

Theoretical Analysis of the Communication System for Chemical Mass Recruitment in Ants

KLAUS JAFFE†

Department of Biology, The University, Southampton, SO9 3TU, England

(Received 9 July 1979, and in revised form 10 January 1980)

Different possible communication systems for chemical mass recruitment in ants are investigated and the results from computer models simulating recruitment are compared with experimental observations reported in the literature. The communication system more likely to be used by ants in chemical mass recruitment is one in which the pheromone concentration on the trail is maintained constant by scout ants and is related to the quality of the food. Equilibration of recruitment is achieved by the ants by reacting to increasing ant densities on the food source, and on the trail, with decreasing recruitment efforts. The general conclusions that can be drawn from this theoretical analysis are the following:

(a) The participation of an important proportion of scout ants in the recruitment process is essential. The optimum proportion depends mainly on the distance to the food. The net result is a high percentage of ants on the trail returning to the nest without carrying any food.

(b) Orientational cues different from the trail pheromone increase the recruitment efficiency.

(c) Attraction to the trail and orientation along the trail to the food source need to be maintained as separate events. This can be achieved if there are two different behavioural thresholds towards the same pheromone (*Atta* for example) or if there are different pheromones for each purpose (*Myrmica* for example).

(d) A decrease in recruitment effort at increasing ant densities on the trail produces more efficient recruitment.

(e) Complete depletion of food sources at long distances from the nest are unlikely. As the food available decreases, the probability that the colony will be unable to exploit it increases.

1. Introduction

Recruitment to a food source by means of an odour trail (trail-pheromone) is well known in many ant species. In some species the odour trail is complementary to other forms of recruitment, such as tandem-running or group-

† Present address: Departamento de Estudios Ambientales, Universidad Simon Bolivar, Apartado 80659, Caracas 108, Venezuela.

recruitment, where a guiding ant is needed to recruit workers to the food source. In other ant species, the odour-trail alone is sufficient to produce full recruitment. This kind of system has been called chemical mass recruitment (Wilson, 1971) and has been studied in *Solenopsis* (Wilson, 1962), *Lasius fuliginosus* (Hangartner, 1967), *Pogonomyrmex* (Hölldobler, 1976) *Myrmica rubra* (Cammaerts, 1974) and *Atta cephalotes* (Jaffe & Howse, 1979).

Using some of these results, Wilson (1971) suggested a mass recruitment mechanism which operates as follows. The number of workers leaving the nest to a food source is controlled by the amount of trail substance on the trail. The amount of trail substance in turn is a result of an "electorate response". This is, the more attractive the food, the higher the percentage of trail-laying ants, the greater the trail-laying effort by individuals, the more trail pheromone presented to the colony and hence, the more ants that emerge from the nest. Equilibration of recruitment is achieved because workers unable to reach the overcrowded food turn back without laying trails and because trails evaporate within few minutes. In this way, the outflow of workers is adjusted to the level needed at the food source.

Studies of the recruitment system of *Atta cephalotes* (Jaffe & Howse, 1979) do not agree with Wilson's account. They showed that the amount of recruitment produced is independent of the number of ants initially returning to the nest from a newly discovered food source. The concentration of pheromone on the trail is related to the quality of the food find and the duration of starvation. The recruitment mechanism suggested for *A. cephalotes* includes the following components:

- (a) an ability of the ants to measure the concentration of pheromone on the trail and to relate it to the attractiveness of the food;
- (b) 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;
- (c) an ability of the ants to measure the density of nestmates on a trail or at the food source;
- (d) 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.

Other studies of the recruitment activity of ants in the field reported specific recruitment patterns, which up to now have not been explained. For example Cherrett (1972) reported that only about 42% of the workers of *A. cephalotes* carried food to the nest. The remaining 58% returned to the nest unladen. Lewis, Pollard & Dibley (1974) reported in the same species that only about 13% of the foragers returned unladen to the nest. Gamboa

(1975) found about 33% of unladen returning foragers in the gardening ant. A similar situation has been described for *Pogonomyrmex badius* (Holldobler & Wilson, 1970), in which a certain percentage of ants return to the nest without carrying food but laying trails.

In order to determine which of the communication mechanisms proposed can best explain all the experimental results concerning the recruitment process, a theoretical analysis was undertaken. Previous theoretical studies of recruitment systems in ants have not dealt with the possible communication mechanism involved, but rather with the mathematical nature of the recruitment activity (Holt, 1955) or with the relation between the maximization of net energy intake and the foraging behaviour (Taylor, 1978). Therefore a computer model† seemed useful in clarifying the differences between the two communication systems proposed and in identifying the elements that confer specific advantages to the recruitment process itself or to the ant colony as a whole.

2. The Theoretical Models

In order to construct the theoretical models, the following assumptions were taken:

(i) *Common assumptions.*

The concentration of pheromone on the trail is proportional to the quality of the food and the duration of starvation but inversely proportional to the distance between food and nest. The trail pheromone acts as an attractant and as an orientation signal. Some ants forage and reinforce the trail, have information about the food source and its location but are not involved in collecting and carrying food; these ants are termed scout ants. Ants carrying food also reinforce the trail with the pheromone. Trail-laying may be done in both directions, i.e. from the food to the nest and vice versa by ants which have encountered the food.

(ii) *Equilibration of the number of ants recruited to the food*

- (1) The degree of overcrowding at the food source serves as a feed-back mechanism equilibrating the number of recruited ants needed at the food source. The more crowded the food source, the more ants turn back to the nest without laying trails and the less the trail laying effort of each trail-laying ant.
- (2) A high density of ants at the food source and on the trail will reduce the recruiting efforts made by nestmates. Scout ants, encountering a

† Copies of the Fortran program can be obtained from the author.

high density of ants on the trail going to the food source will stop recruiting nestmates and will begin to collect food, i.e. will become non-scouts.

