The dynamics of collective exploration and trail-formation in *Monomorium pharaonis*: experiments and model

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Abstract. When exploring a chemically unmarked area devoid of food sources, workers of the pest ant *Monomorium pharaonis* L. (Formicidae, Myrmicinae) leave scent marks on the ground and after 30–60 min a network of diverging exploratory trails begins to emerge.

Exploratory activity is affected by the nutritional state of the colony and a period of food deprivation induces a dramatic increase in the number of workers leaving the nest. A mathematical model based on a logistic growth equation is proposed to describe the exploratory recruitment observed. When travelling along exploratory trails the proportion of ants displaying trail-laying behaviour is higher for outbound than for nestbound workers. Outbound ants also show a greater propensity than nestbound ants to follow the scent marks of their nestmates. The chemical used to mark a novel area does not appear to be colony-specific and thus does not have a territorial function *sensu stricto*. The adaptive value of the collective exploratory behaviour observed in this study is discussed in relation to the common features of other pest ant species described in the literature.

Key words. Formicidae, *Monomorium pharaonis*, Pharaoh's ant, pest ant, exploration, chemical communication, recruitment, mathematical model.

Introduction

The ant species *Monomorium pharaonis* L. (Formicidae, Myrmicinae) is one of the best-known example of the so-called 'tramp ants' (Hölldobler & Wilson, 1990; Passera, 1993) the world-wide dispersion of which is a consequence of international trade. Spreading from its supposed native tropical Asiatic environment (Berndt & Eichler, 1987), it has adapted to the artificial environment created by man and is now thriving in most of the world's big cities. In the northern hemisphere it is commonly found in heated buildings where it is considered a pest and a potential vector of pathogen (Beatson, 1972; Edwards & Baker, 1981). Because of this, its physiology and control have been thoroughly investigated (see review by Berndt & Eichler, 1987). Comparatively few studies have been devoted to its behaviour. However, a better understanding

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of its foraging behaviour could be essential in designing more efficient methods of baiting for its control.

The foraging behaviour of *M.pharaonis* has been described by Sudd (1957, 1960) and Haack & Vinson (1990). Foragers use the mass recruitment system characteristic of several ant species (Hölldobler & Wilson, 1990); upon finding a large food source, they lay a scent-trail on their way back to their nest and arouse their nestmates which subsequently leave the nest and follow the trail to the food. An important aspect of the foraging behaviour of the Pharaoh's ant is the food-searching behaviour of individual scouts (Sudd, 1960). This component of foraging behaviour has often been neglected in the study of ant foraging strategies (Traniello, 1989). A greater efficiency in exploration strategy, however, may allow one species to take the lead when competition for food resources is high. Sudd (1960) did not study the detailed behaviour of individual scouts or the dynamics of exploratory recruitment. Our study intends to fill this gap by investigating the exploratory behaviour of *M.pharaonis* workers in the special

case where they are given access to a novel area devoid of food sources. In this paper we first describe the dynamics of collective exploration and propose a mathematical model to account for the observed phenomena. We then study the marking behaviour of individual workers during exploration and analyse its functional significance in terms of territoriality.

Material and Methods

Colony origin and maintenance. Five experimental colonies of *M.pharaonis*, each including brood and several queens, were obtained by dividing two large colonies collected at two different sites: Berlin (Germany) and Brussels (Belgium). They were kept in the laboratory in Fluon®-coated boxes and were provided for their nest with several glass test-tubes in which a tight cotton-wool plug trapped water at one end. The experimental room was maintained at a temperature of 25–28°C and under a LD 12:12 h regimen; colonies were fed regularly with an artificial diet (Bhaktar & Whitcomb, 1970) and segments of freshly cut mealworms (*Tenebrio molitor*).

Exploration dynamics. An arena (Ø = 2.4 m) covered by a uniformly flat 20 mm thick layer of white sand was used as an exploratory area. A nest-box was placed under the arena and connected to the arena by a glass tube inserted in a hole pierced in the centre of the arena. To avoid visual cues which could influence the direction of exploration, the arena was surrounded by white muslin. During the experiment it was lit by five 100 W 'daylight' Philips® bulbs placed directly 2 m above the centre. A video camera was placed under the arena and the number of nestbound and outbound workers going through the access tube was counted for 1 min every 3 min for a period of 3 h. To assess the total number of foragers in the arena, the net flow of workers was estimated from each minute censused and summed over the 3 h of observation. The influence of the nutritional state of the colony on the exploratory activity was studied by either feeding the colony on the eve of the experiment or starving it for 6–10 days beforehand. To test for the effect of a marked versus. an unmarked area on ant general activity, the flow of workers that had continuous access to the arena for a period of 8 or 15 days was also measured both for fed and starved conditions. Each combination, area unmarked–colony fed/starved, area marked–colony fed/starved was replicated twice. The same colony was used in all experiments and the layer of sand was thoroughly mixed before being levelled between each experiment.

