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Jean-Paul Lachaud. Recruitment by selective activation: an archaic type of mass recruitment in the ponerine ant (*Ectatomma ruidum*). *Sociobiology*, 1985, 11 (2), pp.133-142. hal-02129814

**HAL Id: hal-02129814**

**<https://hal.science/hal-02129814>**

Submitted on 15 May 2019

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**Recruitment by Selective Activation:  
An Archaic Type of Mass  
Recruitment in a Ponerine Ant (*Ectatomma ruidum*)**

by  
Jean-Paul Lachaud<sup>1</sup>

ABSTRACT

The discovery of a rich food-source near to their nest by the ponerine ant *Ectatomma ruidum* Roger results, one time out of four, in several going together to the area in which the food-source was placed. The recruitment appeared to be based on a selective activation by the recruiter of the other foragers whose foraging is specialized in that area. Guidance towards the source seems based more on the smell of the food rather than on chemical trails and is performed without the following of a leader.

INTRODUCTION

A particular type of communication known as recruitment, in which several members of a society cooperate to perform a task, is widespread among social insects. The tasks in which recruitment occurs include the transport of food, nest defense and moving the society to a new nest site. Various recruitment techniques, based to a greater or lesser extent on mechanical or chemical features, have been demonstrated for the Formicidae, with the relative contribution of each depending on the evolutionary level of the species concerned. Thus, tandem running, which is considered to be the most archaic recruitment technique and in which mechanical signalling is the most important component, is frequently observed in the Ponerinae sub-family, which is usually considered primitive (Möglich, 1973; Maschwitz et al., 1974; Agbogba, 1982, 1984). On the other hand, mass and group recruitment, which depend more or primarily on chemical mechanisms which alert large numbers of individuals, are often observed in evolved genera such as *Camponotus* (Wilson, 1965; Hölldobler, 1971), *Solenopsis* (Wilson, 1962) or *Oecophylla* (Hölldobler and Wilson, 1978). This relationship between the complexity of the signals used and the acknowledged evolutionary level is, in fact, only approximately valid and one can cite many instances which violate the rule. For example, tandem running has been observed in several Myrmicinae

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(Wilson, 1959; Dobrzanski, 1966) and Formicinae (Hingston, 1929; Hölldobler et al., 1974) species, and various Ponerine species have been reported to show group recruitment that can be very elaborate (Collart, 1927; Baroni-Urbani, 1973; Maschwitz and Schönege, 1977; . . . etc). The most complex of these latter was Maschwitz and Mühlenberg's report (1975) that *Leptogenys ocellifera* use a highly efficient recruitment process depending only on chemical signals, though, as in all cases reported for the Ponerinae, the recruiter is observed to lead the column of recruited foragers.

We observed several instances of what appeared to be mass recruitment in a neotropical Ponerine, *Ectatomma ruidum* Roger, during the course of an investigation of the foraging strategies used by this species (Lachaud et al., 1984). These observations induced us to investigate this phenomenon more thoroughly.

## METHODS

*E. ruidum* is a diurnal earth-dwelling ant (Lopez and Lachaud, 1983) which is typically found anywhere between southern Mexico and the northern border of Brazil either in plantations or savanna regions, or even damp rain-forests (Weber, 1946; Brown, 1958; Kugler and Brown, 1982). There are two or even three entrances to the nests which contain between 50 and 200 individuals. These entrances lead to annexes used for food and occasionally, brood storage. There is however always one main entrance, upon which most of the society's foragers focus their activity.

In the coffee plantations near to Tapachula (Mexico), where this investigation was carried out, the colonies' foraging areas consist of a mosaic of individual foraging areas. Because of the high density of colonies of this species in this biotope, and the resulting territorial competition, these foraging areas are generally situated close to the nest entrance. By fact, near to this nest entrance, there is a considerable overlap of the individual foraging areas, leading to intensive exploitation of this area by groups of workers that are specialized in the same territorial sector (Lachaud et al., 1984).

All of the experiments were carried out in the field at the end of the rainy season (October-November 1982) at the peak of the daily activity cycle which is between 10:00 and 12:00 hrs. (Lopez and Lachaud, 1983). Having located the nest entrance, circles with diameters of 20cm and 100 cm were drawn around it with a string, and the North, South, East and West coordinates were drawn delimiting the 4 territorial zones: North-East, North-West, South-East and South-West (Figure 1).