(iii) *Communication of the quality of the food*

- (1) The mass communication of quality is achieved by an electorate response; each individual ant modulates the amount of trail-pheromone secreted in accordance to the quality of the food. The sum total of this effort will produce different levels of recruitment, depending on the quality of the food source.
- (2) The amount of recruitment is independent of the number of ants returning to the nest, but dependent on the concentration of pheromone on the trail which is related to the quality of the food only. One or two ants are able to produce the maximum recruitment. The individual ant varies the amount of pheromone secreted in order to maintain a constant pheromone concentration on the trail in accordance with its experience of food quality and ant density on the food source and trail.

(iv) *Proportion of scout ants participating in the recruitment*

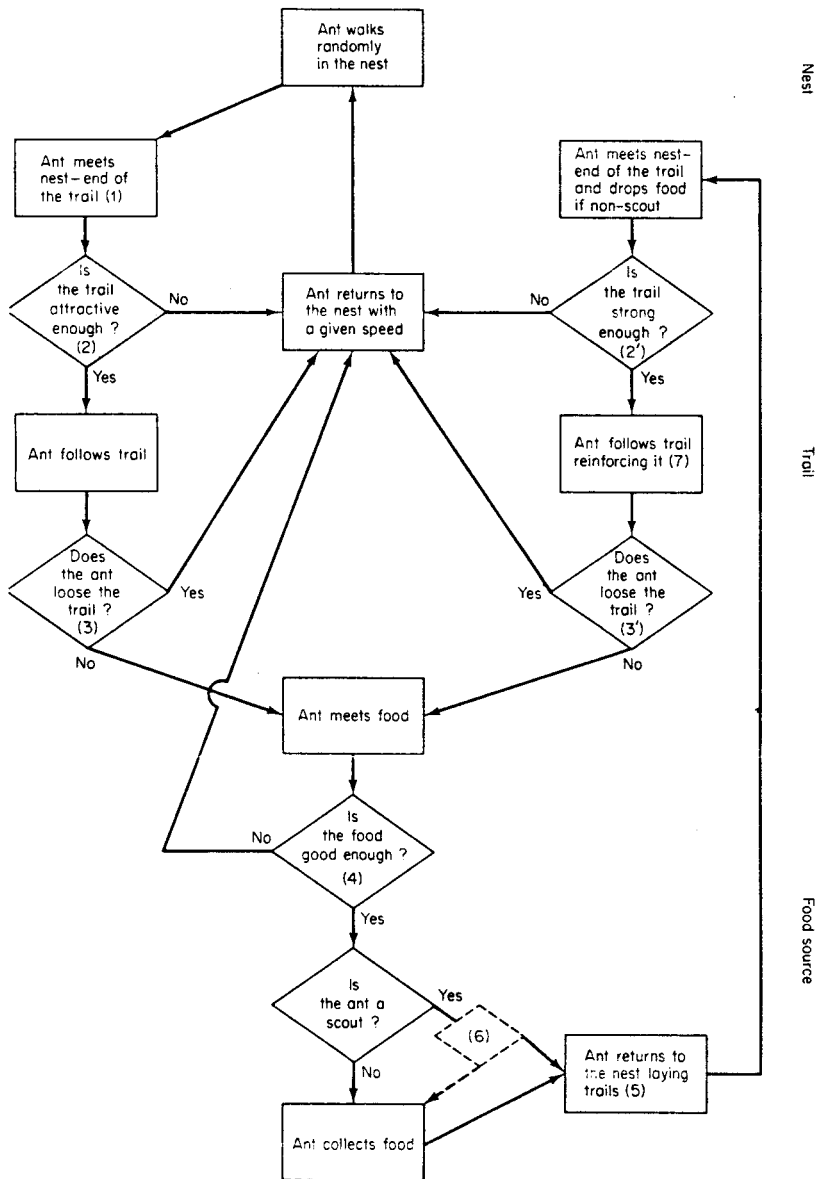
- (1) A fixed proportion of ants are scout ants, which are foragers who may reinforce the trail when they have information about the food source and its location, but are not involved in collecting or carrying food.
- (2) The number of scouts is proportional to the attractiveness of the food source.

The combinations of assumptions ii.1, ii.2, iii.1 and iii.2 produce four different models. Model A applies to the combination of assumptions ii.1 and iii.1; model B to the combination ii.2 and iii.2; model C to ii.1 and iii.2 and model D to ii.2 and iii.1. Assumption iv.1 is used for this four models. The use of assumption iv.1 will be discussed separately.

(A) MATHEMATICAL DESCRIPTION OF THE MODELS

The recruitment in ants was simulated by constructing an ant colony consisting of a nest, a trail and the food source. A thousand ants were initially placed in the nest and then each ant acted according to the following description (Fig. 1). Every individual ant was assigned a pheromone

FIG. 1. Simplified diagram of the sequence of actions for one ant in theoretical models. Discontinuous lines hold only for models B and D. Numbers in brackets refer to equations and relations in the text.



concentration threshold (T_i), such that pheromone concentrations above this threshold would produce behavioural responses. An ant density threshold (A_i), a threshold which regulates responses to ant densities, was given to each individual in models assuming ii.2 (models B and D). These thresholds were selected randomly for each ant from a log-normal distribution, assuming that this is the most common distribution for thresholds in insects (see Clarke, 1969). An initial position in the nest (m_{it}) was selected randomly for each ant from a uniform distribution. Also, a specific caste, either scout (a_i^s) or normal worker (a_i^n), was randomly assigned to each ant. The ratio between the number of scouts and non-scouts could be fixed for any value between 0 and 10.

