

## Memory and chemical communication in the orientation of two mass-recruiting ant species

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### Summary

The relative contribution of visual and chemical components in the orientation of *Lasius niger* and *Iridomyrmex humilis* (Argentine ant) workers during mass recruitment to newly discovered food sources is analyzed over short time intervals. While both species orient in response to the trail pheromone, a large number of *L. niger* foragers rapidly switch to a more individual orientation, based on their memory of environmental cues. *I. humilis* workers, on the other hand, predominantly use collective chemical cues. The effect of the number of reinforcements on visual learning and its interference with chemical communication show that olfactory cues always prevail in the Argentine ant. In *L. niger*, the proportion of ants orienting to visual cues is independent of the trail concentration. Detailed observations of the trail-laying behavior of individually marked foragers show that nearly all the *I. humilis* workers initially lay a trail, whereas only half the *L. niger* foragers do so. This proportion decreases considerably with the number of trips performed by *L. niger* workers, while remaining constant for the Argentine ants. These results are interpreted with respect to the species' behavioral ecology.

### Introduction

Mass recruitment to newly discovered food sources, compared to tandem running and group recruitment, is considered to be the most advanced form of recruitment in ants (Wilson, 1971; Hölldobler, 1978). In this recruitment process, the chemical trails deposited by foragers returning to the nest may stimulate trail following and serve as a guide to orient rapidly to the target area (see review by Passera, 1984; Beckers et al., 1989; Hölldobler and Wilson, 1990). Competition between trail versus visual orientation (sun compass orientation, visual landmarks) during homing or food gathering has been investigated in some species belonging to the genera *Pogonomyrmex* (Hölldobler, 1971; Hölldobler, 1976), *Camponotus* (Hölldobler et al., 1974;

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Klotz and Reid, 1992), *Atta*, *Acromyrmex* (Vilela et al., 1987; Jaffe et al., 1990), *Formica* (Möglich and Hölldobler, 1975; Henquell and Abdi, 1981; Cosens and Toussaint, 1985; Rosengren and Fortelius, 1986, 1987; Fourcassié and Beugnon, 1988) and *Lasius* (Traniello, 1989). Visual and chemical orientation cues are used according to a hierarchy which depends upon the species. The relative contribution of the foragers' memory and collective chemical trails in the workers' orientation during mass recruitment has not, however, been so far analyzed on the individual scale.

We report some aspects of the foraging strategy of the two mass-recruiting species, *Lasius niger* and *Iridomyrmex humilis*, concentrating on individual behavior of the workers rather than collective behavior of the society. We investigate the interplay between individual learning and chemical communication in the foragers' orientation and analyze their trail-laying behavior when moving to and from the nest during foraging. Our results are interpreted according to the species' ecological significance.

## Materials and methods

Colonies of *Iridomyrmex humilis* (*Dolichoderinae*) and *Lasius niger* (*Formicinae*) were collected at Port Leucate (Southern France) and Brussels (Belgium), respectively. They were reared in laboratory nests and fed with sugar water and freshly killed cockroaches.

Both species are generalists. In natural conditions workers forage on various kinds of prey, tend aphids for honeydew, collect nectar, and gather seeds (for *L. niger*: see Donisthorpe, 1927; Wilson, 1955; for *I. humilis*: see Newell, 1908, 1909; De Bach et al., 1951; Markin, 1970a; Buys, 1987). Mass recruitment to newly discovered food sources in the Argentine ant (*I. humilis*) relies on chemical trails originating from the workers' Pavan gland (Wilson and Pavan, 1959; Robertson et al., 1980; Van Vorhis Key et al., 1981). Chemical and behavioral analysis has shown that Z-9-hexadecenal (Z-9-16: Ald) is the trail component to which the workers are the most sensitive (Cavill et al., 1979; Van Vorhis Key and Baker, 1982a, b). In *L. niger*, trail pheromone is produced by hindgut secretions (Lenoir, 1979).

