmid-Hempel 1984) and *Formica schaufussi* (Traniello 1988; Traniello et al. 1992; Fourcassié and Traniello 1993, 1994), the search pattern of a *L. niger* scout ant returning to a previously rewarding site depends on the characteristics of the food it has found. We hypothesized that, if information about food characteristics is conveyed during recruitment, a similar adjustment of search tactic will be observed in recruited ants. To test this, we analyzed the search pattern of workers recruited to food sources of different types (carbohydrate/protein) and quality (different sucrose concentration). In order to identify the stimuli coding for the food characteristics, we then proceeded with additional experiments in which either direct (trophallaxis or physical contacts) or indirect (chemical trail) interactions between scout ants were allowed or not.

Methods

Collection and maintenance of ant colonies

One colony of *L. niger* (Hymenoptera, Formicidae, Formicinae) was collected on the campus of the University of Toulouse, France, in September 1999 and transferred to artificial plaster nests placed in a rearing room under controlled temperature ($25 \pm 2^\circ\text{C}$) and photoperiod (14L:10D) conditions. The colony was queenless and contained approximately 2,000–3,000 workers and brood. It was used as a stock to constitute 5 standardized experimental groups containing 100 workers and an equal quantity of brood (most of it larvae). The size of the experimental groups was kept more or less constant throughout the experiments by taking ants from the stock colony to compensate for the loss and death of workers.

Experimental set-up

Five identical experimental set-ups (Fig. 1) were placed side by side on a large sliding board. During an experiment, the experimental area of each set-up was in turn brought under a Sony CCD-

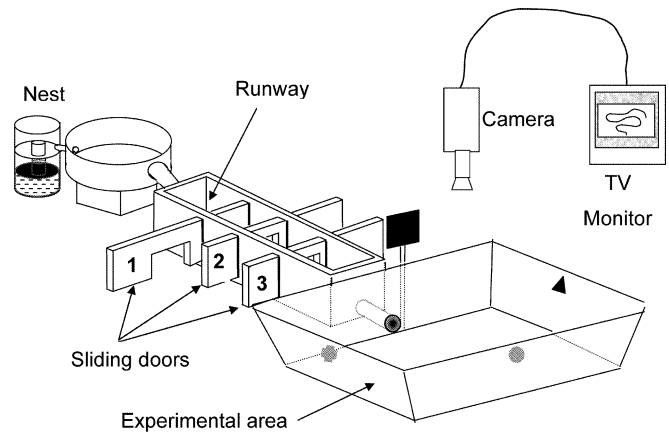


Fig. 1 Experimental set-up. Each nest is linked to a round plastic box (diameter 13 cm) which is itself connected through a plastic tube to a 20-cm-long runway. Three sliding doors in the runway allow the ants' flow to be regulated during the experiments. Ants then have access through a second plastic tube to a white rectangular plastic box (17×28×7 cm) which is used as the experimental area. The walls of all boxes are coated with Fluon to prevent ants from escaping

IRIS video camera, and the ants' trajectories were recorded on S-VHS videotapes with a Panasonic NV-HS 900 videotape recorder. Light homogeneity was ensured by a white tissue hanging from the ceiling and surrounding the set-up.

Experimental procedure

Familiarization phase

Three weeks before the beginning of the experimental sessions, the ants were allowed access to all parts of the set-up. They were fed ad libitum with droplets of 0.06 M (20 g/l) sucrose solution and small dead crickets (first instar of *Gryllus assimilis*). Sugar water was always offered at the same place, in the center of the experimental area, while crickets were placed randomly. The diet of *L. niger* consists mainly of aphid honeydew (carbohydrate) and small prey (protein). Hence, the distribution of sugar water and crickets mimics the spatial distribution of the two types of food in the natural environment of the ants: aggregated for carbohydrate, dispersed and unpredictable for protein. Before each experimental session, the colonies were starved for 4 days to stimulate food-searching behavior. This should be enough since in *Solenopsis invicta*, Cassill and Tschinkel (1999) have shown that after only 2 days of food deprivation worker crop is only 12% of its maximum volume.

Preliminary phase

The day before an experimental session, access to the runway was blocked and all workers present in the experimental area or in the runway were collected and placed in the small circular box connected to the nest. Before each test, the bottom of the runway and the experimental area, as well as the plastic tube leading to it, were cleaned with 95% ethanol to eliminate any chemical cues.

Test phase

Control group. The purpose of this group was to study the exploratory behavior of ants in the absence of food in the experimental area. A single ant (henceforth designated as "worker

no. 1”) was allowed through the runway and its trajectory was recorded as soon as it entered the experimental area. The recording was stopped after 90 s or when the ant left the experimental area for more than 10 s. Meanwhile, the next worker exiting the nest (henceforth designated as “worker no. 2”) was blocked and isolated in the runway. After worker no. 1 left the experimental area and returned to the nest, it was blocked in the runway and allowed to interact with worker no. 2. Meanwhile the bottom of the experimental area was cleaned with ethanol to eliminate any chemical cues. Worker no. 2 was then allowed to enter and explore the experimental area and its trajectory recorded. After completion of the recording, both workers were withdrawn from the experimental nest and replaced by two ants from the stock colony. Twenty pairs of ants were tested, four for each experimental colony.