Initially, three arbitrarily chosen ants encounter the food source and return to the nest laying trails. Ants from the nest encounter the trail, which has a pheromone concentration (C_t) varying in time. This encounter is dependent on the spatial position of the ant in the nest (m_{it}), defined as the time needed to reach the nest end of the trail, and dependent on the concentration of pheromone at the nest entrance at time t (C_t). The position of an ant (a_i) in the nest can be expressed as:

$$Sa_{it} = k_1 \cdot \frac{m_{it}}{C_t - m_{it}}, \quad (1)$$

when $Sa_{it} = 1$, the ant a_i is at the nest end of the trail. Thus, an increase in the pheromone concentration at the nest entrance will reduce the time an ant takes to encounter the trail, simulating the attractive effect of the trail pheromone using the equation derived by Bossert & Wilson (1963).

As soon as an ant encounters the trail it will follow it if the concentration of pheromone (C_t) is sufficiently high:

$$C_t \geq T_i \quad (2)$$

otherwise, the ant will return to the nest to a position which was allocated randomly. Allocation of the ant to a fixed position near the nest entrance (small m_{it}) did not change the recruitment pattern, but increased the number of ants available for recruitment, thus, paralleling the effect of an increased initial amount of ants.

An ant following the trail (of length x) checks the pheromone concentration again at the food end of the trail (C_f). There the pheromone has to serve as an orientation signal alone and no longer needs to exercise its attractive effect. Therefore the detection threshold of the pheromone is different from that at the nest end of the trail:

$$C_f \geq T_i/k_2. \quad (3)$$

If the ant's pheromone detection threshold does not conform to relation (3) it returns to the nest as described above, at a certain velocity.

Eventually the ant arrives at the food source. Once there, it has to determine whether there is enough food left (F_t) and whether the ant density on the food source ($Df_t = Nf_t/F_t$) is not too high, where Nf_t is the number of ants at the food source at time t . For assumption ii.1 if

$$(F_t > 0) \text{ and } [Df_t \cdot k_3 < Rn(0-1)_i], \tag{4a}$$

then a_i responds positively and for assumption ii.2 if

$$(F_t > 0) \text{ and } (Df_t < A_i) \tag{4b}$$

then a_i responds positively where $Rn(0-1)_i$ is a random number between 0 and 1, simulating the chances of reaching a crowded food source. An ant (a_i^s) which conforms to relation (4) i.e. responds positively to equation (4), will collect food or, if it is a scout ant (a_i^s), recruit nestmates. If an ant does not conform in its behaviour to relation (4), it will return to the nest as in equation (3). f_{ii} and f'_{ii} can be defined as:

$$f_{ii} = Df_t \cdot k_3 / Rn(0-1)_i$$

$$f'_{ii} = Df_t / A_i$$

and thus serve to quantify crowding relative to each ant.

A scout ant will recruit nestmates, reinforcing the trail with pheromone when walking both to and from the nest, checking the situation at the food source every time it reaches it. An ant collecting food will spend a time interval (y) on the food source, and then go back to the nest trail-laying. It will also reinforce the trail on its way again to the food source. The amount of pheromone secreted in this process will depend on which end of the trail the ant is situated. For the food end of the trail, the amount of pheromone secreted (Pf_{it}) will be:

$$Pf_{it} = k_4 - k_5 \cdot f_{ii} \tag{5a}$$

assuming iii.1 and if we assume iii.2 it will be:

$$Pf_{it} = \begin{cases} 0 & \text{if } Cf_t \geq k_6 - k_5 \cdot f'_{ii} \\ k_6 - k_5 \cdot f'_{ii} - Cf_t & \text{if } Cf_t < k_6 - k_5 \cdot f'_{ii} \end{cases} \tag{5b}$$

In both cases, the amount of pheromone secreted when the ant reaches the nest (P_{it}) will be:

$$P_{it} = Pf_{i(t-x)}$$

Assuming ii.2, scout ants will not lay trails but will return to the food source and begin to harvest it if:

$$Naf_t > A_i \cdot k_3 \quad (6)$$

where Naf_t is the number of ants arriving at the food source at time t .

The amount of pheromone secreted by each ant in the recruitment process on the way back to the food source will be

$$P_{it} = k_4 - k_5 \cdot f_{i(t-j)} \quad (7a)$$

and assuming iii.2:

$$P_{it} = \begin{cases} 0 & \text{if } k_6 - k_5 \cdot f'_{i(t-j)} \leq C_t \\ k_6 - k_5 \cdot f'_{i(t-j)} - C_t & \text{if } k_6 - k_5 \cdot f'_{i(t-j)} > C_t \end{cases} \quad (7b)$$

where C_t is the pheromone concentration at the nest end of the trail and j the time that has elapsed since the ant last had contact with the food source. The amount of pheromone secreted by the ant when it arrives at the food end of the trail will be for both cases:

$$Pf_{it} = P_{i(t-x)}$$

Thus, the amount of pheromone secreted by each ant can have a maximum value of k_4 and k_6 respectively for assumptions iii.1 and iii.2, but is normally smaller depending on the ant density at the food source. In the case of assumption iii.2 the amount of pheromone secreted depends also on the pheromone concentration on the trail, so that the concentration on the trail will never exceed k_6 .

An ant which has already been on the food source and which conformed to relation (5), will have information about the quality and location of the food source and therefore the attraction by the trail is not essential for it. At the same time it requires fewer orientation signals than an ant going to the food source for the first time. For these ants, relation (2) and (3) will assume the form:

$$C_t \geq T_i/k_2 \quad (2')$$

and

$$Cf_t \geq T_i/k_2 \cdot k_7 \quad (3')$$

(B) CALCULATING THE DIFFERENT PARAMETERS

- (i) The parameters calculated at the nest end of the trail are:
Number of ants leaving the nest:

$$Na_t = \sum_i a'_{it}$$

where a'_{it} is an ant a_i which obeys relation (2) at the time $(t-1)$.