Trail formation and stability. To investigate the formation of the trails created by ants from a starved colony during the exploration of a novel area, an area of 100 mm radius around the arena entrance was filmed by a second camera placed above the arena. The number of ants going through each 10° sector of a 70 mm radius circle centred on the arena entrance was then counted for 5 min every 15 min for a period of 3 h, beginning 15 min after the ants were given access to the arena. The number and location of the trails were determined by the most frequented sectors over the 3 h observation period. Variation over time of the percentage of total traffic across those sectors was used to study the formation of the trails.

Access to the arena was kept unobstructed and the stability of the trails was examined during the 2 subsequent days by filming the same area for 5 min every 2 h during the photophase (12 h). Ant traffic was sampled for the first 30 s of the 5 min recording. The variation of the percentage over time of the total traffic supported by each trail was used to assess their stability.

Marking behaviour during exploration. Marking behaviour was studied with simple binary choice experiments composed of two parts (Fig. 1). In the first part a 5 mm broad V-shaped piece of cardboard was used as a bridge between a nest-box and a chemically unmarked area devoid of food sources which was used as an area of free exploration. A unidirectional outbound flow of workers was created by immediately removing with a vacuum-cleaner all ants as they arrived in the exploratory area. The experiment was videotaped and the number of ants going over the bridge was subsequently counted. In order for the bridge to be marked by a variable number of workers, the duration of the experiment was varied between 1 and 30 min. In the second part the whole experimental set-up was rotated by 180° to cancel out any visual cues and the bridge was removed and incorporated as one of the branches of a diamond-shaped bridge freshly cut from a piece of cardboard which was installed between the exploratory area and the nest-box. All ants that had been captured in the first part of the experiment were then released in the nest-box. To determine whether ants prefer one of the branches, the number of outbound workers going over each branch was then measured for 10 min.

To investigate whether workers lay a scent trail when returning to the nest, workers were first given access to the exploratory area for a period of 30 min. A V-shaped bridge was then installed between the exploratory area and the nest-box and a unidirectional nestbound flow of workers was created by immediately capturing all ants arriving in the nest-box. These ants were then released on the exploratory area and the second part of the experiment was similar to that described in the preceding paragraph. For each situation the protocol was replicated twenty and twenty-three times respectively.

Trail-laying behaviour of individual workers was studied by recording on videotape the ants' movements on a 20 mm portion of a simple 5 mm broad cardboard bridge installed between the nest-box and an exploratory area. The tapes were then analysed frame-by-frame and marking was recorded each time an ant lowered the tip of its gaster to contact the bridge (Aron *et al.*, 1989). The percentage of nestbound and outbound moving ants displaying at least one instance of marking behaviour was measured for each 3 min interval of a 45 min period. The bridge was then removed and replaced by a new one. A unidirectional flow of nestbound workers was created by removing with a vacuum-cleaner all ants as they arrived in the nest-box and the percentage of nestbound workers displaying marking
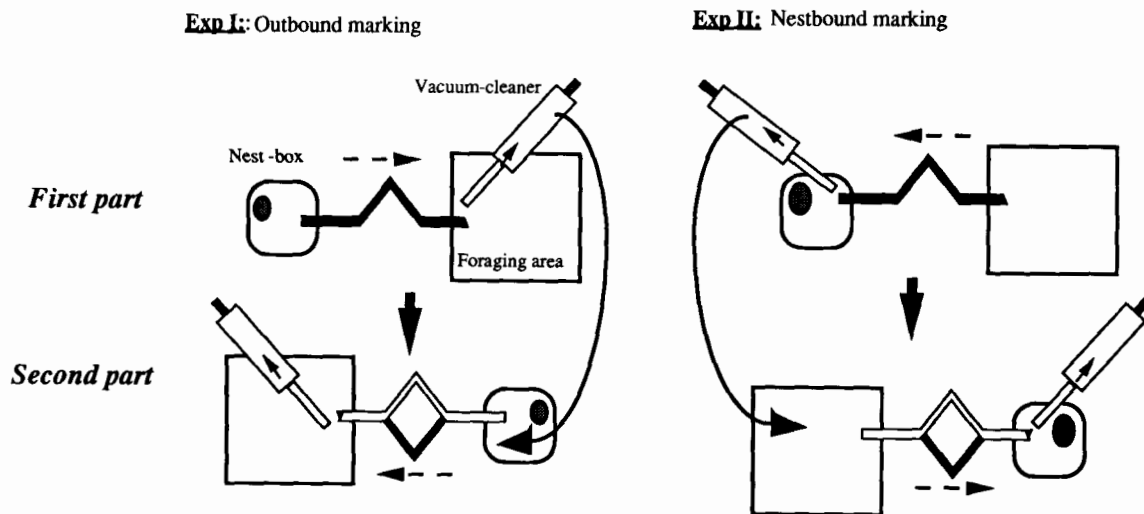
Fig. 1. Experimental set-up and procedure used to study trail-laying behaviour in outbound and nestbound workers during the exploration of a novel area. A unidirectional flow of workers is created by immediately removing with a vacuum-cleaner all ants reaching the end of the bridge.

behaviour was measured for a period of 30 min. The results were pooled over five replicates of the experiment.

