

THE MASS RECRUITMENT SYSTEM OF THE LEAF CUTTING ANT, *ATTA CEPHALOTES* (L.)

By K. JAFFE & P.E. HOWSE

Chemical Entomology Unit, Department of Biology, The University, Southampton, SO9 3TU

Abstract. The recruitment system of *Atta cephalotes* workers was studied in the laboratory. The number of ants recruited to a food source depends on the quality of the food and on the duration of starvation of the colony, and is related to the concentration of trail pheromone on the trail but not to the number of ants initially returning to the nest from the food source. There is a relationship between the concentration of pheromone on the trail and the attractiveness of the food. A component of the trail pheromone, methyl 4-methylpyrrole-2-carboxylate, was found to elicit similar recruitment behaviour to a natural trail. Individual workers of *A. cephalotes* appear to modulate the number of ants recruited for food retrieval by varying the quantity of pheromone secreted from the poison sac during trail-laying.

Introduction

The social insects, and especially ants, have evolved a multitude of ingenious mechanisms which serve to assemble workers for joint efforts in food retrieval. A variety of strategems is used by ant species in recruiting nest-mates to a new food source. These strategems may involve the use of motor displays, visual orientation, chemical communication and tactile stimulation.

A primitive recruitment system that occurs in ants has been termed 'tandem running' (Wilson 1971). Here odour trails, if present, serve only as orientation signals, and an ant recruits only one nest-mate at a time. In the more efficient system of group recruitment, a recruiting ant guides a group of five to ten workers to the food source (Traniello 1977). In both systems, trail pheromones provide only directional information and are unable to induce recruitment.

In the advanced systems of chemical mass communication, it is the amount of trail pheromone discharged by workers that determines the number of ants leaving the nest for food. This kind of recruitment has been studied in *Solenopsis* (Wilson 1962), *Lasius fuliginosus* (Hangartner 1967), *Pogonomyrmex* (Hölldobler 1976) and *Myrmica rubra* (Cammaerts 1977).

In fungus growing ants of the tribe Attini, a trail pheromone component (methyl-4-methylpyrrole-2-carboxylate) has been identified by Tumlinson et al. (1971, 1972) from the poison sac of *Atta texana*, and by Riley et al. (1974) from *Atta cephalotes*. Robinson et al. (1974) found that *Acromyrmex octospinosus* also followed a trail of the carboxylate.

The foraging activity of these ants has been studied by Cherrett (1968, 1972a), Robinson & Cherrett (1978), Lewis et al. (1974), Rockwood (1976) and others in the field.

We have made a detailed analysis of the recruitment system of *Atta cephalotes* in the laboratory and investigated the information transferred by the trail pheromone. The following features were studied: (i) the recruitment to different kinds of foods (experiments A & B), (ii) the fidelity to a trail (experiment C), (iii) the response to poison sac extracts (experiment D), and (iv) the response to the pheromone presented as a trail (experiments E & F) or at a single point near the nest entrance (experiment G).

Materials and General Methods

Cultures

Three small colonies of *Atta cephalotes* collected in Trinidad, West Indies, were cultured on pairs of tables (53 × 38 cm) in an insectary maintained at 28 ± 2 C and 70 to 90% R.H. with a 12 h light/12 h dark cycle. The light source was fluorescent strip light. Nest chambers placed on one table (T1, Fig. 1) consisted initially of plastic boxes, and subsequently of inverted 1350 ml museum jars on plaster of Paris bases. These were filled with fungus and brood as the size of the colony increased. Food was supplied on the second table or in some cases a third table (T2 & T3, Fig. 1). Tables were connected by wooden bridges. The insects were fed with cabbage (*Brassica* sp.) and during some experiments bramble (*Rubus fruticosus*) was used as forage material. The experiments were performed between 11.00 hours and 14.00 hours (lights out 16.00 hours). Not more than one experiment a day was performed on each colony.

Chemicals

A pure sample of the synthetic pheromone, methyl-4-methylpyrrole-2-carboxylate, was dissolved in redistilled diethylether (BDH Chemi-

cals Ltd., Eng.). The solutions were applied with a micropipette.

Statistical Treatment of the Data

Results are expressed as arithmetic means of the number of ants per minute, crossing a particular point on the trail, at different times during each experiment. The curves representing the number of ants on the trails in different experiments were compared using: (a) the total number of ants passing a certain point during the seventh and the ninth minute after the start of the experiment. The sum of these is referred to as the 'cumulative rate' in the text. (b) The 'initial slope' is defined as the regression line (determined by the method of least squares) of the means between 1 and 5 min in experiments A and B (where recruitment is spontaneously initiated after $t = 0$ min) and between -1 and 3 min in all other experiments.

Results

Preliminary Observations: Finding a New Food Source

Methods. Food was placed on the foraging table (T2, Fig. 1) and the first ten or fifteen scout ants (see below) to arrive at the food source were marked with a spot of acrylic water paint on the metathorax or the abdomen. The marking was done during their return without their removal from the table.

Results. The ants found on a food source could be classified into at least three different categories: leaf-carrying workers; scouts; and other workers to which a specific function could not be assigned, but which were seen walking on the nest table or over the food source. The leaf-carrying workers were those which cut the leaves and/or transported them to the nest, generally laying trails in the process. The scouts were those workers which reached the food source and returned to the nest, without food, but laying a trail.