Experimental groups. The purpose of these groups was to study the search behavior of ants that had either found food in the experimental area during a preceding trip, or that had just made contact with a worker coming back to the nest with food. The food was either a 3- μ l droplet of sucrose solution or a patch of four freshly killed small crickets (easily carried by a single worker). The two types of food were always offered in the center of the experimental area. Three different concentrations were used for the sucrose solution: 0.06 M (20 g/l, the concentration of the food offered during the familiarization phase), 0.29 M (100 g/l), and 0.60 M (200 g/l). These concentrations fall within the range of the sucrose concentration of the honeydew of several species of Homoptera exploited by *L. niger* in its natural environment (Völkl et al. 1999). Seven experimental groups were created, differing in the type and quality of food offered and in whether or not the recruitment behavior was manipulated (removal of chemical trail or contacts allowed or not between scouts and recruited workers). Table 1 gives the details of the test procedure used in each group. The experimental groups have been named according to the test procedure employed: the letter S refers to the groups in which ants received a sucrose reward; the numbers following the letter S refer to the concentration of the sucrose solution offered to the group; finally, the letter C refers to the groups in which contact was allowed between scout and recruited worker, and the letter T refers to the groups in which the experimental area was not cleaned and thus where a chemical trail could potentially persist.

The general test procedure for all experimental groups was as follows: First, a scout ant was allowed through the runway and into the experimental area. While collecting food (either sucrose solution or cricket), it was gently marked with a spot of paint on the abdomen so as to be subsequently easily identified. Just after it left the food location, we noted whether or not it laid a chemical trail. We considered that a trail was laid when we observed, at least once, the ant lowering its abdomen onto the ground. Except for groups S0.60 and S0.60T, the scout ant was then allowed to interact with a second worker in the runway. Meanwhile, any remaining food in the experimental area was removed and, except for groups S0.60CT and S0.60T, the bottom of the experimental area was cleaned with ethanol. The scout ant was then allowed to enter the nest and exchange food with nestmates while the recruited worker was allowed access to the experimental area. Once its trajectory had

been recorded, it was withdrawn from the set-up and the experimental area was cleaned again with ethanol. The scout ant was then allowed access a second time to the experimental area and its search path recorded.

Twenty pairs of ants were tested in each group except for groups S0.60C and S0.60T in which only 19 individuals were tested. Each pair was taken from one of the five experimental colonies picked at random. At the end of an experiment, both workers were withdrawn from the experimental nest and replaced by two ants from the stock colony. For the groups S0.60CT, S0.60, and S0.60T, only the search pattern of recruited workers was recorded and analyzed.

Trajectory acquisition and analysis

We used an automatic tracking software (Ethovision by Noldus Information Technology, <http://www.noldus.nl/>) to record the paths of the ants at a rate of 10 fixes per second on the computer (Fourcassié and Traniello 1995). The files were then analyzed using the analysis module of Ethovision.

In order to quantify the spatial organization of the search, the experimental area was divided into four different zones:

1. an entrance zone, corresponding to a 4 cm \times 2 cm area adjacent to the entrance of the experimental area.
2. a central zone, corresponding to a circle 6 cm in diameter drawn around the center of the experimental area (i.e. the prior location of the food source).
3. a marginal zone, corresponding to an area 2 cm wide along the edge of the experimental area, excluding the entrance zone.
4. an intermediate zone, which comprises the area between the marginal and the central zone.

The following path characteristics were computed:

1. linear velocity: the mean distance covered between two fixes, excluding pauses, expressed in cm/s;
2. angular velocity: the average of the absolute change in direction between two successive segments of a trajectory, expressed in degree/cm. A high angular velocity characterizes a meandering path;
3. the time spent in the central and
4. marginal zones of the experimental area.

Statistical analysis

We compared (for scout and recruited workers separately) the performance of the ants from the different groups by applying a one-way ANOVA on the path characteristics. Post-hoc multiple comparison tests were subsequently used to compare the ants' performances in pairs of groups. We used a three-step procedure for the analysis. First, we compared the performance of the control group and of the groups S0.06C, S0.29C, S0.60C, and Cricket to assess the influence of the quality and of the type of food on the

Table 1 Test procedure used in each experimental group (C contact, T trail)

Code of the experimental group	Sample size	Type of food	Quality	Contact allowed between scout and recruited worker	Pheromone trail allowed
S0.06C	20	Sucrose	0.06 M	✓	
S0.29C	20	Sucrose	0.29 M	✓	
S0.60C	19	Sucrose	0.60 M	✓	
S0.60CT	20	Sucrose	0.60 M	✓	✓
S0.60	20	Sucrose	0.60 M		
S0.60T	19	Sucrose	0.60 M		✓
Cricket	20	Cricket	1 st instar	✓	
Control	20	No food		✓	

search pattern. Second, we compared the performance of the control group and the groups S0.60C, S0.60CT, S0.60, and S0.60T to investigate the influence of direct and indirect interactions on the search pattern of recruited workers. Finally, the performances of scout and recruited ants in each group were compared by applying a Student's paired *t*-test and computing a Spearman's rank correlation coefficient on all groups. All analyses were conducted with SPSS for Windows, version 10 (SPSS: <http://www.spss.com/>).