Concentration of pheromone on the nest end of the trail:

$$C_t = C_{t-1}/k_8 + \sum_i [P_{it} + Pf_{i(t-x)}] \quad (8)$$

(ii) The parameters calculated at the food end of the trail are:

Number of ants arriving at the food source:

$$Naf_t = \sum_i a''_{it}$$

where a''_{it} is an ant $a'_{i(t-x-1)}$, which obeys relation (3) at time $(t-1)$.

Number of food carrying ants returning to the nest:

$$Nl_t = \sum_i a'''_{it}$$

where a'''_{it} is an ant $a''_{i(t-y)}$ which obeys relation (4) at time $(t-y)$, and is of the caste type a''_i .

Number of scout ants returning to the nest:

$$Ns_t = \sum_i a^{s'}_{it}$$

where $a^{s'}_{it}$ is an ant $a''_{i(t-1)}$ which obeys the relation (4) at time $(t-1)$ and is a scout ant (a^s_i).

Number of ants returning to the nest not carrying food:

$$Ne_t = Ns_t + \sum_i a^{iv}_{it}$$

where a^{iv}_{it} is an ant $a''_{i(t-1)}$ which do not obey relation (4) at time $(t-1)$.

Total number of ants returning to the nest:

$$Nr_t = Nl_t + Ne_t$$

The amount of food remaining at the food source:

$$F_t = F_{t-1} - Nl_{t+y}$$

The number of ants at the food source:

$$Nf_t = Nf_{t-1} + Naf_{t-1} - Nr_{t-1}$$

And the concentration of pheromone at the food end of the trail:

$$Cf_t = Cf_{t-1}/k_8 + \sum_i [Pf_{it} + P_{i(t-x)}] \quad (9)$$

(C) THE CONSTANTS

k_1 – k_8 are constants. From these, only k_2 , k_4 , k_6 , k_7 and k_8 have specific meaning:

k_2 [relation (3) (2') and (3')]. Represents the difference in the thresholds between the attractive effect and the orientation function of the trail pheromone(s).

k_4 [equation (5a) and (7a)]. Represents the amount of pheromone released by an individual ant at a given quality of food, when no overcrowding at the food source occurs (Assuming iii.1).

k_6 [equation (5b) and (7b)]. Is the optimal pheromone concentration on a trail, which leads to a food source of a given quality, when the ant-density at the food source is low (Assuming iii.2).

k_7 [relation (3')]. Quantifies the precision in orientation due to cues other than the trail pheromone.

k_8 [equation (8) and (9)]. Represents the evaporation rate of the pheromone on the trail.

k_1 , k_3 and k_5 are arbitrarily constants with no direct biological meaning. k_1 relates pheromone concentrations to chances of encountering the trail; k_3 relates ant densities to crowding, i.e. to the number of collisions between ants; and k_5 relates crowding or ant densities to pheromone concentrations. Other constants are those used, defining the probability distributions from which the values for A_i , T_i , m_{ii} , and a_i^n/a_i^s are derived.

(D) CRITERIA FOR THE COMPARISON BETWEEN THE DIFFERENT MODELS

A fixed set of values was chosen for k_2 , k_7 and k_8 . The values for the other constants were varied for each model, until the best conditions could be obtained (see Appendix). Naf_i and Nr_t were calculated for different times and these results compared to similar ones obtained experimentally from *Atta cephalotes* in laboratory cultures (Jaffe & Howse, 1979), from *Myrmicine* ants (Taylor, 1977), and from *Pogonomyrmex badius* (Hölldobler & Wilson, 1970).

The best set of values for the constants were taken as those which produced results closest to the following:

1. The curves representing the number of ants arriving at the food source at different time intervals have four distinct and consecutive phases.
 - (a) Initial phase or fast increase phase ($Naf_i \gg Naf_{i-1}$)
 - (b) Maximum recruitment phase ($Naf_{i-1} < Naf_i > Naf_{i+1}$)
 - (c) Equilibrium phase ($Naf_i \cong Nr_t$)
 - (d) Decrease of recruitment ($Naf_i < Naf_{i-1}$)

2. The quality of the food (values of k_4 and k_6) must be directly related to:
- The number of ants per time unit, in the maximum recruitment phase
 - The number of ants per time unit, in the equilibrium phase
 - The rate of increase of the number of ants arriving at the food source in the initial phase.

3. Discussion of the Results

(A) THE EFFECT OF THE CONSTANTS

Any change in the relative values of the constants will change the recruitment pattern produced by the models. Some of these changes are interesting because they are the same in the four models and at the same time have possible biological meanings.

k_7 (orientation to the food source)

An increase in the value of k_7 , which represents a greater use of alternative cues to the trail pheromone for orientation to the food source, produced more efficient recruitment to the food. A higher value of k_7 with the other conditions constant, produced recruitment with nest-food distances larger than otherwise possible with low values of k_7 .

If we make ants, which contacted the food, return to the food from the nest depending only on the orientation effect of the trail we have:

$$C_i \geq T_i/k_2 \cdot k_7$$

Using this relation instead of (2'), we obtain an excess of ants at the food source, even if no food is left. This suggests that the scout ants, which are recruiting nestmates, must use the concentration of the trail pheromone in order to obtain information about the recruitment activity, so that they can then regulate it.

k_2 (orientation vs. attraction)

The effect of k_2 on the recruitment process was very similar to that of k_7 . The higher the value of k_2 , the longer the distance over which a trail could be effective in recruiting and leading ants to the food. The greater the ratio between the thresholds for attraction and orientation, the more efficient the chemical trail becomes, i.e. less ants are needed to collect equivalent amounts of food in an equivalent time period.

k_8 (the volatility of the trail pheromone)

The lower the value of k_8 , the longer the trail remains effective in recruiting ants, and the greater can be the distance over which a trail could

be used. With very low values of k_8 however, recruitment occurs long after the food source is depleted.