When a scout arrived at a new food source, it touched the food with its antennae and mouth parts and ran quickly back towards the nest without food, touching the tip of its abdomen to

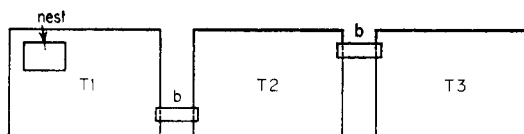


Fig. 1. Nest arrangement showing nest table T1 and two consecutive foraging tables T2 and T3, connected by wooden bridges b.

the ground (trail-laying). When the ant arrived at the nest, it turned and ran back to the food source again, touching the abdomen on the ground. Often the scout did not reach the nest, but turned back again when it met other ants coming towards it. Typically, a scout would make the trip several times from the food to the nest or to the point where it met other ants. Only after 30 to 60 min was the first marked scout seen carrying leaves to the nest.

It was frequently observed that, on its way to the nest or back to the food source, the scout stopped beside other ants and was touched by their antennae. These ants then ran towards the food source. Other ants, as soon as they got near the fresh trail, ran towards the food source without any physical contact with the scout.

Five or six minutes after a new food source had been offered to the ants, the first leaf-carrying ant was observed on its way to the nest. The ants then began to arrive in large numbers and covered the food, many of them cutting leaves or carrying them to the nest. Approximately 10 min after the mass arrival of workers at the food source, an equilibration of the recruitment took place, in which the number of ants arriving at the food was similar to the number returning to the nest.

Conclusions. These observations indicate the existence of at least two different kinds of communication in the recruitment of *A. cephalotes*. One is chemical (trail-laying) and another involves direct contact between two individuals.

The recruitment process, according to these observations, can be divided into three phases. The initial phase corresponds to the first 5 min after the food has been offered, and before the first leaf-carrying ant is seen on its way to the nest. The second phase, of mass recruitment, corresponds to the maximum amount of recruitment reached in the whole process. It begins approximately 5 min after the food has been offered. In the third, equilibrium, phase, the number of ants returning to the nest approximately equals the number of ants reaching the food source. This phase is reached at about 15 min after the food has been offered.

Experiment A: Recruitment of a New Food Source: Cumulative Measurements

Methods. The number of ants per minute going to a new food source and to the nest was measured at different time intervals before and after the new food had been placed on the food

table. The following parameters were varied in this experiment: (a) type of food, (b) distance of the food from the nest in metres, and (c) duration of starvation before the food was presented, measured in hours. The schedule of testing is shown in Table I.

Results. The rates of recruitment (Fig. 2a) show that experiments A1 and A3 give similar patterns. Thus, a more attractive food source (A3) has a similar effect on the recruitment process as a long period of starvation (A1), as measured by the comparison of initial slopes in the initial phase of recruitment, and the comparison of the cumulative recruitment rates in the mass recruitment phase (Table II).

Experiment A4 (Fig. 2a and Table II) shows that a less preferred food and a shorter period of starvation results in a slower rate of increase in the number of ants going to the food source and in a lower maximum in the mass recruitment phase. Experiment AC is a control, in which the number of ants going to an empty table was recorded after food had been offered on a table on the opposite side of the nest. The control is significantly different from all other experiments as shown by analysis of variance and Hartley's test (Table II).

The effect of the distance from the food to the nest on the recruitment process is shown in experiment A1 (short distance) and A2 (long distance) (Fig. 2b). In both we see a rapid increase in number of ants recruited to the food, but this increase occurred 3 min later in A2 than in A1. The slopes of both curves in their rapid increase phase, i.e. the part of the curve where the greatest increase in the recruitment rate is observed (which is between min 1 and 5 in A1 and min 3 and 7 in A2) are not statistically different ($P > 0.1$, Student's *t*-test). However, the initial slopes (first 5 min) are different ($P < 0.05$, Student's *t*-test).

Table I. Schedule of Experiment A

Experiment	<i>n</i>	Food on T2	Distance from the nest (m)	Duration of starvation (h)
A1	6	Cabbage	0.5	48
A2	6	Cabbage	1.0	48
A3	5	Bramble	0.5	12
A4	8	Cabbage	0.5	12
AC	9	Cabbage on opposite food table	0.5	48

The mean time an ant took to walk an approximate distance of 0.5 m, following a natural trail, was 96 ± 18 s ($n = 10$). Therefore the time needed for the rapid increase phase to take place is twice as long as the time an ant takes to go from the food source to the nest.

In both experiments A1 and A2, a decrease in the number of ants returning to the nest was observed (Fig. 2b, A1' and A2') simultaneously with the rapid recruitment phase. This decrease in the number of ants is significant ($P < 0.05$, sign-test) if the minimum number of returning ants ($t = 3$ min in A1 and $t = 7$ min in A2) is compared with that occurring 2 min previously or 4 min subsequently.