Colonies were starved for 4 days before conducting food recruitment experiments towards a sugared food source (1 M sucrose solution).

### *Visual and chemical components in the foragers orientation*

The experimental procedure was similar to that used in Aron et al. (1988). Ants were given access to a food source placed on a foraging arena connected to the nest by a Y-shaped cardboard bridge (30 cm long, 1 cm wide). The bridge had one fixed branch (15 cm long) connected to the nest entrance, and two removable branches (the fork of the Y) each leading to a foraging arena (Petri dishes 14 cm  $\varnothing$ ), and diverging from each other at an angle of 60°. Experiments were based on binary choices by outbound foragers between visual and/or chemical orientation cues. They were performed in two successive periods.

Feeding period: foragers were given access to a food source placed at the end of one of the branches (left or right) of the Y-shaped bridge, and were marked with a drop of paint (Humbrol Enamel®) while feeding.

Testing period: after 10 min, the experimental setup was modified in order to force the ants to choose between visual (laboratory surroundings or 60 watt light bulb) or chemical cues (trails). The orientation of marked (experienced) and unmarked (inexperienced, newly recruited) workers crossing the bridge was reported during the next 10 min.

In order to avoid spatial left/right laterality effect, the food source was randomly placed at either branch of the bridge.

### *Trail-laying behavior*

Trail laying was studied by monitoring the behavior of individually color-marked foragers crossing a cardboard bridge (30 × 0.5 cm) placed between the nest and a food source. The ants were observed laterally on a 20-cm section of bridge. We assumed that an ant lays a chemical mark each time its gaster touched the substrate (for more details on this technique, see Aron et al., 1989; Beckers et al., 1992). We considered a trailing passage as a passage on the bridge during which the ants made at least one mark. The results obtained for *I. humilis* were compared with that reported for *L. niger* by Beckers et al. (1992) in the same experimental conditions.

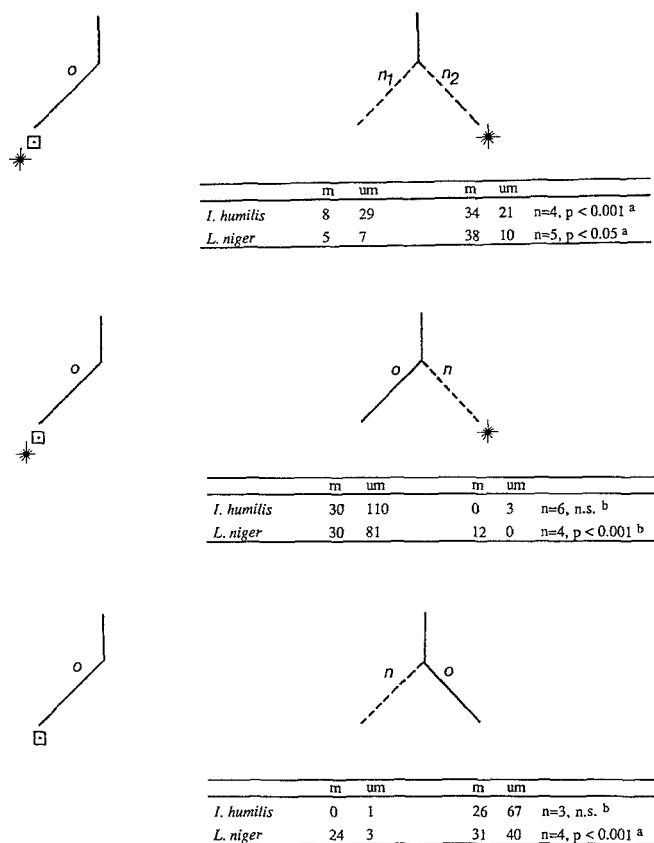
### *Individual memory and communication*

Binary choice experiments were performed with a cardboard Y-shaped bridge.