These three constants illustrate the relationship between requirements for a long lasting orientation effect, and a short-lived attraction effect of the trail. Both effects are increased with k_8 , whereas k_2 and k_7 increase only the orientation efficiency of the trail, without affecting its attractive function. Therefore the best combination of these constants is one with a low value for k_8 and high values for k_2 and k_7 .

In biological terms, this means that in order to improve recruitment, the ants could use at least one of three possible solutions:

- (a) The use of orientation signals other than the trail pheromone.
- (b) The development of different behavioural thresholds for the same trail pheromone. High concentrations of pheromone are attractant, and stimulate the ants for food retrieval, whereas very low concentrations are still detected and can be used for orientation.
- (c) The use of two different pheromones with different volatilities; one to be used as attractant and the other as an orientation signal.

Probably all ant species apply solution (a) to a certain degree. For example, visual orientation, sun compass orientation or the use of polarized light are known to occur in many ant species. (Carthy, 1951; Hölldobler, 1976; Wehner, 1976; Plekhanov & Kaul 1977).

Solution (b) seems to have been adopted by *Atta cephalotes* (Robinson *et al.*, 1974; Jaffe & Howse, 1979), where the sensory threshold for the detection of the pheromone is more than 250 times lower than the threshold for directed orientation, i.e. attraction (Jaffe, Bazire-B & Howse, 1979). In ants of the genus *Leptogenys*, the orientation pheromone is also used for attraction, (Maschwitz & Schönegege, 1977) a fresh trail will attract ants for only half an hour, whereas it will still be used in orientation for 5 h. *Megaponera foetens* uses the poison gland secretion as an attractant and orientation signal at the same time, with different threshold concentrations for both effects (Longhurst, pers. comm.).

Solution (c); the use of two different pheromones in recruitment; seems to have been adopted by *Pogonomyrmex badius* (Hölldobler & Wilson, 1970) and *Myrmica rubra* (Cammaerts, 1974). Both species secrete an orientation pheromone on the way from the food to the nest and a recruitment pheromone on the journey back to the food.

(B) COMPARISON OF THE MODELS

With fixed constants, comparisons between models A, B, C and D are possible (Fig. 2). They show that the assumptions of equilibration of

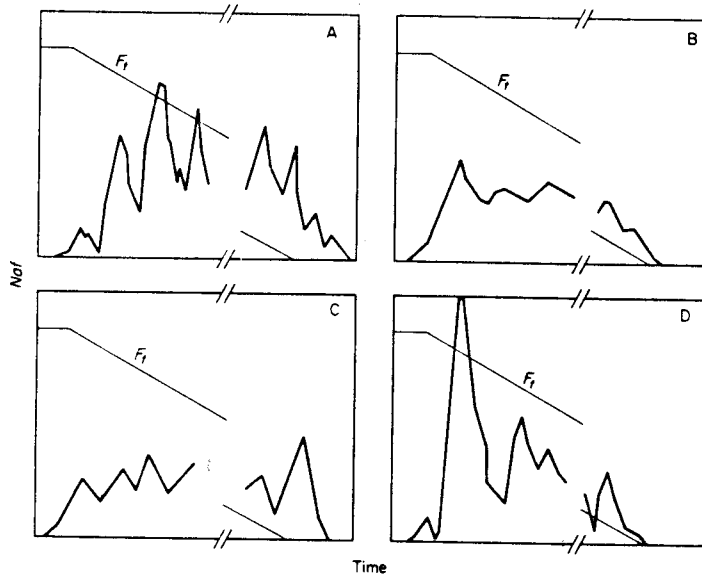


FIG 2. Variations in the number of ants arriving at the food source (N_{af}) during a recruitment process simulated by models A, B, C and D respectively.

recruitment (ii.1 and ii.2) and the assumptions of communication of food quality (iii.1 and iii.2) are not related and have totally different effects on the recruitment patterns. Assumptions ii.1 and ii.2 are related to the speed of food retrieval and the effort needed for it; whereas assumptions iii.1 and iii.2 are related to the effectiveness of transmitting the information about the quality of the food. Model D (ii.2, iii.1) produces faster food depletion with less trips from the nest to the food than model A (ii.1, iii.1); and model B (ii.1, iii.2) faster depletion than model C (ii.1, iii.2). Therefore, we may conclude that assumption ii.2 produces a more efficient recruitment than assumption ii.1. In assumption ii.2 (models B and D) there is a difference in that the number of ants recruited to the food decreases as the food source is exhausted. Models assuming ii.1 (models A and C) have a high number of ants recruited to the food after the food source is exhausted. We also observe in models A and C absence of a maximum recruitment phase immediately after the initial phase, which is present in models B and D (Fig. 2).

No fundamental difference in the general pattern of recruitment between models assuming iii.1 (models D and A) and those assuming iii.2 (models B and C) can be observed (Fig. 2). But if the food quality is varied (k_4 in models

A and D and k_6 in models B and C), for different distances between food source and the nest, we observe that in those models assuming iii.1, an increase in the food-nest distance (x) reduces the amount of recruitment drastically (Fig. 3). The models assuming iii.2, show a recruitment pattern in which the amount of recruitment is not affected by the food-nest distance, but only by the quality of the food (Fig. 3).