Home-range marking and territoriality. To test for possible colony-specific home-range marking, two experimental colonies of different origin (Brussels and Berlin) were used. First, we tested nestmate recognition by putting a group of ten workers of the first colony in a 55 mm diameter Petri dish, the bottom of which was covered with a fresh piece of filter paper. After 5 min a worker of the second colony was introduced and all interactions noted during 3 min. The test was then repeated with a group of ten workers of the second colony and a worker of the first colony. Each protocol was replicated twenty times.

To test for colony-specific territorial marking the standard method described in Hölldobler & Wilson (1977) was used. In the foraging area of each colony two pieces of papers (100×100 mm) were placed at equal distance from the entrance to the nest. Colonies were fed *ad libitum* and after 3 days the foraging area was filmed for 10 min in each of the following situations: situation 1 (control for spatial bias) with the position of the papers unchanged; situation 2 (control for the effect of paper manipulation on the exploratory activity of the workers) with the position of the papers inverted; situation 3 (test for the existence of a home-range marking) with one piece of paper replaced by a fresh one; and situation 4 (test for colony specific marking) with one piece of paper replaced by another one previously marked by the other colony.

For each recording, the number of ants present simultaneously on each paper at 1 min interval was noted and pooled over the 10 min observation time. The average time spent on each piece of paper for a random sample of ten workers was also computed. The results of three replications with the same colony were pooled.

Results

Exploration dynamics

The cumulated net flow of workers from a fed colony which had free access to the arena for a period of 15 days increased slightly over the 3 h of observation (Fig. 2: thin dashed lines), indicating that the turning on of the lights at the beginning of the observation triggers an increase in the number of outbound workers. This effect was more pronounced when the colony was starved for 8 days (Fig. 2: thick dashed lines). Access to an unmarked area induced a dramatic increase in the net flow of outbound workers. The rate at which the flow increased during the first hour of the experiment was almost doubled when the colony was subject to a 10 day compared to an 8 day starvation period (Fig. 2: thick solid lines; mean net flow of workers per minute $\pm$SD: 73.90 ± 49.15, 45.85 ± 24.30, respectively); in the former case the colony actually almost emptied of its content after 3 h. In contrast, a fed colony showed only a weak exploratory activity on an unmarked area (Fig. 2: thin solid lines). Thus we observed the following sequence in the exploratory activity: (starved colony–area unmarked) > (fed colony–area unmarked) > (starved colony–area marked) > (fed colony–area marked) and we conclude that whether or not the substrate has been previously marked is more important than the nutritional state of the colony in eliciting the exploratory activity of the workers.

Based on our experimental data, the following mathematical model was designed to describe the dynamics of the exploratory recruitment observed towards a chemically unmarked area.

Let X be the population of ants in the area at time t, the mean flow of ants leaving the nest and arriving on the area is given by the logistic equation:

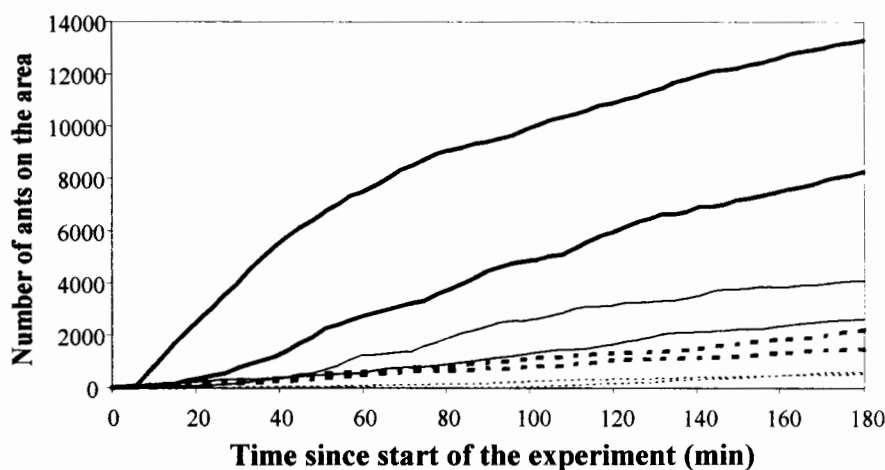$$F_{area} = aX (N - X) + c(N - X) \tag{1}$$

Fig. 2. Estimated number of ants on the arena as a function of time. Solid lines, unmarked area; dashed lines, area previously marked; thick lines, colony starved; thin lines, colony fed.

where a is the recruitment rate in number of ants per minute and per recruited worker, N the total number of ants available in the nest for the exploration at the start of the experiment, and c the spontaneous leaving rate in number of ants per minute.

a, N and c are determined empirically by the second-degree polynomial equation describing the relationship between the number of ants on the area (cumulated net flow of workers) and the flow of workers leaving the nest, F_{area}. Let

$$F_{area} = C_2 X^2 + C_1 X + C_0$$

then $C_2 = -a$, $C_1 = aN - c$, and $C_0 = Nc$.