Feeding period: during food recruitment, foragers were given access to two food sources, each placed at one end of the bridge. The first source was associated with a 60 watt light bulb. The workers feeding at this source were individually marked with a color spot. They were allowed perform one to four passages towards the food. After each passage of a marked ant, the branch leading to the source was replaced by a virgin one. Simultaneously, the trail-laying behavior of the foragers having fed on the second source was observed on the other branch of the bridge, using the same technique as described above. This allowed us to approximate the trail pheromone concentration on the second branch of the bridge. This last parameter was estimated with two different experimental procedures according to the species studied. In *I. humilis*, the trail concentration corresponded to the number of passages on one branch of the bridge during which trail laying is observed (number of trail reinforcements). For *L. niger*, it was given by the total number of marks deposited by the foragers crossing the bridge (see text).

Testing period: workers having performed one to several passages towards the bulb were given the choice between visual cue and various trail pheromone concentrations.

Statistical tests used were taken from Siegel and Castellan (1988).



**Figure 1.** Experimental device and number of foragers crossing on each branch of the Y-shaped bridge during the testing period. m: marked (experienced) foragers; um: unmarked (naive) foragers. n: number of tests performed. <sup>a</sup>: Chi-square test; <sup>b</sup>: Fisher exact probability test. o: old branch (used during feeding period); n: new branch; □: food source; ☆: 60 watt light-bulb

## Results

### *Visual and chemical components in the foragers orientation (Fig. 1)*

Taking into account that both *I. humilis* and *L. niger* are typical mass-recruiting species that use strong chemical trails during foraging, we first tested how the workers orient in the absence of any chemical cues. The ants were given access to a food source placed at the end of one of the branches (left or right) of the bridge, and associated with a 60 watt light bulb added as a possible visual cue. The second branch of the fork was not placed during the feeding period. Once the first foragers were marked, the branch O leading to the food source was removed from the experiment and replaced by a new unmarked one ( $n_1$ ). The second branch of the fork, also unmarked ( $n_2$ ), was added to the experimental setup. Simultaneously, the light bulb was rotated 60° from

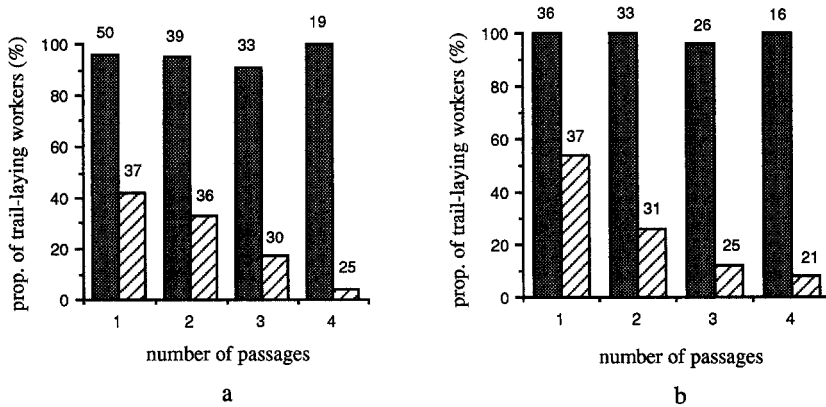
its initial position, in the direction of the second unmarked branch of the fork. For both species, most of the experienced (marked) foragers oriented according to the visual cue, whereas naive (unmarked) ones randomly crossed both branches of the bridge. Such a difference in behavior equally observed in both species illustrates a learning process in which the foragers are able to orient to visual cues in the absence of any chemical cues.

In the next two series of experiments, we tested the contribution of visual and chemical cues on workers orientation during foraging. In the first test, the ants were given access to a food source associated with a light bulb. At the onset of the testing period, the visual cue was moved ( $60^\circ$  rotation) to the newly placed unmarked branch (n). In the second experiment, no light bulb was used and only the influence of the laboratory surroundings (walls, furnitures, experimenter, etc.) was tested as orientation cues. For the testing period, the branch leading to the food source was then rotated  $60^\circ$ , and replaced by a new unmarked one (n). In both situations, experienced as well as inexperienced *I. humilis* workers followed preferentially the branch previously used during the feeding period (O) and maintained a chemical orientation, suggesting that olfactory cues dominate over visual cues. The results obtained for *L. niger* are different. Although a majority of workers followed the trail, our data indicate a difference in behavior between experienced and inexperienced workers: a significant number of marked foragers oriented according to visual cues, while naive ones crossed the marked (trailed) branch of the bridge (O), following chemical cues.