The total number of ants returning to the nest in the initial recruitment phase is relatively small,

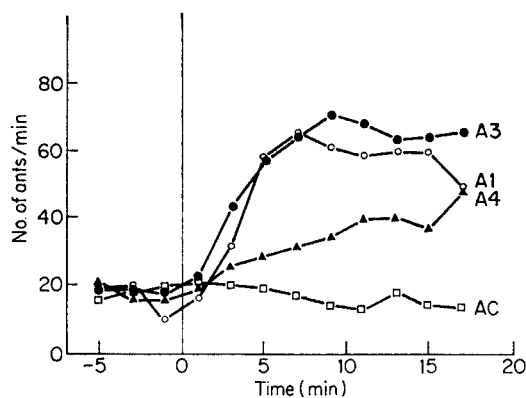


Fig. 2(a)

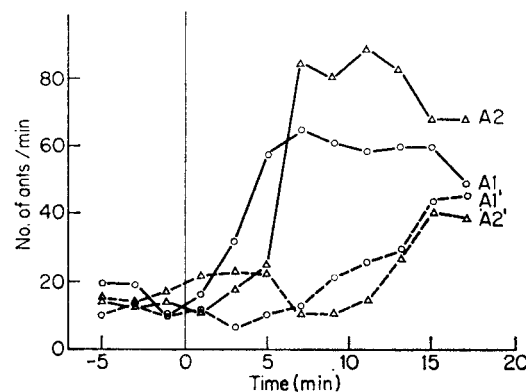


Fig. 2(b)

Fig. 2. Number of ants per min going to and also coming from (A1', A2'; 2b) the food source at different times before and after the food had been placed on the foraging table (see also Table I).

and is not related to the number of ants recruited in the mass recruitment phase. The relationship between these numbers can, however, be expressed in terms of a modification of the previously defined cumulative rate of returning ants. If we take the cumulative rate of returning ants from min 1 and 3 and compare them with the cumulative recruitment rate at min 7 and 9, the results are: for A1, 20 ± 6 returning ants to 125 ± 16 recruited ants; for A3, 17 ± 5 to 138 ± 29 ; and for A4, 26 ± 8 to 69 ± 32 . A chi-squared test shows that the ratio in A3 is not different from that in A1 ($P > 0.1$), but the ratio in A4 differs from those of A1 and A3 ($P < 0.001$) There is no constant relationship between the number of ants returning to the nest in the first 3 min of the recruitment process and the number of ants recruited to the food source later.

Conclusion. The kind of food and duration of starvation are important in determining the level of recruitment to a food source in the ants. On the other hand, the number of ants recruited to the food source is not dependent on the number of ants which leave the food and return to the nest to recruit nest-mates. This

suggests that a mechanism exists which enables an individual ant to modulate the recruitment process.

When nest-mates begin to arrive in numbers at the food source the number of unladen ants returning to the nest drops, and observation indicates that a proportion of the returning ants turn back towards the food. This suggests that the ants may be able to regulate their recruiting activity along a trail according to the number of foragers on that trail.

Experiment B: Discrimination between two Recruitment Processes

Methods. These experiments were designed to study the interference between a new recruitment process and one already in progress. The colony of ants was connected by means of bridges to two tables in series (T2 and T3, Fig. 1). Two sets of experiments were performed. In both, cabbage was placed on T2, and 15 min later an alternative food source of either bramble (B1) or cabbage (B2) was placed on T3. The number of ants going from T2 to T3 and from T3 to T2 was measured on the bridge separating the two tables. Each set of experiments consisted of five replicates.

Results. The mean time an ant took to go from T2 to the nest was approximately the same as that from T3 to T2 (96 s and 88 s respectively). If the results of these experiments are compared (Fig. 3) with those of experiment A (Fig. 2b) it should be possible to show whether the recruitment process is initiated mainly from the nest or from the food source on T2.

Table II. Analysis of the Data from Fig. 2a

A. Analysis of variance

Source of variation	Sum of squares	Deg. of freedom	Mean square	F
Experiments	39 318.6 (452.5)	3 (3)	13 106.20 (150.83)	23.5*** (42.3)***
Error	8 943.2 (57.1)	16 (16)	558.95 (3.57)	
Total	48 261.8 (509.6)	19 (19)		

Upper values are obtained from cumulative rates ($t = 7$ and 9 min) while those in parenthesis are taken from initial slopes. (***) = $P < 0.001$

B. Multiple range test (Hartley's test)

Values taken from	Mean values in experiments:			
	A1	A3	A4	AC
Cumulative rates	125.0	138.0	69.0	27.6
Initial slope	10.4	10.2	2.6	-0.6

Any two means joined by the same line are not significantly different ($P > 0.05$).

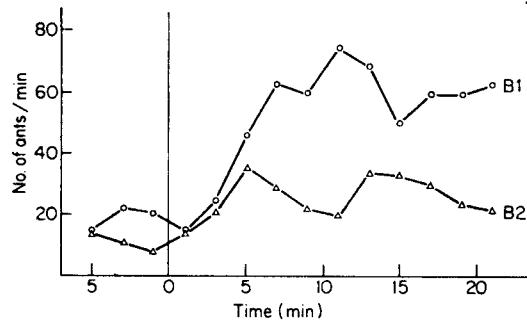


Fig. 3. Number of ants per min going to the food source on T3 before and after cabbage (B2) or bramble (B1) had been placed on T3, 15 min after cabbage was offered on T2.