The mean flow of ants leaving the area and returning to the nest is given by the equation:

$$F_{nest} = bX = X/T_{mean} \qquad (2)$$

where b is the departure rate in number of ants per minute.

b is determined empirically by the slope of the regression line describing the relationship between the number of ants on the area and the flow of workers coming back to the nest and is equal to the inverse of the mean time spent by a worker on the area, T_{mean}.

The general equation describing the rate of change of X, the total number of ants on the area, as a function of time is then given by:

$$\begin{aligned} dX/dt = F_{area} - F_{nest} &= (1) - (2) \\ &= c(N - X) + aX(N - X) - bX \qquad (3) \end{aligned}$$

The temporal evolution of X is given by the resolution of the integral of (3):

$$X = (A - RB)/(1 - R)$$

where A and B are the two roots of the right-hand term of equation (3) and

$$R = (A/B)e^{-at(A-B)}$$

when the population on the area at time $t = 0$ is null (exploration of an unmarked area).

When t tends towards infinity, X reaches an asymptote which is equal to the positive root of the right-hand term of equation (3).

The number of ants present on the area at time $t = 0$ in experiments where the colony had had free access to the arena for a period of $8-15$ days could not be estimated without serious disturbance of the ants as well as the substrate. The model was therefore tested only for the experiments where ants explored an unmarked area. Another problem was the choice of the period of time that had to be considered to estimate the parameters of the model. Indeed, our model was conceived to describe the dynamics of exploratory recruitment towards an area of infinite size. However, our experimental set-up imposed artificial boundaries on the movements of the workers. This led to changes in the pattern of exploration of the colonies which were not accounted for by our model. For example, because ants show a tendency to follow natural discontinuities, a circular scent-trail running along the edge of the arena progressively appeared as the exploration proceeded and an increasing number of workers got trapped on this trail. This was bound to affect several parameters of the model in an unpredictable manner. Based on our visual monitoring of several exploration experiments, we estimated that these boundaries effects began to be particularly important after 2 h of exploration. The parameters of the model were therefore estimated by considering as a basis the data collected during the first 2 h only of the experiments and the model was tested for this initial period of time. Table 1 gives the values of the parameters of the equation computed in different experimental conditions and Fig. 3 gives two examples of the fitting of an experimental curve with the model. The number of workers available for the exploration is always larger when the colony is starved than when it is fed. The other parameters are not affected in a consistent manner by the nutritional state of the colony.

Table 1. Parameter values computed according to equations (1) and (2) of the text for the first 2 h of exploration of an unmarked area in different experimental conditions. Nutritional state: +, fed colony, −, starved colony, with number of days of starvation in parentheses. a: recruitment rate in number of ants per minute and per recruited worker. N: number of ants available for the exploration. c: rate of spontaneous exit in number of ants per minute. T_{mean}: mean time spent by a worker in the area in minutes.

Experiment	Nutritional state	a	N	c	T_{mean}
1	−(10)	33.62×10^{-7}	11919	7.07×10^{-3}	259
2	−(8)	41.18×10^{-7}	8700	2.61×10^{-3}	191
3	+	152.30×10^{-7}	3850	1.55×10^{-3}	209
4	+	42.07×10^{-7}	4760	1.53×10^{-3}	328

Trail formation and stability

When workers at the exit of the test-tube leading to the arena encountered a chemically unmarked ground, they first moved hesitantly and randomly back and forth about the entrance to the arena. After 3−5 min, as the number of workers leaving the nest begins to grow rapidly, a few isolated individuals move away from the exit of the tube and slowly progress in the novel area. These workers tend to be followed closely by succeeding nestmates and in about 30−60 min, a network of diverging exploratory trails extending towards the periphery of the arena begins to appear. This network continues to develop, even in the absence of food sources on the arena. At the end of the 3 h observation period, 74% of the traffic was concentrated on five of the thirty-six 10°-angular sectors (30−50°, 110−120°, 230−240°, 260−270°), thus defining four trunk-trails starting from the arena entrance. The trunk-trails were formed rapidly: 15 min after the beginning of the exploration, the proportion of traffic on those sectors delimiting the trunk-trails was already greater than would be expected if the ants were dispersing randomly (Fig. 4: $\chi^2 = 12.45$, d.f. = 1, $P < 0.001$) and at 45 min the proportion stabilized

around 75%. It remained relatively stable thereafter, accounting for 60−90% of the total traffic of ants. The proportion of traffic on each trunk-trail did not vary over the first 2 days of the experiment. On the thrid day the level of general activity was too low to determine whether there was a change in this proportion.