The mechanisms involved in the workers' orientation in *I. humilis* and *L. niger* during food recruitment are obviously different. In the first case, the workers follow almost exclusively collective chemical trails. Chemical communication also dominates for *L. niger*; nevertheless, the individual memory is competitive and enables the foragers to maintain a visual orientation, even when visual information is in conflict with chemical cues.

### *Trail-laying behavior*

We then compared the dynamics of trail-laying behavior during food recruitment in both ant species. More specifically, we concentrated on how trail-laying varies as a function of the number of trips made by an individual. Previous studies on the trail-laying behavior during food recruitment have revealed that foragers of both *I. humilis* and *L. niger* deposit chemical marks when following trails towards and away from the nest (Van Vorhis Key and Baker, 1986; Beckers et al., 1992). Our results show, however, that the dynamics of the foragers' trail-laying as a function of the number of trips made by the individuals greatly vary according to the species studied (Fig. 2). Firstly, in *L. niger* only 50% of individually marked foragers laid a trail during their first trip to or from the nest, while this proportion reaches  $\geq 90\%$  in the Argentine ants. Secondly, while the proportion of trailing passages both to and from the nest decreased considerably with the number of trips made by each *L. niger* individual, this parameter remained more or less constant for *I. humilis*. For both species, once a worker stopped trail laying, it generally did not resume the behavior at a latter passage.



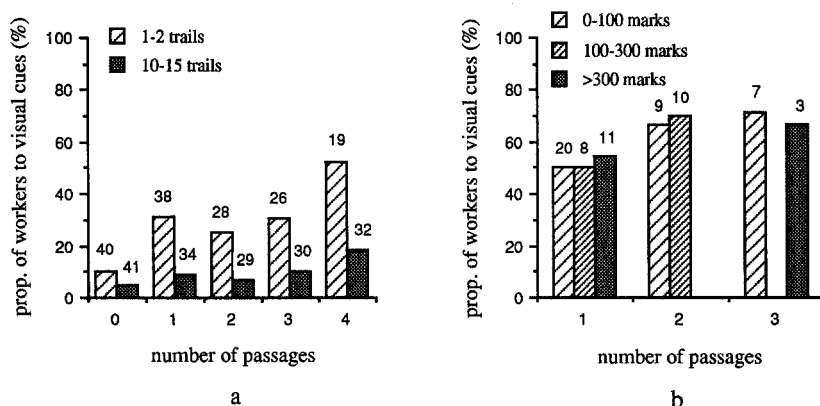
**Figure 2.** Proportion of trail-laying workers after 1, 2, 3 or 4 passages performed: (a) towards the nest and; (b) towards the food source. ■: *I. humilis*, ▨: *L. niger*. The total number of workers is reported on top of each column

### *Individual memory and communication*

To gain a better understanding of the factors affecting the interplay between individual memory of the visual cues and chemical communication, we carried out detailed analyses of the foragers' orientation, taking into account the trail pheromone concentration (see materials and methods) and the number of trips performed by the individuals towards the food source associated with a visual cue.

The results obtained for *I. humilis* are illustrated in Fig. 3a. It appears that for very weak trail concentrations (1–2 trail reinforcements) a large majority of foragers preferentially followed chemical trails, even after 1, 2, or 3 passages previously performed towards the food source ( $p < 0.05$  for all comparisons, Binomial Test). After 4 trips, however, about 50% of the workers followed the visual cue. Furthermore, there was a significant difference in behavior between experienced and naives foragers (0 passages previously performed towards the light bulb), as a larger proportion of experienced foragers oriented toward the visual cue ( $p < 0.05$  for all comparisons, Chi-square test). For higher trail concentrations (10–15 trail reinforcements) the proportion of foragers following visual cues decreased. These results suggest that the number of trips previously performed only weakly influenced the foragers' preference for visual cues.