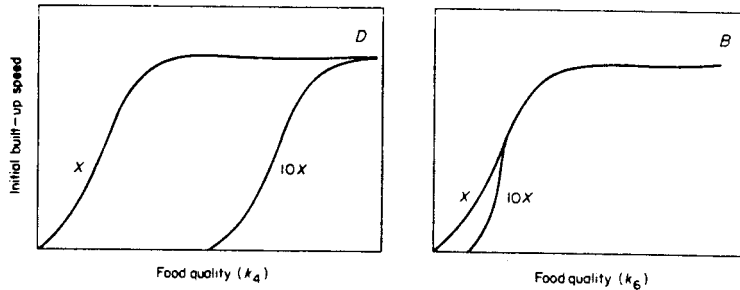


FIG 3. Changes in the initial slope of the recruitment curve due to different qualities of food at food-nest distances of x and $10x$ using models D and B respectively.

These results show that if assumption iii.1 is the one used by the ants in their communication system, they have to increase their trail-laying efforts at increasing food-nest distances in order to produce similar recruitment for food of equivalent quality. Even a lower amount of recruitment at longer distances will require a greater trail-laying effort by individuals. The experimental findings do not show this behaviour in individual ants (Hangartner, 1969). The longer the distance of the food source from the nest, the lower the trail-laying effort of individual ants. This finding, is consistent with assumption iii.2 (model B): in order to reduce the attractiveness of distant food sources, the individuals must reduce their trail-laying efforts (reducing k_6) per unit distance along the trail. The curves showing the recruitment pattern in *Solenopsis saevissima* (Wilson, 1962), for which a recruitment system of the kind of model A had been thought to hold (Wilson, 1971), can be reproduced using model B, but not with model A. Also the experimental results from *Pogonomyrmex*, *Myrmica* and *Atta* suggest that model B is the more accurate one.

(C) EFFECT OF THE PROPORTION OF SCOUT ANTS ON RECRUITMENT

The proportion of scout ants foraging at short food-nest distances is not very important, but at long distances, it turns out to be the main limiting

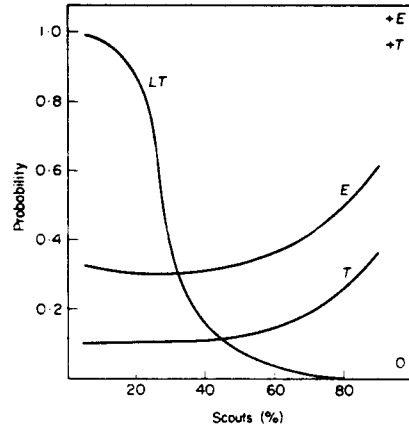


FIG. 4. Effect of different percentages of scout ants participating in the recruitment, simulated by model B, on the total number of trips to the food (E), on the time needed to retrieve 50% of the food (T) in successful recruitments; and on the probability of losing the trail before 90% of the food was retrieved (LT) at a long nest-food distance ($x = 20$).

factor in recruitment (Fig. 4). The efficiency of recruitment is directly related to the proportion of scout ants participating in the process. In successful recruitments the efficiency can be measured as the recruitment effort (number of trips to the food: $\sum_i Na_i$) or as the speed of food retrieval (half-time of food depletion i.e. the time 50% of the food is collected). If the proportion of trails lost, before 90% of the food has been collected, is measured, the effect of the scout ants on the efficiency of recruitment is even more dramatic. At short food-nest distances, more than 90% of the food is eventually taken. At long distances, many of the recruitments started retrieve less than 50% of the food if the proportion of scout ants is low.

The optimum proportion of scout ants thus depends on the average distance of the food source the ants exploit. At short distances the optimum seems to be between 10% and 30% of scout ants (Fig. 4) because no trails are ever lost. At long food-nest distances, many trails can be lost, and the optimum proportion of scouts is around 50%. These optimum proportions are similar for all four models, and also for different initial numbers of ants available for recruitment in model B. The time spent by the colony in model B for the collection of food at long food-nest distances and with the optimum proportion of scouts, increases with decreasing amounts of food remaining. At the same time, the probability that the ants will lose the food source, because the trail fades, also increases as amounts of food remaining at the food source decrease. This mechanism would provide the ants with a

regulatory device, which insures them against over-exploitation of their surrounding food sources. For the food sources close to the nest, this mechanism does not work, and probably another device, altogether different, exists (Cherrett, 1968; Rockwood, 1976).

Different proportions of scout ants give rise to different proportions of ants returning without food to the nest, relative to those returning with food at different times of the recruitment process. These patterns (Fig. 5), if

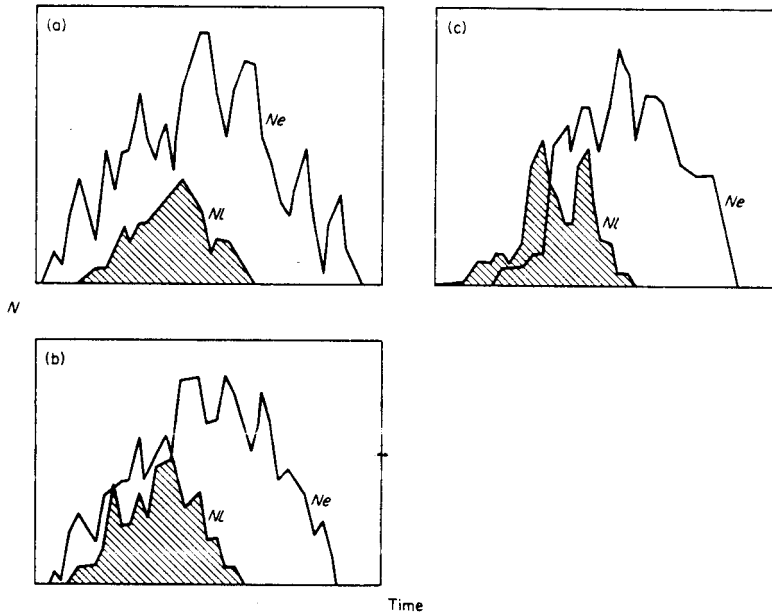


FIG. 5. Variations in the number of food carrying ants (N_f) and unloaded ants (N_e) returning to the nest during a recruitment process simulated by model B with different proportions of scout ants participating in the recruitment; (a) 75%, (b) 50%, (c) 10% of scouts.