Results

Influence of food type and quality on the search patterns of the foragers

Scout ants

Scout ants belonging to the sucrose groups moved faster (Fig. 2a; black bars, group S0.06C, S0.29C, S0.60C; ANOVA: $F_{4, 94}=7.8$, $P<0.001$) and had more sinuous trajectories (Fig. 2b; ANOVA: $F_{4, 94}=9.0$, $P<0.001$) than those belonging to the cricket or the control group. The path characteristics of ants of these two last groups did not differ significantly. Scout ants that found crickets spent more time in the marginal zone than either ants that found sugar or those of the control group (Fig. 2c; black bars, ANOVA: $F_{4, 94}=5.5$, $P<0.001$). Scout ants that were rewarded with the highest concentration of sugar, however, concentrated their search in the central zone (Fig. 2d; black bars, ANOVA: $F_{4, 94}=4.6$, $P<0.01$). The

concentration of the sucrose solutions offered to the scout ants did not otherwise induce notable differences in the search trajectories of scout ants, either at the kinetic or spatial levels (Fig. 2).

We conclude that in *L. niger*, as in other species of ants, scout ants returning to a previous rewarding site adjust their search pattern, both at the spatial and kinetic level, according to the type of food (prey/sugar) they have found in their previous foraging trip.

Recruited ants

The search patterns of the recruited ants contacted by a worker returning without food (control group) did not differ from those of the workers that were recruited towards a cricket (Fig. 2; white bars). The trajectories of the recruited ants of the four experimental groups, i.e. the three groups rewarded with sugar and the group rewarded with cricket, differed only at the kinetic level: workers recruited toward sugar had more sinuous trajectories than workers recruited toward crickets (Fig. 2b; white bars; ANOVA: $F_{4, 94}=10.9$, $P<0.001$). The search characteristics of the workers recruited towards sugar, however, did not depend on the concentration of the sucrose solution offered (Fig. 2, white bars, groups S0.06C, S0.29C, S0.60C).

Fig. 2a–d Influence of food type and quality on the characteristics of scout ants' (*black bars*) and recruited ants' (*white bars*) trajectories. Note that for recruited ants, information was only conveyed via physical contacts with the scout ants; **a** linear velocity, **b** angular velocity, **c** time spent in the marginal zone, **d** time spent in the central zone of the experimental area. Mean values \pm SE. The bars bearing the same *letters* indicate values that are not significantly different at the 5% level of significance [one-way ANOVA followed by a Student-Neuman-Keuls post-hoc test; a separate analysis was conducted for scouts (*roman letters*) and recruited ants (*italic letters*)]. For each group, the performances of scout ants and recruited ants were compared by a Student *t*-test for matched samples (*S* significant: $P<0.05$; *NS* non-significant)