The results show no time lag before the onset of the recruitment phase; this indicates that the majority of ants recruited to T3 came from T2 and not from the nest. This can be deduced from the comparison of the initial slopes between experiments B1 (initial slope 9.7) and A1, which show no significant difference ($P > 0.1$, Student's *t*-test) and between B1 and A2, which are different ($P < 0.05$, Student's *t*-test). In a similar way, B2 (initial slope 2.1) does not differ from A4 ($P > 0.1$, Student's *t*-test). As in the previous section, bramble produced more recruitment than cabbage (B1 versus B2 using initial slopes: $P < 0.002$, Student's *t*-test).

Conclusions. A new recruitment process does not necessarily have to be started from the nest. The ants recruited to a certain food source are able to participate in a new recruitment process without having to return to the nest.

Experiment C: Fidelity to a Trail

Methods. The mechanisms that enable the ants to distinguish between two different food sources were investigated next. The same experimental design was used as in experiment B. Food was placed on T3 (Fig. 1), and, 15 min later, food was offered on T2 approximately 1 cm from the trail made by the ants for recruitment to T3, without removing the food on T3. The experiments differed in the kind of food offered (Table III).

Results. Experiment C2 (Fig. 4) shows a decrease in the number of ants going to the cabbage on T3 after bramble was placed on T2, but experiments C1, C3 and C4 do not show this decrease. The initial slope of C1 is -0.6 , of C2: -6.2 , of C3 -0.7 and of C4 -1.7 . The initial slope of C2 is significantly different from all the others using analysis of variance ($F = 9.55$, $P < 0.001$) and Hartley's test ($\alpha = 0.05$). The slopes of C1, C3 and C4 do not differ ($P > 0.05$). In experiment C2 some leaf-carrying ants arriving at the bramble on T2 eventually dropped their pieces of cabbage and began to cut the new food.

In experiment C1, there was a diminution in the number of ants going to T3 during the

Table III. Schedule of Experiment C

Experiment	<i>n</i>	Food on T3	Food on T2
C1	7	Cabbage	Cabbage
C2	6	Cabbage	Bramble
C3	6	Bramble	Cabbage
C4	5	Bramble	Bramble

period 13 to 17 min after placing the food on T2. This reduction is significant ($P < 0.001$, Student's *t*-test) if compared with C2 and C3 in the same range, but is not different if compared with the initial slope of C2 ($P > 0.1$, Student's *t*-test).

Conclusions. An ant recruited to a food source may change its objective only if it finds a more attractive food on its way, but not if the food offered is equally or less attractive than those to which it is recruited. The recruited ant therefore has some information about the food to which it is recruited; this information must at least concern the degree of attractiveness. Experiment C1 suggests that, after a time period of at least 13 min, the ants recognize a nearer food source of the same kind as they are collecting, and an increasing proportion ignores the more distant one. The long time interval suggests that separate recruitment is involved.

Experiment D: Artificial Trail with Poison Sac Extracts

Methods. Poison sacs of workers were dissected out under a microscope and stored in diethyl-ether for 24 h. This solution was diluted with diethyl ether before use and deposited as an artificial trail with a micropipette on the food table (T2, Fig. 1) with no food on it, continuing over a bridge, where the number of ants going in both directions was counted, and leading to the nest entrance on T1. The concentration was measured in terms of poison sac contents per metre of trail (DC: 0.0; D1: 8.0; D2: 0.4; D3: 0.04 glands m^{-1}). The duration of starvation was 12 h and five replicates were carried out for each experiment.

Results. All the initial slopes from the experimental curves are significantly different from

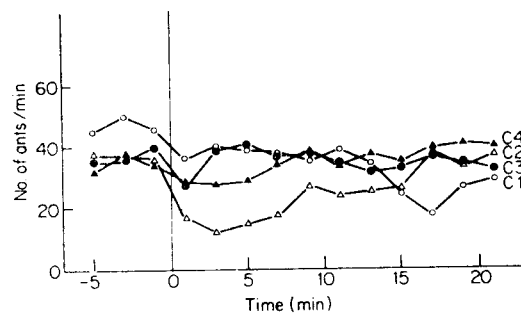


Fig. 4. Number of ants per min going to the food source on T3 before and after food had been placed on T2 (see also Table II).

each other (Fig. 5) as an analysis of variance ($F = 31.9$, $P < 0.001$) and Hartley's test ($\alpha = 0.05$) show. The values of the initial slopes were: D1: 32.2, D2: 17.5, D3: 6.2, DC: -1.0. The number of ants recruited was related to the concentration of poison sac extracts; the more concentrated the trail, the more recruitment produced. A concentration of 0.4 glands m^{-1} (experiment D2) produced more recruitment than the maximum amount observed under the conditions of experiments A (A1, Fig. 2a) as is shown by comparison of the initial slopes ($P < 0.01$, Student's *t*-test).