compared with experimental results, lead to the following conclusions: In *Decamorium* (Longhurst, Johnson & Wood, 1979) and in *Pogonomyrmex* (Hölldobler & Wilson, 1970), the recruitment pattern reported resembles most nearly that with a 10% of scouts, whereas in *Atta*, (Cherrett, 1968; Jaffe; unpublished observations) the recruitment pattern most closely resembles one with 50% of scout ants. The apparently contradictory reports of the number of foragers returning to the nest without a load in *Atta* Cherrett (1972), reported 42%, whereas Lewis *et al.* (1974) reported about

13%, could be explained by different colony sizes. Larger colonies have longer foraging trails (Lewis *et al.*, 1974) and therefore different optimum scout proportions for the recruitment process. *Decamorium* and *Pogonomyrmex* should have shorter foraging trails than *Atta*. *Decamorium* forage on average up to about one thousand times its body length, whereas *Atta* forage for about ten thousand times its body length. (See Cherrett, 1972, and Longhurst *et al.*, 1979.)

The proportion of scout ants can be related to the quality of the food find and to the amount of food left (assumption iv.2), using the criteria: very attractive food induces an ant to be a scout, less attractive one induces it to collect, and low attractive food makes the ant return to the nest without laying trails. The attractiveness can be assessed as the product between quality and amount of food left. Each ant will then have its own threshold for each of the three alternatives. The results show that with models A and B, this assumption does not change the recruitment pattern substantially. The efficiency of recruitment decreases much faster as the food-nest distance increases compared to the same models but assuming iv.1.

4. Conclusions

The communication system used by ants in mass recruitment is one which probably works in the following way.

An ant, finding new food, will lay a trail from the food to the nest, in such a way that the concentration of pheromone on the trail will have a certain value, according to the quality of the food and the distance from the nest. The pheromone on the trail attracts a certain number of nestmates which will reinforce the trail, maintaining its original pheromone concentration or a similar one according to information about the food that the trail-laying ant has obtained. Scout ants will continuously walk on the trail in both directions, without cutting food, maintaining the concentration of pheromone on the trail at an adequate level. Overcrowding on the food source will cause the ants to choose a lower concentration level, therefore less trail-laying effort will be observed, because a smaller amount of pheromone is required in order to maintain the pheromone concentration at its new level. A very large number of ants arriving at the food source will result in some scout ants ceasing to maintain the trail and beginning to cut food. Food-carrying ants will reinforce the trail in a similar way to the scouts. Trail-laying is performed in both directions on a trail. In all recruitments, a large proportion of the ants are scout ants. The longer the trail leading to the food sources, the larger the proportion of scouts needed to maintain the pheromone concentration on the trail at its optimal level. In ant species

using two different pheromones for attraction and orientation, the concentration level of the recruitment pheromone (attraction) will be maintained constant by the ants. The orientation pheromone must be maintained above a certain threshold concentration for effective recruitment.

From this analysis we may suggest that the recruitment system in ants includes three important features: scouts, orientation pheromones and attraction to the trail. The order of importance correlates with the evolutionary development of the species concerned. Primitive recruitment systems involve tandem running (Wilson, 1971), where scouts have the main role and where odour trails, if present, serve only as orientation signals. In more advanced species, odour trails are always present, and play an important role, as in the case of *Camponotus sericeus* (Hölldobler, 1974). The next step of sophistication in recruitment is group recruitment, in which the scout ant does not need to be in direct physical contact with its followers, i.e. the orientation trail is used by the following workers. An example of this kind of recruitment occurs in *Camponotus socius* (Hölldobler, 1971). In this species, in addition to the orientation pheromone, a stimulatory substance from the poison sac is secreted on to the trail. The "waggle" motor display is essential for attracting nestmates to the trail.

Camponotus pennsylvanicus (Traniello 1977) has a similar system to that of *C. socius*, but some recruitment can be achieved with odour trails alone, although the "waggle" motor display of the scout ant intensifies the recruitment process. This appears to be an intermediate step towards a pure chemical mass recruitment system. *Decamorium uelense* (Longhurst *et al.*, 1979) uses both recruitment systems: The first ants are recruited using group recruitment, and some time later, the process begins to change to chemical mass recruitment.

Following the development of the recruitment system to the level of specialisation of chemical mass recruitment it can be seen that the role of scout ants does not vary considerably. The main variable is the efficiency and speed of the recruitment process. The advantage of chemical mass recruitment lies not so much in a reduction in the number of scout ants, but in the speed that a certain food source can be made available, and the reduced effort required by the ants.

Taylor (1978) showed mathematically that the recruitment system in ants will select the type of food collected in accordance with the energy requirements of the specific recruitment system used. One important element is the minimisation of interference among workers at the food source. He reconfirmed these results experimentally in two species of Myrmicine ants (Taylor, 1977). This hypothesis implicitly assumes that the ants may change their communication system in order to obtain the optimum recruitment in

relation to net energy gain, but do not take into account the energy requirements of the communication system itself. In his experimental work, he made one finding that did not fit his hypothesis: the ants did not choose a narrower range of seed sizes as the distance to the patch increased. In order for the ants to be able to do this, they would require a mechanism which could provide them with information about the range of seed size available. This could be obtained either by individual exploration of the food source, which would increase "y", and therefore the time an ant spends on the food source and the rate of energy expenditure per worker (t_d and c_d in Taylor, 1978); or by using a new pheromone the concentration of which could indicate the range of sizes. This would require a physiological effort which probably would not be compensated for by the energy gain.