In *L. niger*, as shown in Fig. 3b, the proportion of ants that oriented to visual cues slightly increased for 1 or 2 passages previously made towards the light bulb. After 2 passages a majority of ants oriented to visual cues, whatever the trail pheromone concentration. This proportion remained constant after 3 trips performed by the foragers; note, this could nevertheless result from the small sample size due to the difficulty in following a large number of workers crossing the bridge several times. The trail concentration thus does not seem to affect the forager's choice. For a given number of passages, the proportion of workers orienting to visual cues remained



**Figure 3.** Proportion of workers which orient according to visual cues after 1, 2, 3 or 4 passages performed towards the food source and for various trail pheromone concentration: (a) for *I. humilis*, the trail concentration corresponds to the number of passages during which trail-laying is observed; (b) for *L. niger*, the trail concentration is given by the number of marks laid by the recruiters. The total number of workers is reported on top of each column.

relatively constant, independently of the number of marks deposited (about 50%, 68%, and 70% for 1, 2, and 3 passages, respectively).

## Discussion

Both ant species studied perform cooperative foraging coordinated by collective chemical trails. However, as recruitment proceeded, the interplay between individual memory of the visual cues and chemical communication in the forager's orientation was clearly different according to the species.

As first suggested by Skaife (1955), and later by Van Vorhis Key et al. (1981), our results show that the Argentine ant relies essentially on collective chemically mediated orientation processes during food recruitment. Preliminary experiments (Aron, unpublished data) suggest that even in presence of long-lasting food sources (3 weeks), most of the foragers orient to chemical rather than visual cues. When several reinforcements of visual learning interfere with only one or two chemical trails, most of the foragers maintain an olfaction-based orientation. Although it is doubtful that such an experimental situation occurs in natural conditions, it clearly indicates the prevalence of chemical communication over individual memory during foraging. Only in the absence of olfactory cues do experienced foragers orient to visual cues (60 watt light bulb) when returning to the food. This leads us to suppose that both visual and chemical orientation mechanisms co-exist under natural conditions, and that visual cues could improve the foragers' orientation efficiency along the trail.

It is important to note that our experiments were carried out on a relatively short scale from a spatial and temporal point of view. Assuming that Argentine ant

societies exploit long-lasting food sources, one may not exclude that on longer time scales foragers develop an individual memory of the nest surroundings, which would therefore lead them to orient mostly to visual cues. Indeed, spatial fidelity to a particular nest hole, trails, and honeydew sites has been reported for the closely related Australian meat ant, *I. sanguineus* Smith in natural conditions (McIver, 1991).

Compared to *I. humilis*, a large proportion of *L. niger* foragers orient on their own memory of the visual cues when these latter are in competition with olfactory cues. Our results indicate that on a short-term scale (the feeding period lasting for 10 min) a chemical orientation dominates, although a large number of experienced foragers orient with respect to visual cues (laboratory surroundings, light source). Additional data (Gérard, 1987) obtained with a comparable experimental setup with two food sources suggest that after one hour, ants remain faithful to the source where they had previously fed, thus showing that a visual memory of the orientation cues is predominant. Our detailed experiments on the interplay between individual memory and chemical communication in *L. niger* are in accordance with these observations. Once the recruitment is well under way, the foragers' orientation appears more affected by the number of trips performed towards the food source rather than by the trail pheromone concentration. The proportion of workers orienting to visual cues is not influenced by trail concentration. These results suggest that the recruitment trail in *L. niger* would essentially function as a guideline for newly recruited nestmates, which would allow the workers to memorize the visual cues of the environment. Once this learning process is achieved, most of the foragers orient to visual cues. These results agree with those reported by Traniello and Levings (1986) and Traniello (1989) showing the use of precise information on their environment by homing *L. neoniger* foragers. In this species, recruitment trails are colony-specific and the trails of various colonies are spatially divergent in order to avoid confrontation between adjacent nests (Traniello, 1980). Although the initial phase of foraging activities is chemically mediated by hindgut trail pheromone, visual cues predominate later in the workers' orientation, which also shows a strong fidelity to their nest crater.