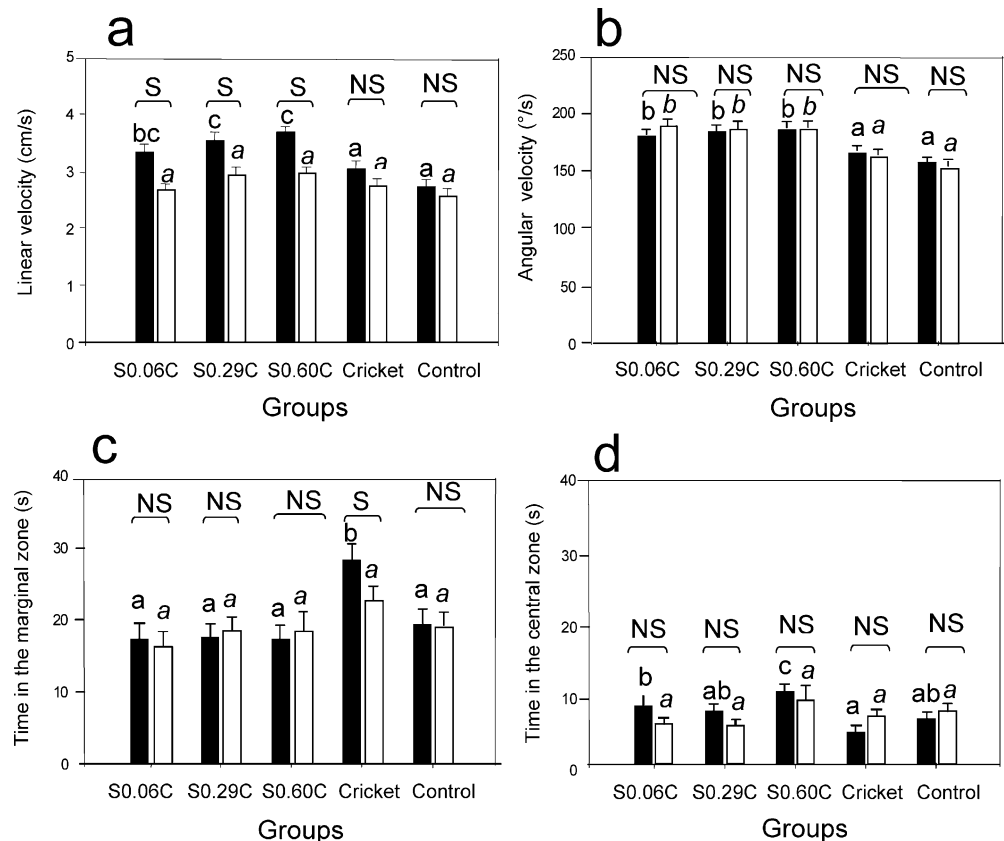
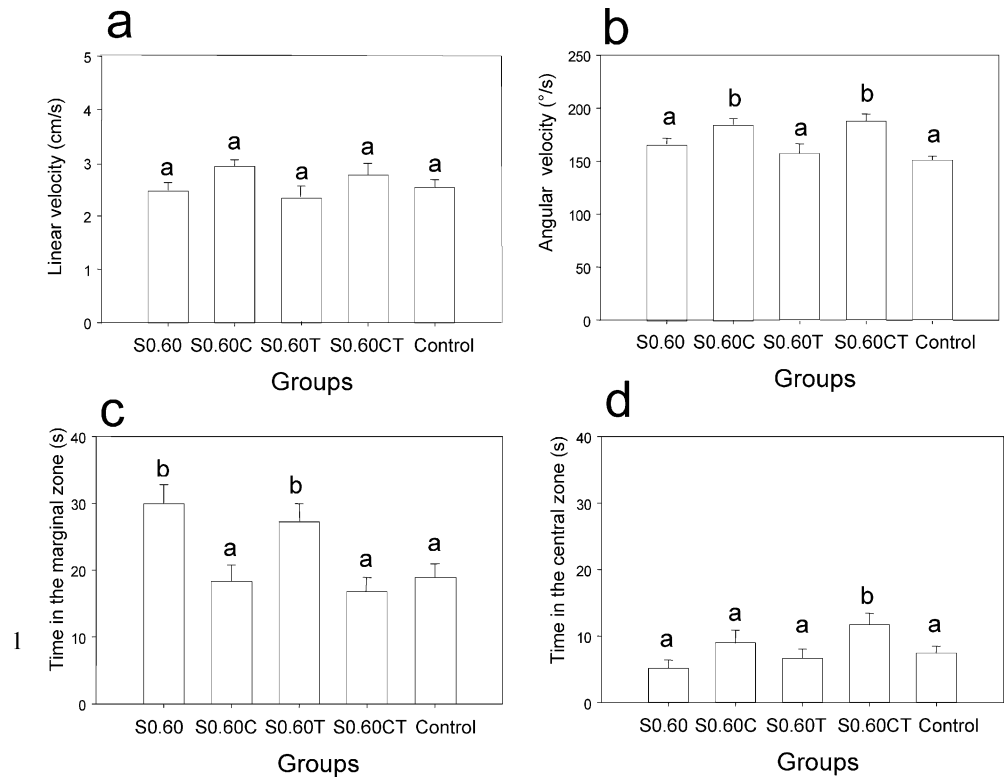


Fig. 3a–d Influence of the trail and the physical contacts with scout ants on the characteristics of recruited workers' trajectories: **a** linear velocity, **b** angular velocity, **c** time spent in the marginal zone, **d** time spent in the central zone. Mean values \pm SE. The bars bearing the same letters are not significantly different at the 5% level of significance (one-way ANOVA followed by a Student-Neuman-Keuls post-hoc test)



Comparison of the search patterns of scout versus recruited ants

When all pairs of workers were considered, a significant positive correlation was found between the trajectory characteristics of scout ants and recruited ants for all variables ($r=0.247$, $r=0.361$, $r=0.256$, for linear velocity, angular velocity and time spent in the marginal zone, respectively, $P<0.01$, $N=99$ for all tests), except for the time spent in the central zone ($r=-0.016$, $P=0.910$, $N=99$). When the performances of ants within the same group were compared with a test for matched samples, the only group for which significant differences were never found was the control group (Fig. 2). Scout ants of the experimental groups that were rewarded with a droplet of sugar solution moved significantly faster than recruited ants, independently of the concentration of the sucrose solution offered (Fig. 2a). The sinuosity of the trajectories (Fig. 2b), and the time spent searching in the marginal (Fig. 2c) and in the central zones of the experimental area (Fig. 2d) were not significantly different for the two categories of workers. Finally, in the group of ants searching for crickets, scout ants spent significantly more time in the marginal zone than recruited ants (Fig. 2c).

On the whole, recruited ants thus behave in the same way as those of the control group, the only exception being that they increase the sinuosity of their search trajectories when they are contacted by a scout returning with sucrose. Therefore, as we hypothesized, recruited ants do modify their search pattern according to the type of food found by scout ants. However, this is only true for

sucrose. In the next section, we investigate in which way information about sucrose discovery can be conveyed by scout ants.