The ants follow the artificial trail made with poison sac extracts in the same way as a natural trail, the only difference being that no ants were observed laying trails. A large proportion of ants following a naturally laid trail dip the tip of the abdomen on the ground. After some minutes, the the artificial trail loses its attractiveness towards the ants (Fig. 5). This can be ascribed to the lack of trail-laying behaviour. When an artificial

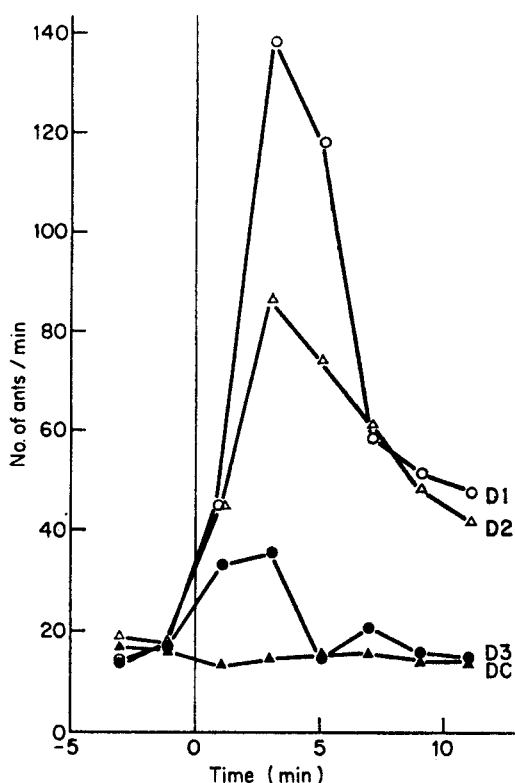


Fig. 5. Number of ants per min following an artificial trail made with poison sac extracts.

trail is laid to a new food source, trail-laying behaviour is observed 5 to 6 min later.

Conclusions. A single ant can produce almost the maximum amount of recruitment possible with the contents of its own poison sac. There is a direct relationship between the concentration of poison sac extract on the trail and the number of ants recruited. These two behavioural components would be sufficient to provide a mechanism in which an individual ant is able to modulate the amount of recruitment to a food source.

The fact that the trail loses its attractiveness with time, indicates that the ants do not reinforce the artificial trail, and that in order to do so, they need to have direct contact with the food source.

Experiment E: Recruitment with Artificial Trails Made with Synthetic Trail Pheromone

Methods. An attempt was made to reproduce the effects observed above with the aid of synthetic trail pheromone (methyl 4-methylpyrrole-2-carboxylate). A complete artificial trail was laid down, beginning from the food table (T2, Fig. 1), with no food on it, continuing over a bridge, where the number of ants, going in both directions was counted, and leading to the entrance of the nest. The following conditions were varied: (a) concentration of trail pheromone in $ng\ cm^{-1}$ and (b) duration in hours of starvation of the colony before the experiment. The pheromone was dissolved in distilled diethyl ether. The schedule of the experiment is shown in Table IV.

Results. Ants followed an artificial trail made with the synthetic trail pheromone in a way slightly different from those following a natural trail. They followed the artificial trail more slowly and did not seem to be as active as when they followed a natural trail, in spite of the fact that the concentration of pheromone used was the same or higher than that used by the ants in

Table IV. Schedule of Experiment E

Experiment	<i>n</i>	Concentration of pheromone on the trail ($ng\ cm^{-1}$)	Duration of starvation (h)
EC	5	0.0	12
E1	6	1.0	12
E2	5	0.05	12
E3	5	0.05	48

making their trail (the approximate concentration can be deduced from the number of ants recruited).

Experiment EC (Fig. 6) served as control, in which ether alone was used to lay the trail. In all the experiments shown in Fig. 6, with the exception of EC, there was an increase in the number of ants going to the food table after the artificial trail was laid. An analysis of variance of the initial slopes ($F = 10.3$, $P < 0.001$) and a subsequent Hartley's test ($\alpha = 0.05$) show that the recruitment obtained in E1, E2 and E3 was significantly different from EC (initial slopes: 16.2, 8.0, 12.2 and -1.0 respectively). The more concentrated trail (E1) recruited significantly more ants than the diluted one (E2) under the same conditions ($P < 0.05$). Starvation of the colony seemed to increase the response of the ants to the trail (E3) but the difference is not statistically significant ($P > 0.05$) if compared with E1 or E2. The slope of the initial part of the curve of E3 is thus intermediate between those of E1 and E2, and, with the statistical methods used, it was not possible to separate the response curves.

A reduction of the responsiveness of the ants to the artificial trail was observed 7 min after the trail was laid. This can be explained as in the experiment above (experiment D), by the

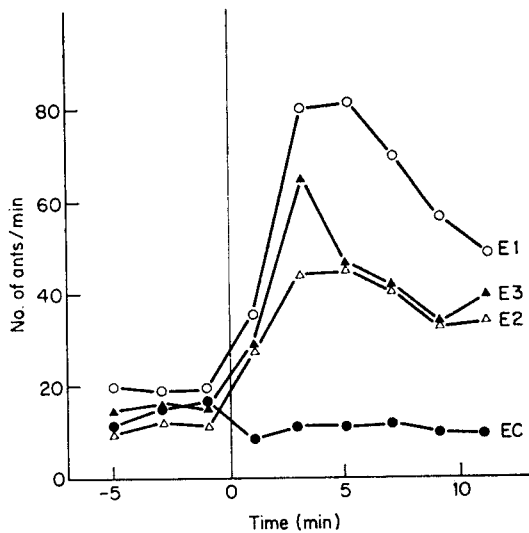


Fig. 6. Number of ants per min following an artificial trail made with synthetic trail pheromone. EC: 0.0 ng cm^{-1} , E1: 1.0 ng cm^{-1} , E2 & E3: 0.05 ng cm^{-1} ; EC, E1 & E2: 12 h starvation; E3: 48 h starvation before the experiment.

volatilization of the pheromone which is replaced by the ants only if a food reward is present.