Marking behaviour during exploration

When given a choice between an unmarked branch and a branch which was previously used by outbound workers only, ants heading towards the exploratory area in most experiments expressed a significant preference for the marked branch (seventeen out of twenty experiments). Ants heading to the nest, however, did not show any preference when faced with a choice between an unmarked branch and a branch previously used by nestbound workers only (significant choice for the latter branch occurred in eleven out of twenty-three experiments). Moreover, for both nestbound and outbound workers there was no relationship between the number of ants that went over the bridge in the first part of the experiment and the choice
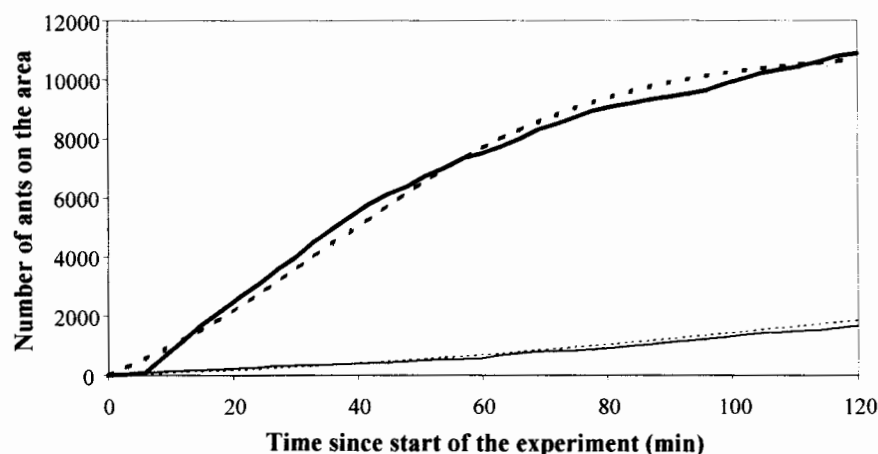

Fig. 3. Two examples of a fitting of an exploratory recruitment curve with equation (3). Solid lines, experiment; dashed lines, model; thick lines, experiment 1; thin lines, experiment 4 of Table 1.
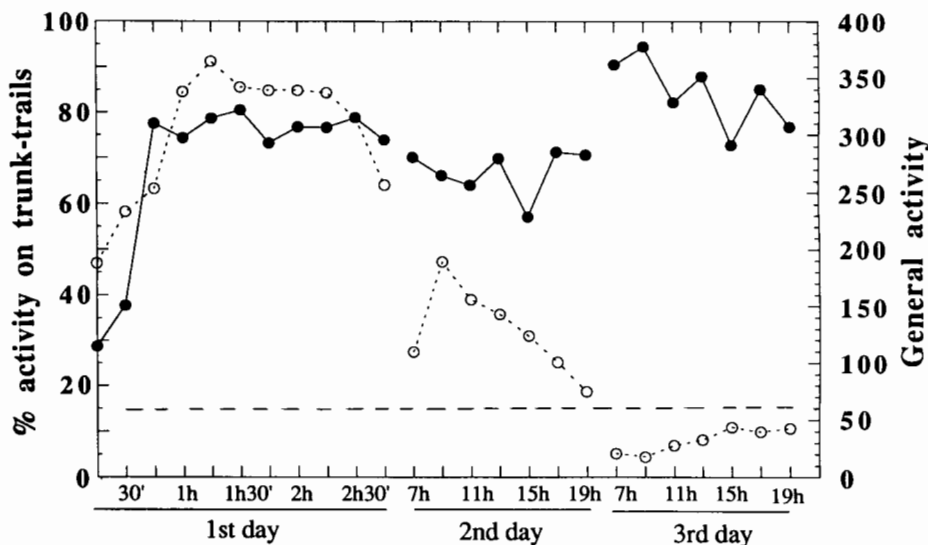
Fig. 4. Level of general activity over time (dashed line and open circles) measured as the number of ants crossing a 70 mm radius circle drawn around the nest entrance and percentage of activity on trunk-trails (unbroken line and filled circles) measured at the same distance as the proportion of ants travelling in the 10° sectors in which the trunk-trails were later found. Dashed line: percentage of activity expected on those sectors delimiting the trunk-trails if ants were dispersing randomly. Note the change in time scale between the first and the second and third days of observation.

expressed by the ants in the second part of the experiment (Spearman's rank coefficient: $\rho = 0.191$ and $\rho = 0.119$ respectively).

On a simple bridge with workers going in both directions, 70% of outbound ants displayed trail-laying behaviour, whereas for nestbound ants this proportion was only 27% (Table 2, part 1). For both outbound and nestbound workers there was a slight decrease in the percentage of ants marking over the 45 min of observation. On a previously unmarked bridge supporting a unidirectional nestbound flow of workers about 42.5% of workers displayed trail-laying behaviour (Table 2, part 2). In all cases the percentage of ants displaying marking behaviour was inversely proportional to the absolute number of ants involved in the traffic.