Information transfer during recruitment towards a source of sucrose

Contact

Whether recruited ants were contacted or not by scout ants did not affect their linear velocity while searching in the experimental area (Fig. 3a). However, recruited ants contacted by scout ants coming back to the nest with food (groups S0.60C and S0.60CT) moved with a higher angular velocity than both the recruited ants that were not allowed contact with scout ants (groups S0.60 and S0.60T) and the ants of the control group contacted by scout ants coming back to the nest without food (Fig. 3b; ANOVA: $F_{4, 93}=7.0$, $P<0.001$). This result suggests that when recruitment occurs to a source of sucrose, the contact with the food retrieved to the nest by scout ants is important in the modulation of the angular velocity of the recruited workers. However, contacting food does not seem to affect the spatial distribution of the search effort since no differences were found in the time spent searching in the different zones of the experimental area between ants from group S0.60C and those from the control group (Fig. 3c,d), and only a slight but statistically significant difference was found between ants from group S0.60 CT and those from the control group. Note,

however, that the mere physical contact with a scout ant, whether loaded with food or not, seems to be important in the distribution of the search effort. Indeed, the time spent searching in the marginal zone was significantly higher when contact was not allowed between scout and recruited ants (groups S0.60 and S0.60T) than when it was allowed (groups S0.60C, S0.60CT, and control group) (Fig. 3c).

Chemical trail

The presence of a chemical trail in the experimental area (group S0.60T) did not induce any modifications in the workers' linear or angular velocity compared to the ants from the control group or from group S0.60, for which the experimental area had been cleaned (Fig. 3a,b). However, when contacted by scout ants (group S0.60CT), recruited ants had more meandering paths (Fig. 3b). Moreover, contrary to what could be expected, the presence of a trail did not induce a large and systematic increase in the time spent searching in the central zone when the experimental area was not cleaned with alcohol (groups S0.60T and S0.60CT; Fig. 3d). Note also that the presence of a trail had a different effect on recruited ants, depending on whether or not they were contacted by a scout: when chemical marks were left on the floor, recruited ants spent significantly more time in the marginal zone (Fig. 3c) and less time in the central zone of the exploratory area (Fig. 3d) when contact was allowed with a scout ant than when it was not allowed. One explanation could be that ants recruited to a source of sugar could have a higher probability of ignoring the chemical marks if they have not been contacted directly by a scout. This will consequently lead them to move away from the central zone of the exploratory area and spend more time in its marginal zone.

Discussion

In ants, as in other animals (see review by Bell 1990), local search is generally characterized by both a decrease in locomotory rate and an increase in turning rate (Harkness and Maroudas 1985; Crist and MacMahon 1991; Traniello et al. 1991). In our experiments, however, we found that scout ants searching in the experimental area after having found a sucrose solution in their previous foraging trip moved not only with a higher turning rate but also with a higher locomotory rate when compared to ants from the control group that spontaneously explored the experimental area. Higher running speed when returning from the nest to the site of a prior carbohydrate find is a well-known fact in ants, and has been reported repeatedly, although most often in qualitative and not quantitative form (e.g. Hangartner 1969; Szlep-Fessel 1970; Burkhardt 1998). Increase in running speed in our experiments may result from a high level of excitement triggered by interactions with other workers

inside the nest. It could also be directly linked to the ingestion of sucrose in the previous foraging trip. Further evidence of this is provided by the fact that there was a trend for the running speed to increase with increasing concentrations of the sucrose solution offered. For scout ants returning to the site of a prior protein find, however, only a slight nonsignificant increase in running speed was noted. Fourcassié and Traniello (1994) reported similar results in the ant *Formica schaufussi*. These authors found that protein food was more often rejected than carbohydrate food, which could mean that in species of ants characterized by a mixed diet of protein and carbohydrate, the latter type of food is more stimulating than the former and may trigger a higher level of excitement. This result also agrees with observations by Portha et al. (2002) indicating that protein food in *L. niger* usually induces no recruitment or a low level of recruitment compared to carbohydrate food.

Ants from the control group distributed their search efforts over all parts of the experimental area, whereas those that were offered a droplet of sucrose tended to search more centrally and those that were offered a cricket spent significantly more time in the marginal zone. This latter behavior could be interpreted as an attempt by the foragers to extend their search beyond the limits of the experimental area. The distribution of the search effort is thus affected by the type of food found on the previous foraging trip. This result agrees with that obtained in field experiments with *Cataglyphis bicolor* (Schmid-Hempel 1984) and in field (Traniello 1987, 1988, 1989; Traniello et al. 1992) and laboratory (Fourcassié and Traniello 1993, 1994) experiments with *F. schaufussi*. Moreover, as in the giant tropical ant *Paraponera clavata* (Breed et al. 1996) and the species *F. schaufussi* (Traniello et al., unpublished results), in the absence of chemical trails, no significant effect of reward concentration was found on the distribution of search effort in foraging ants.