Conclusion. The major component of the trail pheromone (methyl 4-methylpyrrole-2-carboxylate) recruits ants but does not reproduce all the aspects of natural recruitment. The reduction with time of the response to the synthetic compound confirms that the ants lay a trail only when they have tested or found the food, and therefore they will not reinforce the artificial trail in the absence of food.

The amount of recruitment induced is proportional to the concentration of the pheromone on the trail and, to a lesser extent, to the duration of starvation of the colony.

Experiment F: Fidelity to an Artificial Trail Made with Synthetic Trail Pheromone

Methods. The possible relationship between the concentration of the pheromone on the trail and the attractiveness of the food source was examined. An artificial trail was laid starting from T3 (Fig. 1) with no food on it, across T2 leading to the nest entrance on T1. Three minutes later, food (bramble) was offered on the first food table (T2) approximately 1 cm from the trail. The ants were counted on the bridge between T2 and T3. The concentration of methyl-4-methylpyrrole-2-carboxylate on the trail was 1.0 ng cm^{-1} for F1 and 0.05 ng cm^{-1} for F2. Four replicates were carried out for each experiment.

Results. The results (Fig. 7) show that the ants on a trail with high pheromone concentration (F1) did not stop at the food offered near the trail. When the pheromone concentration on the trail was low (F2) the ants stopped at the food source on T2. Comparison of the initial slopes of the recruitment curves (initial slope for F1: 6.1; for F2: -4.1) gave a statistically significant difference ($P < 0.002$, Student's *t*-test). Comparing the curves for normal recruitment with artificial trails (experiment E) and those where food was presented near the artificial trail during the recruitment process (experiment F), it can be seen once more that only with a dilute artificial trail and with the preferred food on the trail (F2) was there an interruption in the build-up of the number of ants due to the food offered on T2. Comparing the slopes, starting from the time the trails were laid; that is, from $t = -3$ to 1 min in experiment F, and from $t = -1$ to 3 min in experiment E, we have 13.2 in F1 versus 16.2 in E1, which is not significantly different ($P > 0.1$, Student's *t*-test), and 0.8 in F2 versus 8.0 in E2,

which is significantly different ($P < 0.001$, Student's *t*-test).

Conclusion. The ants are able to relate the attractiveness of the food source to the concentration of the pheromone on the trail. Ants on a concentrated trail do not divert to food sources nearby that are less attractive than those they are exploiting, but ants following a dilute trail may divert.

Experiment G: The Trail Pheromone as an Attractant

Method. The attractive effect of the major component of the trail pheromone (methyl 4-methylpyrrole-2-carboxylate), and its ability to induce foraging in the ants, were examined. A spot of 1.0 ng of pheromone dissolved in ether was placed near the nest entrance. In two cases this spot was also over a natural trail laid by the ants some 15 min earlier (GC and G1). In GC the spot consisted of ether alone. In G2 the spot of pheromone solution was laid at the nest entrance when foraging was not taking place. The duration of starvation in all experiments was 12 h. The number of ants going to T2 (Fig. 1) was measured on the bridge between T2 and T1. Five replicates of each experiment were carried out.

Results. In experiment G1 there was an increase in the number of ants going to the food source 3 min after the pheromone solution was

placed at the nest entrance (Fig. 8). This increase, based on the comparison of the initial slopes, is statistically significant ($P < 0.05$, *t*-test) if compared with either the control GC, or G2. The slopes of G2 and GC do not differ ($P > 0.1$) (initial slopes of G1: 5.3, G2: 0.9, GC: 0.5). In G2 there was an accumulation of ants around the spot of pheromone solution, and a general increase of foraging activity, but no specific increase in the number of ants going to T2 (Fig. 1).

Conclusion. The trail pheromone component, methyl 4-methylpyrrole-2-carboxylate, attracts ants to the trail and therefore increases the number of ants recruited to the source. In the absence of a trail, the pheromone attracts ants, and induces a general and non-specific increase in foraging activity.

Discussion

The experiments suggest that the ants use mainly the major component of the trail pheromone, methyl 4-methylpyrrole-2-carboxylate, as an orientation signal and as an attractant when recruiting nest-mates to a new food source. Antennal contact, or components of the poison sac other than the pyrrole, do not seem to be essential in the recruiting process. The ants can modulate their recruitment signal by controlling the concentration of trail pheromone on the trail. This modulation seems to be done by individual ants and is not a result of the total

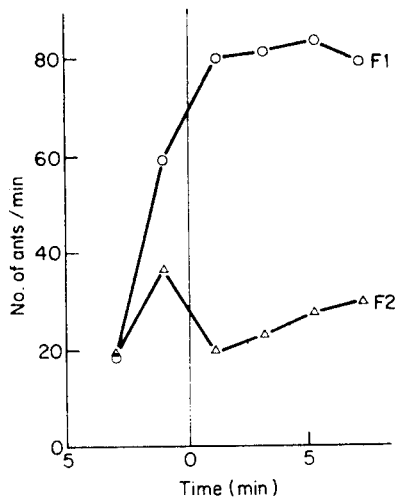


Fig. 7. Number of ants per min following an artificial trail, made with synthetic trail pheromone, to T3 before and after bramble had been placed on T2. F1: 1.0 ng cm⁻¹, F2: 0.05 ng cm⁻¹ of synthetic trail pheromone.