The communication system used varies in accordance with the kind of food or conditions for food collection which the colony experiences. For example, seasonal food abundance determines the form of the foraging activity in some desert ants (Bernstein, 1974). The same has been observed in *Megaponera foetens* (Longhurst & Howse, 1979), in the Nigerian guinea savanna, where recruitment can vary from individual foraging, to chemical recruitment or to group recruitment, according to the density and distribution of the food.

One remarkable finding is that chemical mass recruitment is used for two completely different types of food, i.e. predatory ants of the genus *Leptogenys* (Maschwitz & Mühlenberg, 1975) feed on termites, and other animals, whereas ants of the genus *Atta* collect leaves. Both ants use trunk trails and chemical mass recruitment with pheromones for attraction and orientation. This suggests that the competition for food with other animals and fast communication of new food sources are equally important factors in predatory ants and herbivorous ants, and that chemical mass recruitment is probably the optimum possible system for effective food retrieval in non-nomadic ants. A computer model, considering more than one trail at a time, perhaps could give more information about this subject.

Thanks are given to CONICIT of Venezuela for the award of a postgraduate scholarship. I also want to thank Dr P. E. Howse and Dr B. Scharifker for their critical reading of the manuscript, Dr C. Longhurst for his helpful discussions, Mrs C. Riggs for the secretarial work, and Mrs M. Ribbi and Dr A. Ribbi-Jaffe for drawing the figures.

REFERENCES

- BERNSTEIN, R. A. (1974). *Am. Natur.* **108**, 490.
BOSSERT, W. A. & WILSON, E. O. (1963). *J. theor. Biol.* **5**, 443.
CAMMAERTS-TRICOT, M. C. (1974). *J. Comp. Physiol.* **88**, 373.

- CARTHY, J. D. (1951). *Behaviour* **3**, 275.
 CHERRETT, J. M. (1968). *J. Animal Ecol.* **37**, 387.
 CHERRETT, J. M. (1972). *J. Animal Ecol.* **41**, 647.
 CLARKE G. M. (1969). *Statistics and Experimental Design*. London: E. Arnold.
 GAMBOA, G. J. (1975). *Oecologia* **20**, 103.
 HANGARTNER, W. (1967). *Z. vergl. Physiol.* **57**, 103.
 HANGARTNER, W. (1969). *Z. vergl. Physiol.* **62**, 111.
 HÖLDOBLER, B. (1971). *Z. vergl. Physiol.* **75**, 123.
 HÖLDOBLER, B. (1974). *J. Comp. Physiol.* **90**, 105.
 HÖLDOBLER, B. (1976). *Behav. Ecol. Sociobiol.* **1**, 3.
 HÖLDOBLER, B. & WILSON, E. O. (1970). *Psyche* **77**, 385.
 HOLT, S. J. (1955). *Animal Ecol.* **24**, 1.
 JAFFE, K., BAZIRE-BENAZET, M. & HOWSE, P. E. (1979). *J. Insect Physiol.* **25**, 833.
 JAFFE, K. & HOWSE, P. E. (1979). *Animal Behav.* **27**, 930.
 LEWIS, T., POLLARD, G. V. & DIBLEY, G. C. (1974). *J. Animal Ecol.* **43**, 129.
 LONGHURST, C. & HOWSE, P. E. (1979). *Insectes Soc.* (in press).
 LONGHURST, C., JOHNSON, R. A. & WOOD, T. G. (1979) *Oecologia* **38**, 83.
 MASCHWITZ, U. & MÜHLENBERG, M. (1975). *Oecologia* **20**, 65.
 MASCHWITZ, U. & SCHÖNEGGE, P. (1977). *Naturwissenschaften*, **64**, 389.
 PLEKHANOV, G. F. & KAUL, R. M. (1977). *Zool. Zh.* **55**, 1573.
 ROBINSON, S. W., MOSER, J. C., BLUM, M. S. & AMANTE, E. (1974). *Insectes Soc.* **21**, 87.
 ROCKWOOD, L. L. (1976). *Ecology* **57**, 48.
 TAYLOR, F. (1977). *Behav. Ecol. Sociobiol.* **2**, 147.
 TAYLOR, F. (1978). *J. Theor. Biol.* **71**, 541.
 TRANIELLO, J. F. A. (1977). *Behav. Ecol. Sociobiol.* **2**, 61.
 WEHNER, R. (1976). *Sci. Am.* **235**, 106.
 WILSON, E. O. (1962). *Animal Behav.* **10**, 134.
 WILSON, E. O. (1971). *The Insects Societies*. Harvard: Belknap Press.

APPENDIX

Values of the Constants Used

$$\begin{aligned}
 k_1 &= m_{it} \\
 k_2 &= 50-200 \\
 k_3 &= 20 \\
 k_4 &= 0.001-0.2 \\
 k_5 &= 1.5 \\
 k_6 &= 0.03-2.0 \\
 k_7 &= 1-5 \\
 k_8 &= 1.2-1.3
 \end{aligned}$$

Mean and standard deviation for distributions for:

$$T_i: \ln(1) \pm \ln(2)$$

$$A_i: \ln(20) \pm \ln(2)$$

CHEMICAL COMMUNICATION IN ANTS

Limits to the uniform distributions for

$$m_1 = 1-60$$

m , after returning to the nest:

1-10 for ants returning before trying the food

1-3 for ants returning carrying food for recruiting

$$a^s/a^n = 0-10$$