As noted by Traniello (1988), the search behavior of ants appears to be correlated with the spatial and temporal distribution of food resources in the natural environment: carbohydrate food sources such as honeydew produced by aphid colonies or the secretion of extra-floral nectaries are more persistent and more spatially concentrated, whereas protein food sources, such as dead or live arthropods, are spatially and temporally unpredictable. It is therefore more profitable for a forager that found carbohydrates in its previous trip to concentrate its search in the vicinity of the site of its prior find, whereas it is more profitable for a forager that found a single prey to reduce its search time around this site and rapidly extend its search. This food-correlated search behavior is probably the result of evolutionary pressures since it is observed in naive foragers and is only slightly modified through foraging experience (Fourcassié and Traniello 1993).

Changes in search behavior were noted in all groups in which recruited workers were allowed to establish contact with scout ants returning to the nest with sucrose. Their angular velocity was indeed significantly higher than that of the workers from the control group that established

contact with scout ants returning unloaded from the experimental area. This suggests that recruited workers perceive, directly or indirectly, that scout ants have discovered sucrose and subsequently actively modify their locomotor behavior when searching in the experimental area. The search pattern of ants recruited to protein was not significantly different from that of the control group, despite the fact that recruited ants had contact with the cricket carried by the scout ant. Contact with a prey, therefore, does not elicit a specific search movement.

Information about the presence of a sucrose reward could be transmitted either indirectly, through some chemical marks left by scout ants upon their return to the nest, or directly through physical contact. Different types of chemical substances could be left by scout ants to signal the nature of the food they have found. The trail pheromone, which is produced by the hindgut in *L. niger*, would be the first candidate. Trail-laying behavior was indeed almost always observed in ants collecting sucrose while it was observed only once out of 20 tests in ants retrieving a prey. Yet the presence of a trail did not induce any modifications in the trajectory of recruited ants: significant changes in angular velocity were observed only when physical contact was allowed between scout and recruited ants. During this contact, several signals could convey information about the type of food discovered. First, information could obviously be transmitted through trophallaxis. However, the frequency of food exchanges was too low (it occurred in less than 20% of the total number of encounters) to explain our results. Second, information could be transmitted through mechanical signals or motor displays (Hölldobler 1999). For example, “jittering” (a rapid back and forth movement of the ant body along its longitudinal axis) was sometimes observed in scout ants. However, their frequency was also too low to constitute a reliable source of information. Finally, information could be transmitted through antennation. In fact, this was observed in all encounters. However, although several authors have attempted to demonstrate the semantic value of these antennations (Torossian 1973; Lenoir and Jaisson 1982; Bonavita-Cougourdan and Morel 1984; Reznikova and Ryabko 1996), there is hitherto no convincing evidence that antennal signals code for a specific type of food.

To learn about the type of food found by scout ants, recruited ants could use either signals or cues. Seeley (1998) has emphasized the difference between these two terms: signals are stimuli such as chemical trails, which are shaped by natural selection to convey specific information, while cues are behavioral acts conveying information incidentally. For instance, residues of sucrose on the mandibles or the antennae of the scouts could be perceived by recruited ants and act as a cue conveying information about the nature of the food discovered. In the same way, it is well documented that in honeybees (von Frisch 1967) and bumblebees (Dornhaus and Chittka 1999), floral odors attached to the body of the scouts are detected by other workers and are an important source of

information to direct their search once outside the hive. In the fire ant, *Solenopsis invicta*, recruited workers are informed about the quality of a sugar solution transported by the scouts during very brief contacts, without the need of any ingestion (Cassill 2003). The quality of the food is assessed by contacting very briefly the droplet of sugar water held between the mandibles of the scout with the tip of their antennae. In our experiments, the mere contact of the recruited workers with sucrose residues could activate a specific locomotor program leading to an increase in the sinuosity of the search trajectory. Contact with a prey transported by scout ants, however, would not trigger any changes in the locomotor behavior of recruited ants. Increase in trajectory sinuosity following contact with sucrose has indeed been noted in several species of insects, e.g. in the giant tropical ant *P. clavata* (Breed et al. 1996), the domestic fly *Musca domestica* (White et al. 1984), and the fruit fly *Drosophila melanogaster* (Bell et al. 1985). It would have been interesting to see whether the trajectory sinuosity of recruited workers would have increased in the same way if they had been prevented from establishing a direct contact with a scout but just allowed to contact with their antennae a drop of sucrose before entering the experimental area.

It is interesting to note that the perception of sucrose does not seem to raise the level of excitement of recruited ants since their linear velocity, contrary to scout ants, was not significantly different from that of the ants from the control group. An explanation could be that the mere contact of sucrose with the antennae is not sufficient to raise the level of excitement of recruited ants because the chemoreceptors of the antennae are not sensitive to sucrose concentration. Ingestion of sucrose, directly as in scout ants, or indirectly, through trophallaxis, may be required to detect the concentration of sucrose and modify the ants' motivational state.