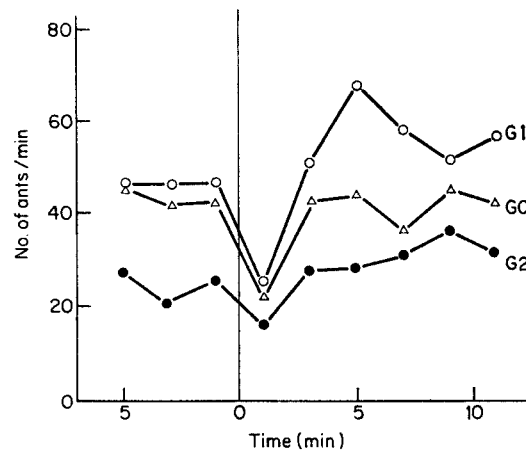


Fig. 8. Number of ants per min following a natural trail before and after a spot of synthetic trail pheromone solution had been placed at the nest entrance. GC: spot of ether on a natural trail, G1: pheromone on trail, G2: pheromone at nest entrance when foraging activity was not taking place.

number of ants laying trails. Hangartner (1969), working with *Solenopsis geminata*, suggested that an individual ant is able to contribute to the effectiveness of the mass-communication system by controlling the continuity of its trail. At the same time he described a direct relationship between either the duration of starvation of the ant colony or the quality of the food, and the continuity of the individual trail. The mechanism used by leaf-cutting ants for mass recruitment here includes an ability to relate the concentration of pheromone on the trail to the attractiveness of the food. This mechanism seems to be very similar to the one described by Hangartner (1969), and suggests that an individual trail that is more or less continuous may also have a higher concentration of pheromone, and that the ants might be able to detect the concentration of trail pheromone rather than the continuity of the trail itself.

In both tandem running and in group recruitment, individual ants control the recruitment process. Hölldobler (1971) found in *Camponotus socius* that 'mass foraging is organized by the behavioural activity of individual recruiting ants'. Cammaerts (1977) suggested a mechanism for *Myrmica rubra* similar to that found in *Solenopsis* (Hangartner 1969), but with two secretions involved, one acting as an orientation signal and the other as an attractant.

Wilson (1971) describes mass communication in *Solenopsis saevissima* as the information that can be transmitted only from one group of individuals to another group of individuals. That is, the number of workers leaving the nest is controlled by the amount of trail pheromone emitted by returning foragers. This quantitative relationship results in the adjustment of the outflow of workers to the level needed at the food source. Wilson suggests that an equilibrium is then achieved in the following manner. The initial build-up of workers at a newly discovered food source is exponential, and reaches a limit as workers become crowded on the food mass, first because workers unable to reach the food return without laying trails and secondly, because trails laid by single workers evaporate within a few minutes. The mass communication of quality is achieved by means of an 'electorate' response, in which individuals choose whether to lay trails after inspecting the food find. If they do lay trails, they adjust the quantity of pheromone according to circumstances (Hangartner, loc. cit.). The more desirable the food, the higher the percentage of trail laying, the greater the trail-laying effort by

individuals, the more the trail pheromone presented to the colony, and hence, the more ants that emerge from the nest (Wilson 1971).

The findings in the present work suggest that the number of ants that recruit nest-mates does not depend on the quality of the food (Fig. 2b), but that the number of ants recruited to the food source does depend on it (Fig. 2a). This can be explained only if we assume that in the 'electorate' response described by Wilson, the 'trail-laying effort' by individuals is much more important than the percentage of ants responding positively to the food source by laying a trail. That is, individual ants have a primary role in the release of the mass recruitment. On the other hand, the equilibration of the build-up of workers at the food source can not be achieved without adjustment of the trail laying response of the individual ants after the discovery of a new food source. Even at an overcrowded food source, the number of ants reaching the food, and therefore returning to the nest laying trails, would produce excessive recruitment if they all laid trails in the same way as the first ants to return to the nest. This suggests that the returning ants reduce the amount of pheromone they secreted on to the trail in accordance with the density of ants at the food source. This is supported by the finding that the trough in the numbers of ants going from the food to the nest coincides with the maximum rate of increase in the number of ants going to the food (Fig. 2). The interpretation could be that the ants that have found the new food and recruit nest-mates by laying trails from the food source to the nest, stop doing so as soon as they detect large numbers of ants coming towards them.

This mass recruitment mechanism probably includes the following components: (1) an ability of ants to detect the concentration of pheromone on the trail and to relate it to the attractiveness of the food; (2) modulation by individual ants of the amount of trail-pheromone released in accordance with the quality of the food and the concentration of pheromone already present on the trail; (3) an ability of the ants to measure the density of ants on a trail or at a food source; and (4) an effect of the duration of starvation on the trail-laying activity of the individuals and probably also on the responsiveness of the ants towards the trail pheromone. This would provide a highly sensitive recruitment system which would enable the ants to determine whether to begin to follow a new trail or not, depending on their motivation to collect food from known sources

which they may be already exploiting, and depending on the concentration of trail pheromone on a new trail. This would enable the colony to concentrate on the best food available. This recruiting system can work only if the ants laying the trail have precise information about the new food source. Therefore only the ants that have actually contacted or tasted the food lay trails until the number of ants recruited reaches a maximum. Only after this has happened does a kind of equilibration take place, in which the individual ant modulates the concentration of trail pheromone on the trail according to the factors listed above. In spite of the susceptibility of this system to individual 'errors', the colony as a whole gains greater flexibility to adapt to a changing environment.