In order to follow the changes in activity in the different sectors, and any influence of these changes on the activity in other sectors, minute by minute records of all entrances and exits and the directions followed by

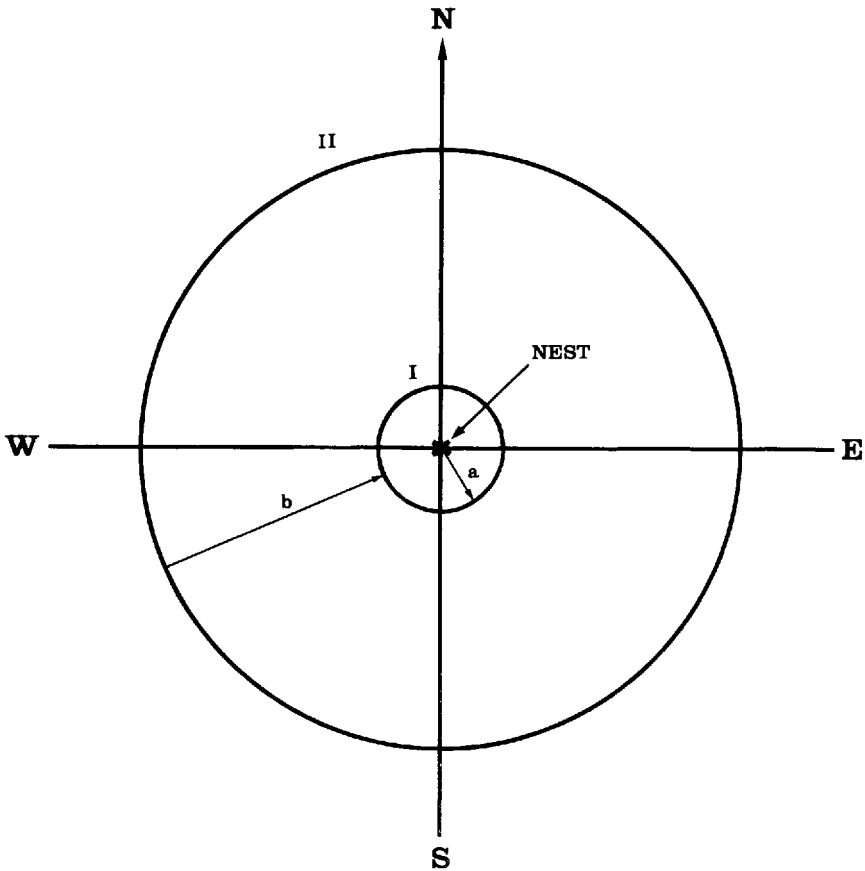


Fig. 1. Schematic representation of the observational arrangement used. The diameter of circle I was 20cm, and that of circle II was 100cm. Those components of the foragers' trajectories that were used to determine their orientation are shown by "a" for exits and by "b" for entries.

the foragers, were taken. Exit directions were established on the basis of the ant's orientation between the nest entrance and the first circle (a on Figure 1), and entrance directions were based on the path between the outer and inner circles (b on Figure 1).

This procedure was adopted because the ants' orientation when leaving the nest area tended to be fairly constant, but on returns, especially if prey was being carried, the ants often changed direction repeatedly close to the nest, turning around while probing the ground with the abdomen, apparently searching for the nest entrance, the localization of which seemed upset in this specific instance. Furthermore, most of the time, the workers enter the nest backwards when carrying prey. This makes it easier for the position of the prey to be adjusted to fit the narrow nest entrance.

The three periods of observation are outlined in Figure 2:

-The first period, between A and B is a control period of the initial activity, and lasted 21 min.

-During the second period, between C and D, food (tuna crumbs upon a dead leaf) was placed 50cm from the nest entrance in a randomly chosen sector, which was then the "experimental sector". The first two ants (Ants I and II) to discover the food source and return to the nest were considered to be potential recruiters, and were individually marked with a spot of paint on the end of a needle. The durability of these marks (several hours) easily surpasses that of the experiment. This identification was quickly carried out and did not apparently disturb the forager. This stage lasted for 30 min. after the entrance of the first discoverer ant.

-The third period, from D to E, followed the removal of the food source and was aimed to evaluate any modification of the ants' behaviour as a result of the previous stage. This final stage lasted 21 min.

Previous studies investigating *E. ruidum*'s activity cycles (Lopez and Lachaud, 1983 and unpublished data) suggested that, given the time at which the experiments were carried out, and their short duration, the number of foragers should remain nearly constant during the experimental period.

## RESULTS

The present analysis concerns only the twelve complete experiments that were carried out. All the statistical analyses use the Mann-Whitney test.

The histograms on Figure 2 show the averaged general activity levels (from 12 separate replicates) in the foraging area as a function of time. The activity in the experimental sector is compared with that of the three others pooled. These results, grouped into 3-min. periods highlight two important aspects:

There is much more activity in the experimental sector during the C-D phase than in the control A-B period ( $p < .001$ ). This C-D activity averages more than three times the A-B activity in this sector. Indeed, the activity in the experimental sector alone is greater than in the other three sectors combined. Following the removal of the food source, this activity level drops rapidly in the D-E phase ( $p < .001$  between the activity level of C-D and D-E periods) to about the initial level (no-significant difference between activity level of A-B and D-E periods).