Does the contact with the residues of sucrose smeared on the body of scout ants also modify the spatial distribution of the search effort of recruited workers? The answer is no. When contact was allowed and the experimental area was cleaned, no differences were found in the distribution of the search effort of workers recruited to sucrose compared to ants from the control group. Contrary to what we observed in scout ants, there were also no differences in the distribution of the search effort between ants recruited to sucrose and those recruited to crickets. When the experimental area was not cleaned (group S0.60CT), recruited ants spent significantly more time searching the central part of the area than control ants. We conclude therefore that the change observed in the distribution of the search effort of workers recruited to sucrose is not based on their perception of the nature of the food carried by scout ants, but on the chemical marks it has deposited on the ground.

Our results also shed some light on the phenomenon of collective choice observed during recruitment in some species of ants. When a colony of mass recruiting ants such as *L. niger* is simultaneously offered two sucrose rewards of different concentrations at the same distance

from its nest, it generally makes a clear choice and selects the richer food source (Beckers et al. 1993; Portha et al. 2002). This choice is based on a self-organization process that emerges from the trail-laying and trail-following behavior of the ants (Pasteels et al. 1987) and that can be further amplified by a graded invitation behavior of the returning scouts inside the nest (Cassill 2003). The first workers returning to the nest from the richest food source trail-lay more frequently and the small difference in intensity between the two trails leading to the food sources is then amplified by an autocatalytic process prompting the rapid selection of the most profitable source. Our results show that, in *L. niger*, this phenomenon could be further amplified by the fact that scout ants returning to the richer food source have a tendency to run with a higher speed than those returning to the poorer one.

Acknowledgements We would like to thank F. Fayret for technical help, S. Grosset and E. Goldstein for assistance in the experiments, J.C. Biesmeijer for interesting discussions, and R. Jeanson, C. Detrain, R. Bon and Alain Dejean for critically reading the manuscript. Thanks are also due to Andrea Dejean who kindly revised the English. This work was financed in part by Conseil Régional Midi-Pyrénées.

References

- Beckers R, Deneubourg JL, Goss S (1993) Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of food source. *J Insect Behav* 6: 751–759
- Bell WJ (1990) Searching behavior patterns in insects. *Annu Rev Entomol* 35:447–467
- Bell WJ, Tortorici C, Roggero RJ, Kipp LR, Tobin TR (1985) Sucrose-stimulated searching behaviour of *Drosophila melanogaster* in a uniform habitat by period of deprivation. *Anim Behav* 33:436–448
- Bonavita-Cougourdan A, Morel L (1984) Les activités antennaires au cours des contacts trophallactiques chez la fourmi *Camponotus vagus* ont-elles valeur de signal? *Insectes Soc* 31:113–131
- Breed MD, Fewell JH, Moore AJ, Williams KR (1987) Graded recruitment in a ponerine ant. *Behav Ecol Sociobiol* 20:407–411
- Breed MD, Bowden RM, Garry MF, Weicker AL (1996) Giving-up time variation in response to differences in nectar volume and concentration in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). *J Insect Behav* 9:659–672
- Burkhardt JF (1998) Individual flexibility and tempo in the ant, *Pheidole dentata*, the influence of group size. *J Insect Behav* 11:493–504
- Cammaerts MC (1977) Recrutement d'ouvrières vers une source d'eau pure ou d'eau sucrée chez la fourmi *Myrmica rubra* L. (Formicidae). *Biol Behav* 2:287–308
- Cammaerts MC, Cammaerts R (1980) Food recruitment strategies of the ants *Myrmica sabuleti* and *Myrmica ruginodis*. *Behav Process* 5:251–270
- Cassill DL (2003) Rules of supply and demand regulate recruitment to food in an ant society. *Behav Ecol Sociobiol* DOI 10.1007/s002650030639
- Cassill DL, Tschinkel WR (1999) Task selection by workers of the fire ant *Solenopsis invicta*. *Behav Ecol Sociobiol* 45:301–310
- Crawford DL, Rissing SW (1983) Regulation of recruitment by individual scouts in *Formica oreas*. *Insectes Soc* 30:177–183
- Crist TO, MacMahon JA (1991) Individual foraging components of harvester ants: movement patterns and seed patch fidelity. *Insectes Soc* 38:379–396
- De Biseau JC, Pasteels JM (1994) Regulated food recruitment through individual behavior of scouts in the ant, *Myrmica sabuleti* (Hymenoptera: Formicidae). *J Insect Behav* 7:767–777
- Detrain C, Deneubourg JL (1997) Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants. *Anim Behav* 53:537–547
- Detrain C, Pasteels JM (1991) Caste differences in behavioral thresholds as a basis for polyethism during food recruitment in the ant, *Pheidole pallidula* (Nyl.) (Hymenoptera: Myrmicinae). *J Insect Behav* 4:157–176
- Detrain C, Deneubourg JL, Pasteels JM (1999) Decision-making in foraging by social insects. In: Detrain C, Deneubourg JL, Pasteels JM (eds) *Information processing in social insects*. Birkhäuser, Basel, pp 331–354
- Dornhaus A, Chittka L (1999) Evolutionary origins of bee dances. *Nature* 401:38
- Fourcassié V, Traniello JFA (1993) Effects of experience on food-searching behavior in the ant *Formica schaufussi* (Hymenoptera: Formicidae). *J Insect Behav* 6:287–299
- Fourcassié V, Traniello JFA (1994) Food searching behaviour in the ant *Formica schaufussi* (Hymenoptera, Formicidae): response of naive foragers to protein and carbohydrate food. *Anim Behav* 48:69–79
- Fourcassié V, Traniello JFA (1995) Ant search behaviour analysis with a video frame grabber. *Insectes Soc* 42:249–254
- Frisch K von (1967) *The dance language and orientation of bees*. Harvard University Press, Cambridge, Mass
- Hangartner W (1969) Structure and variability of the individual odor trail in *Solenopsis germinata* Fabr. *Z Vgl Physiol* 62:111–120
- Hangartner W (1970) Control of pheromone quantity in odor trails of the ant *Acanthomyops interjectus* Mayr. *Experientia* 26:664–665
- Harkness RD, Maroudas NG (1985) Central place foraging by an ant (*Cataglyphis bicolor*)—a model of searching. *Anim Behav* 33:916–929
- Hölldobler B (1999) Multimodal signals in ant communication. *J Comp Physiol A* 184:129–141
- Lenoir A, Jaisson P (1982) Evolution et rôle des communications antennaires chez les insectes sociaux. In: Jaisson P (ed) *Social insects in the tropics*. Presses de l'Université Paris XIII, Paris, pp 157–180
- Mailleux AC, Deneubourg JL, Detrain C (2000) How do ants assess food volume? *Anim Behav* 59:1061–1069
- Mercier JL, Lenoir A (1999) Individual flexibility and choice of foraging strategy in *Polyrhachis laboriosa* F. Smith (Hymenoptera, Formicidae). *Insectes Soc* 46:267–272
- Michelsen A (1993) The transfer of information in the dance language of honeybees: progress and problems. *J Comp Physiol A* 173:135–141
- Nieh JC (1998) The food recruitment dance of the stingless bee, *Mellipona panamica*. *Behav Ecol Sociobiol* 43:133–145
- Pasteels JM, Deneubourg JL, Goss S (1987) Self-organization in ant societies. I. Trail recruitment to newly discovered food sources. In: Pasteels JM, Deneubourg JL (eds) *From individual to collective behavior in social insects*. Birkhäuser, Basel, pp 155–175
- Portha S, Deneubourg JL, Detrain C (2002) Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. *Behav Ecol* 13:776–781
- Reznikova Z, Ryabko BY (1996) Transmission of information regarding the quantitative characteristics of an object in ants. *Neurosci Behav Physiol* 26:397–405
- Robson SK, Traniello JFA (1998) Resource assessment, recruitment behavior, and organization of cooperative prey retrieval in the ant *Formica schaufussi* (Hymenoptera: Formicidae). *J Insect Behav* 11:1–22