As pointed out by Goetsch (1957) and Cherrett (1968), the polyphagous habit is an important characteristic of fungus growing ants. The recruiting system here described, would not only allow, but also enhance, this polyphagous habit. A new food source, which is almost always more attractive to the ants if compared to an old one (Cherrett, 1972b), is rapidly and effectively made available to the colony. This provides the fungus garden with a proper balance of nutrients and moisture without overloading it with secondary compounds from the plants selected (Rockwood, 1976).

Acknowledgments

K. J. is grateful to the Concejo Nacional de Investigaciones Cientificas y Tecnologicas (CONICIT) of Venezuela for the award of a postgraduate scholarship at Southampton University. We thank Dr J. M. Cherrett for supplying the ant colonies, C. Broomfield and G. Jackson for the synthesis of methyl 4-methylpyrrole-2-carboxylate, Mrs S. Came for the care of the ant colonies, Dr O. T. Jones, Dr C. Longhurst and Dr J. W. Bradshaw for their critical reading of the manuscript, and Miss J. Spear for the secretarial work.

REFERENCES

- Cammaerts, M. C. 1977. Recruitment to food in *Myrmica rubra* 1. *Proc. VIII Congress I.U.S.S.I.*, Wageningen, p. 294.
- Cherrett, J. M. 1968. The foraging behaviour of *Atta cephalotes*. *J. Anim. Ecol.*, **37**, 387-403.
- Cherrett, J. M. 1972a. Some factors involved in the selection of vegetable substrate by *Atta cephalotes* in tropical rain forest. *J. Anim. Ecol.*, **41**, 647-660.
- Cherrett, J. M. 1972b. Chemical aspects of plant attack by leaf-cutting ants. In: *Phytochemical Ecology* (Ed. by J. B. Harborne), pp 13-24. London and New York: Academic Press.
- Goetsch, W. 1957. *The Ants*. Michigan.
- Hangartner, W. 1967. Spezifität und Inaktivierung des Spurpheromones von *Lasius fuliginosus* und Orientierung der Arbeiterinnen im Duftfeld. *Z. vergl. Physiol.*, **57**, 103-136.
- Hangartner, W. 1969. Structure and variability of the individual odour trail in *Solenopsis geminata* Faber. *Z. vergl. Physiol.*, **62**, 11-120.
- Hölldobler, B. 1971. Recruitment behaviour in *Camponotus socius*. *Z. vergl. Physiol.*, **75**, 123-142.
- Hölldobler, B. 1976. Recruitment behaviour, home range orientation and territoriality in the Harvester ants *Pogonomyrmex*. *Behav. Ecol. Sociobiol.*, **1**, 3-44.
- Lewis, T., Pollard, G. V. & Dibley, G. C. 1974. Micro-environmental factors affecting diet patterns of foraging in the leaf-cutting ant, *Atta cephalotes* L. *J. Anim. Ecol.*, **43**, 143-153.
- Riley, R. G., Silverstein, R. H., Carroll, B. & Carroll, R. 1974. Methyl 4-methylpyrrole-2-carboxylate, a volatile trail pheromone from the leaf-cutting ant *Atta cephalotes*. *J. Insect Physiol.*, **20**, 651-654.
- Robinson, S. W., Moser, J. C., Blum, M. S. & Amante, E. 1974. Laboratory investigations of the trail following responses of four species of leaf-cutting ants with notes on the specificity of a trail pheromone of *Atta texana*. *Insectes Sociaux*, **21**, 87-94.
- Robinson, S. W. & Cherrett, J. M. 1978. The possible use of methyl 4-methyl-pyrrole-2-carboxylate, an ant trail pheromone, as a component of an improved bait for leaf-cutting ants. *Bull. Ent. Res.*, **68**, 159-170.
- Rockwood, L. L. 1976. Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). *Ecology*, **57**, 48-61.
- Traniello, J. F. A. 1977. Recruitment behaviour, orientation and organization of foraging in the carpenter ant. *Behav. Ecol. Sociobiol.*, **2**, 61-79.
- Tumlinson, J. H., Silverstein, R. M. & Moser, J. C. 1971. Identification of the trail pheromone of a leaf-cutting ant, *Atta texana*. *Nature, Lond.*, **234**, 348-349.
- Tumlinson, J. H., Moser, J. C. & Silverstein, R. M. 1972. A volatile trail pheromone of the ant *Atta texana*. *J. Insect Physiol.*, **18**, 809-814.
- Wilson, E. O. 1962. Chemical communication among workers of the Fire ant (*Solenopsis saevissima*). *Anim. Behav.*, **10**, 134-164.
- Wilson, E. O. 1971. *The Insect Societies*, p. 548. Cambridge, Mass.: Belknap Press of Harvard University.

(Received 10 August 1978; revised 9 November 1978; MS. number:1800)