Home-range marking and territoriality

Control tests with workers belonging to the same colony did not show any effects of experimental conditions on aggressivity (Table 3). Most encounters between workers of two colonies of different origins immediately resulted in fierce and prolonged attacks (biting of appendages). Attacks were almost always initiated by the single non-resident worker introduced in the group of ten workers.

As shown in Table 4, ants frequented in the same manner and spent the same amount of time on two pieces of paper that had remained in their foraging area for 3 days. There was no effect of the manipulation of the papers on the level of exploratory activity of the workers (average time

±SD spent by the workers on the two pieces of paper when they are left in place: 13.67 ± 9.10; and after their positions have been inverted: 13.45 ± 8.43, $t = 0.135$, two-tailed Student's t test with d.f. = 118). A fresh paper was about 4 times more frequented than a 3-day-old paper from the same colony and ants spent about twice more time on it. There were no significant differences in the frequentation or in the total time spent on 3-day-old papers from the same or from a different colony.

Discussion

As in a number of other ant species (Beckers et al., 1989), mass-chemical communication is used by *Monomorium pharaonis* not only during foraging for food (Sudd, 1957; Haack & Vinson, 1990) but also during exploration of novel areas. While advancing on unmarked ground, workers intermittently lay short streaks of pheromone which tend to be closely followed by their nestmates. After 30–40 min, depending on the number of ants involved, interactions among workers through the trail-pheromone laid on the ground lead to the emergence of a network of diverging exploratory trails. When measured at 70 mm from the entrance tube, the proportion of workers travelling on these exploratory trails rises to 75% in <40 min. This figure remains stable thereafter despite the decrease in the total number of workers travelling to and from the nest. Observations over 3 days show that the spatial organization of the network remains unchanged as long as no food is found on the arena (Fourcassié & Deneubourg, 1992). Exploratory trails form well-defined routes along which

Table 2. Marking behaviour of individual workers observed on a 5 mm broad cardboard bridge placed between the nest and a chemically unmarked area devoid of food sources. Part 1: bi-directional traffic: outbound and nestbound traffic measured for 45 min. Part 2: unidirectional flow: nestbound traffic measured for 30 min. For each experiment, the total number of ants and the absolute and relative frequency of workers displaying at least one instance of marking behaviour on a 20 mm portion of the bridge are given.

Part 1. Bi-directional traffic

	Outbound traffic			Nestbound traffic		
Exp.	Total no. of ants	No. marking	Marking (%)	Total no. of ants	No. marking	Marking (%)
1	413	330	80.0	46	24	52.0
2	645	486	75.3	95	49	51.6
3	894	697	78.0	96	42	44.0
4	1031	588	57.0	463	75	16.2
	Σ2983	Σ2101	70.4	Σ700	Σ190	27.1

Part 2. Unidirectional traffic (nestbound only)

Exp.	Total no. of ants	No. marking	Marking (%)
1	59	50	85.0
2	106	70	66.0
3	311	133	42.8
4	373	108	29.0
	Σ849	Σ361	42.5

Table 3. Nestmate recognition experiments. A worker from an alien colony is introduced in a 55 mm diameter Petri dish containing ten workers from another colony. Interactions are observed for a 3 min period.

Resident colony (ten workers)	Alien colony (one worker)	No. of encounters	Attacks		
			No.	Initiated by resident	Initiated by alien
Brussels	Brussels	20	0	—	—
Brussels	Berlin	20	13	3	10
Berlin	Brussels	20	13	2	11

Table 4. Test for colony-specific home-range marking. The average time in seconds (±SD) spent by a sample of thirty workers on each 100×100 mm piece of paper is given. The number given in parentheses is the number of ants simultaneously present on the paper at 1 min intervals, pooled over the 10 min observation time. A two-tailed Mann-Whitney test is used to compare the samples. NS: $P > 0.05$.

	Paper 1	Paper 2	M-W test
Homocolonial A v. Homocolonial B	13.87 ± 11.45 (75)	13.47 ± 6.13 (84)	$Z = 1.015$ NS
Homocolonial B v. Homocolonial A	15.23 ± 9.38 (73)	11.67 ± 6.13 (85)	$Z = -1.552$ NS
Fresh paper v. Homocolonial	29.93 ± 15.98 (418)	14.47 ± 10.66 (110)	$Z = -4.024$ $P < 0.001$
Heterocolonial v. Homocolonial	14.03 ± 8.46 (112)	17.8 ± 12.29 (110)	$Z = -1.006$ NS

the workers patrol. The discovery of food sources changes the proportion of traffic on each route, rather than the spatial structure of the network (Fourcassié & Deneubourg, 1992).

The foraging and exploratory activities of the Pharaoh's ant seem to be affected by the intensity of the light illuminating the arena; illuminating the arena induced an increase in the flow of workers leaving the nest. Since this increase occurred rapidly, it is unlikely that it was due to a rise in the temperature of the substrate or ambient air. Although *M.pharaonis* is not known as being a strictly diurnal species (Berndt & Eichler, 1987), Sudd (1960) reports that most colonies he observed in Nigeria became inactive during the night, and we repeatedly observed a marked decline in the foraging activity when the colonies were placed in the dark. It is likely that *M.pharaonis*, as do a number of other ant species, shows a positive phototropism which is responsible for the phenomena observed.