The results obtained on the trail-laying behavior of both species are closely related to our observations on the contribution of visual and chemical components in the workers' orientation. In *L. niger*, only half the foragers laid a trail and they stopped trail laying after a few trips, even though they continued to move to and from the source (see also Beckers et al., 1992). One may suppose that because of spatial memory, trail following becomes less necessary and therefore reduces trail-laying behavior. This is supported by evidence showing that *L. niger* workers rapidly learn visual cues. Nelson et al. (1991) have reported similar results for the mass-recruiting Ponerinae *Paraponera clavata*, and have showed that the number of trail-laying ants decreases with time during food gathering, which could be associated to the use of other orientation cues by the foragers. On the contrary, even after 4 trips performed between the source and the nest, almost all Argentine ants maintained a trail-laying behavior. Workers thus reinforce the chemical cues and collective orientation processes during recruitment, which agrees with our results on visual versus olfactory orientation.



The relative weight of visual and chemical orientation in both ant species may be tentatively interpreted with respect to their respective society size and their natural foraging habits. *L. niger* and *I. humilis* show extremely different society size. Argentine ants constitute dense polygynous populations consisting of several thousand workers, whereas *L. niger* societies are monogynous and reach 5000–6000 individuals (Stradling, 1970). The differences observed in the foraging strategy between the species could be related to their respective society size. This prediction is consistent with the hypothesis which suggests that the larger the society, the more it relies on chemically based foraging strategies (Deneubourg et al., 1986, 1987; Pasteels et al., 1987a, b; Beckers et al., 1989). Following this hypothesis, the organization of foraging activities in small-sized societies would mostly rely on individual capabilities, allowing the foragers to develop a good memory of the surrounding landmarks. This memory could lead to a spatial fidelity of the workers to parts of their foraging area and to the division of this area among several individuals. In large societies, such an organization based on individual performances could be harder to achieve, as the coordination of the activities of a large number of workers is more difficult. Foraging activities would then be mediated mostly by collective chemical communication. This mechanism gives large societies the opportunity to quickly concentrate a worker force on several feeding sites, allowing both a rapid exploitation of new discoveries and a massive defense against competitors. In this context, trail laying in societies of intermediate size such as in *L. niger* could perform two important functions: firstly, a rapid mobilization of the workers by mass recruitment to newly discovered food sources; and secondly, olfactory trails could serve as a guide during the acquisition of a visual memory of the environmental cues by the individuals. This latter would allow the societies to exploit many food sources simultaneously. In huge societies like *I. humilis*, the presence of a large number of individuals allows the collective exploitation of several food sources by chemical trails. The individual spatial memory seems therefore to play a minor role.

According to a more ecological interpretation, *L. niger* is a sedentary species usually foraging at long-lasting food sources, like honeydew produced by aphid colonies. Foraging to such highly predictable and stable resources may lead to a spatial specialization of the workers relying on the development of an individual memory of spatially organized visual cues, and to more individual foraging strategies (Rosengren, 1971; Rosengren and Fortelius, 1986; Cherix, 1987; Quinet and Pasteels, 1991). On the contrary, the Argentine ant is extremely restless and frequently emigrates during the course of a single season (Skaife, 1955; Markin, 1970 b; Benois, 1973). In this situation, it is probably more efficient that the foragers' orientation relies mostly on collective mechanisms allowing rapid displacement of a large population in response to any local disturbance, rather than on the development of an individual memory of the condition of environment by the foragers.

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