- Roces F (1993) Both evaluation of resource quality and speed of recruited leaf-cutting ants (*Acromyrmex lundii*) depend on their motivational state. *Behav Ecol Sociobiol* 33:183–189
- Roces F (2002) Individual complexity and self-organization in foraging by leaf-cutting ants. *Biol Bull* 202:306–313
- Schmid-Hempel P (1984) Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Behav Ecol Sociobiol* 14:263–271
- Seeley TD (1998) Thoughts on information and integration in honey bee colonies. *Apidologie* 29:67–80
- Szlep-Fessel R (1970) The regulatory mechanisms in mass foraging and the recruitment of soldiers in *Pheidole*. *Insectes Soc* 18:233–244
- Torossian C (1973) Etude des communications antennaires chez les Formicoidea: analyse du comportement trophallactique d'échanges alimentaires pratiqués entre ouvrières de la fourmi *Dolichoderus quadripunctatus*. *CR Acad Sci Paris Ser D* 227:1381–1384
- Traniello JFA (1987) Social and individual responses to environmental factors in ants. In: Deneubourg JL, Pasteels JM (eds) *From individual to collective behavior*. Birkhauser, Basel, pp 63–80
- Traniello JFA (1988) Variation in foraging behavior among workers of the ant *Formica schaufussi*: ecological correlates of search behavior and the modification of search pattern. In: Jeanne RL (ed) *Interindividual behavior variability in social insects*. Westview, Boulder, Colo, pp 91–112
- Traniello JFA (1989) Foraging strategies of ants. *Annu Rev Entomol* 34:191–210
- Traniello JFA, Fourcassié V, Graham TP (1991) Search behavior and foraging ecology of the ant *Formica schaufussi*: colony-level and individual patterns. *Ethol Ecol Evol* 3:35–47
- Traniello JFA, Kozol AJ, Fournier MA (1992) Resource-related spatial patterns of search in the ant *Formica schaufussi*: a field study. *Psyche* 99:87–93
- Völkl W, Woodring J, Fischer M, Lorenz MW, Hoffmann KH (1999) Ant-aphid mutualisms: the impact of honeydew production and honeydew sugar composition on ant preference. *Oecologia* 118:483–491
- White J, Tobin TR, Bell WJ (1984) Local search in the housefly *Musca domestica* after feeding on sucrose. *J Insect Physiol* 30:477–487
- Wilson EO (1971) *The insect societies*. Harvard University Press, Cambridge, Mass