The dynamics of collective exploration which we observed can be compared in many respects with the dynamics of food recruitment that has been described in ants using mass chemical communication (review by Hölldobler & Wilson, 1990). During the first 2 h of exploration the number of ants present in the arena follows a logistic growth equation which can be described by a mathematical model similar to that used in modelling mass recruitment to a food source (Verhaeghe & Deneubourg, 1983; Deneubourg *et al.*, 1983).

Whether the area had been previously marked or not, food deprivation induced a greater number of workers to leave the nest. In a chemically unmarked area the effect of starvation on exploratory activity was correlated with the number of days of starvation. This was particularly clear after 10 days of starvation, whereupon the colony almost emptied when given access to a novel area. Our mathematical model suggests that the only parameter which is affected in a consistent way by a period of starvation is the number of ants available for the exploration. One hypothesis, often mentioned in the literature, is that food deprivation acts by lowering the threshold of foraging activity of the workers. This would increase the size of the population available for the exploration.

At the individual level, the exploratory behaviour of the workers of *Monomorium pharaonis* is essentially the same as that observed in *Lasius pallitarsis* (Nonacs, 1991), *Iridomyrmex humilis* (Aron *et al.*, 1989), *Pheidole pallidula* (Detrain *et al.*, 1991), in army-ants *sensu stricto* (see review by Hölldobler & Wilson, 1990), as well as in other ants characterized by legionary behaviour such as *Pheidologeton diversus* (Moffett, 1988) and some species of the genus *Leptogenys* (*L.processionalis*: Ganeshaiah & Veena, 1991; *L.distiguenda*: Maschwitz *et al.*, 1991; *L.nitida*: Duncan, 1992). Although the composition and origin of the chemical substance left on the ground is very different among these species, the same basic operational rule is followed by exploring workers. Whenever an unmarked area is encountered, they lay scent-marks. If, on the other hand, they come across scent-marks laid by other workers, they are reinforced and closely followed. The collective

pattern of exploration emerging from this simple individual behaviour, however, varies greatly among species. Whereas *Iridomyrmex humilis* forms a moving exploratory front much like the one observed in species with legionary behaviour (Deneubourg *et al.*, 1989, 1990), the collective pattern of exploration in *Monomorium pharaonis* is closer to what is observed in *Pheidole pallidula* (Detrain *et al.*, 1991), where one or more exploratory trails slowly emerge as the workers disperse on the novel area. Our observations show that in the Pharaoh's ant, on a bridge supporting a bi-directional traffic of ants, the proportion of ants displaying trail-laying behaviour is much higher for ants travelling from than for ants travelling to the nest (Table 2), whereas in *Iridomyrmex humilis* (Aron *et al.*, 1989) and in *Pheidole pallidula* (Detrain *et al.*, 1991) the proportions are the same in both directions. We do not know, however, whether this difference is offset by nestbound workers trail-laying more frequently and depositing longer pheromone streaks than outbound workers. The fact that only four out of ten nestbound workers show trail-laying behaviour when moving on a bridge supporting a unidirectional traffic of workers (Table 2, part 2) could explain why ants heading towards the nest did not show any preference when faced with a choice between an unmarked branch and a branch previously used by nestbound workers only. In addition, Pharaoh's ant workers are known to possess some visual orientation capabilities (Sudd, 1960) and therefore nestbound workers may rely as much on sparsely distributed scent marks as on visual cues available within the experimental set-up to find their way back to the nest. Outbound workers, on the other hand, may be more reluctant to move off the scent-trails, because these may allow them to disperse over distant areas which have not already been swept by other workers. As they progress along the trail, the pheromone concentration decreases. Thus the further they move from the nest, the more likely they are to wander off from it (Pasteels *et al.*, 1986), and this could explain why no clear fanning exploratory front is observed at the end of the trail. Our hypothesis is that the collective patterns of exploration observed in the ant species using mass chemical communication emerge as a result of a self-organizing process based on the relatively simple trail-laying and trail-following behaviour of individual workers. Differences among species in the patterns of exploration could be explained by differences in the chemical properties of the pheromone (rate of evaporation and/or adsorption), in the number of workers involved or in the value of the parameters intervening in the exploration behaviour of individual workers, e.g. directionality of their movements, amount of pheromone laid and manner in which it is deposited (continuous/discontinuous), propensity to follow the scent-marks left by other workers. For example, using the same mathematical model with different parameter values, Deneubourg *et al.* (1989) have been able to generate the different collective patterns of raiding observed in three species of the army-ant genus *Eciton*.

The network of exploratory trails in *M.pharaonis* acts as a system of mass recruitment which allows a rapid occu-

pation of a novel area. As soon as a portion of chemically unmarked ground has been discovered, it is immediately occupied and marked by the workers. This behaviour has been described in numerous species of ants (*Oecophylla longinoda*: Hölldober & Wilson, 1977; *Atta cephalotes*: Jaffé *et al.*, 1979; *Myrmica rubra*: Cammaerts *et al.*, 1977; *Camponotus rufipes*: Jaffé & Sanchez, 1984; *Solenopsis geminata*: Jaffé & Puche, 1984; *Pseudomyrmex termitarius* and *Pseudomyrmex triplarinus*: Jaffé *et al.*, 1986; *Leptothorax unifasciatus*: Aron *et al.*, 1986; *Solenopsis invicta*: Gordon, 1988). Providing the portion of unmarked ground and the number of workers are large enough, this process can sometimes lead to the emergence of one or several exploratory trails, as observed in our experiments. However, whereas in most of the species mentioned above, workers have been found to discriminate between a surface marked by their nestmates and a surface marked by workers of another conspecific colony, in *M.pharaonis*, despite strong agonistic interactions between workers of different origins, no evidence of such discrimination was found. The pheromone used to label a novel area therefore lacks colony-specificity, and the marking behaviour of the Pharaoh's ant should be termed home-range marking rather than territorial marking (see Hölldobler & Wilson, 1990, p. 286, for definitions); it is used by the foragers as a way to assess that they are on familiar ground but does not deter workers of other conspecific colonies from entering their foraging area. For the same reason, the term exploratory rather than territorial recruitment is more appropriate to describe the recruitment process to a novel area observed in our experiments. *M.pharaonis* forms large polydomous colonies, and workers of the same area do not show any aggressive interactions between each other. A colony-specific territorial pheromone would thus be of little adaptive value for this species. It is likely that, as in *Iridomyrmex humilis* (Aron *et al.*, 1989) and *Pheidole pallidula* (Detrain *et al.*, 1991), the same chemical substance (Faranal, originating from Dufour's gland: Hölldobler, 1973; Ritter *et al.*, 1977) mediates both exploratory and food recruitment.

Since there are no reports on the foraging ecology of *M.pharaonis* in its native habitat, it is difficult to assess the original adaptive value of the collective exploration behaviour described in this paper. However, a few suggestions can be made as to the adaptive value of this behaviour in the human environment, and some of these suggestions should apply equally to the native environment of the species. First, ants patrolling on the exploratory trails can be used as a worker force immediately available for recruitment by successful scouts coming back from a newly discovered food source. *M.pharaonis* is known to have a preference for protein baits (Haack & Vinson, 1990). It does not collectively retrieve large prey but dissects them on site. A prompt mobilization of workers around prey items is therefore essential in preventing their appropriation by competing species. Recruited workers aggregate around prey items, show extreme interspecific aggression, and defend the resource by smearing it with a substance from their poison gland which has a strong repellent effect

on other species (Hölldobler, 1973). Although *M.pharaonis* foraging indoors are likely to meet few ant competitors in Europe, excursions outdoors to rubbish dumps often occur in the summer (personal observations in Belgium) and competition with other tramp species ants has been observed indoors in Brazil (Fowler *et al.*, 1993). *M.pharaonis* is a small ant and is likely to be vulnerable to most competitors. Chemical interference may thus provide the best means to defend and secure food resources. Second, *M.pharaonis*, like other tramp species (Passera, 1993), settles in precarious sites and frequently moves nests (Berndt & Eichler, 1987). A rapid occupation of a novel area can be secured by collective exploration and this behaviour should therefore be of particular advantage to establish a new foraging area and pre-empt other ant colonizers (Fowler, 1993; Fowler *et al.*, 1993). In a human environment it should also allow a fast recovery of the foraging area after a heavy washing. Finally, *M.pharaonis* is a highly polygynous species and colony multiplication and foundation occurs by budding in which a group of individuals with at least one fertilized queen emigrates from the main nest to a new nest site (Petersen & Buschinger, 1971). Workers of large colonies nesting in limited space should therefore explore as much for food as for new sites. In fact, during the early phase of collective exploration we often observed a few queens leaving the nest and travelling along the exploratory trails.

The three species of 'tramp' ants most commonly encountered throughout the world in the human environment are *Iridomyrmex humilis*, *Monomorium pharaonis* and *Wasmannia auropunctata* (Passera, 1993). These three species share a number of biological and behavioural characteristics which are likely to have been determinant for their ecological expansion, e.g. an opportunist diet and the formation of highly polygynous and polydomous colonies (Ulloa-Chacon, 1990). Because it allows the rapid occupation of a novel area, collective exploration by means of mass-chemical communication may well be another important asset for the colonization and the establishment of dominance of environments modified by human activities. In fact, exploratory recruitment and the formation of a network of exploratory trails has been demonstrated in *I.humilis* (Deneubourg *et al.*, 1990) and observations of *W.auropunctata* workers foraging in the field in New Caledonia (Jourdan, personal communication) seem to indicate that this species uses a similar exploration strategy.

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