The increase in the experimental sector activity occurs independently of activity levels in other sectors which show very little change (no-significant differences between the activity level of A-B and C-D, C-D and D-E, A-B and D-E periods). The increase is therefore not accounted for by a rearrangement of the foragers in the territory.

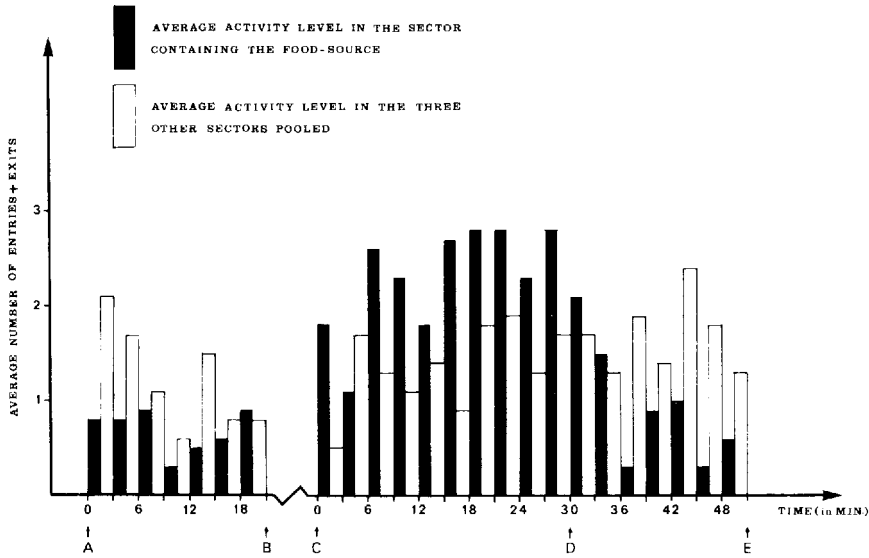


Fig. 2. Histogram showing the average level (from 12 separate experiments) of activity by *E. ruidum* on its territory. The activity level (the 3-minutes average number of entries and exits per hour) is shown as a function of time. A: beginning of the control period; B: end of the control period, and deposit of food-source; C: entry to the nest of the first forager having discovered the food-source; D: removal of the food-source; E: end of the experiment.

A detailed analysis of each experiment reveals the existence of two fundamentally different types of behavioral response during the C-D and D-E periods.

1) In most instances (75% of those analyzed) the large increases of activity levels during the C-D phase were due primarily to the response of the first one or two foragers that discovered the food source. This response consisted of shuttling repeatedly between the food source and the nest.

Figure 3a illustrates the distribution of the experimental sector activity compared with the total activity, and the importance of the contribution of certain groups of foragers to this type of response. During the C-D period ants I and II alone produced nearly 85% of the activity recorded in that sector (which represents about 60% of the entire colony's activity during this period). The remaining 15% of the activity was produced by a small number of workers (from 0 to 2), whose contribution increased to about 60%, compared to 40% for ants I and II, in the D-E period.

Worker I typically appeared very agitated when bringing a piece of tuna back to the nest, and had difficulty both in finding the nest entrance, and in entering with its prey. Other workers soon left the nest (apparently roused either by the smell of the tuna which partially blocked the entrance passage, or by the guards at the nest entrance) and mustered around worker I, further obstructing its progress. This latter individual often then

abandoned its burden, to return to the food source, while the other workers broke up the prey, and brought it into the nest. It appears that it is this activity of the other workers, and the consequent blockage of the nest entrance, that explains the low activity level in the experimental sector by ants other than workers I and II.

2) In about 25% of the cases however (Figure 3b), there was a considerable proportion of activity by ants other than I and II. After a variable time following ant I's return to the nest with prey, a group of several ants was seen to enter the experimental sector together, each individual then scattering out over the entire territorial region, without following any fixed route. In this case, workers I and II accounted for only 35% of the activity in that sector (which is 17% of the total activity during this period). The remaining 65% of the experimental sector activity was produced by a larger number of workers (from 5 to 7). The observed exit rate occasionally reached as much as 12 workers per minute which, considering the normally low activity rate observed in this species (Lopez and Lachaud, 1983 and unpublished data), was particularly striking. Concerning the participation to the activity developed in the experimental sector performed by the ants I and II and by the other workers, the difference between the two situations (no-recruitment, Figure 3a, and recruitment, Figure 3b) is highly significant for the C-D period ( $p < .01$ ) and the D-E period ( $< .02$ ).

It is however important to note that these workers seldom found the food source, and the food retrieval rate was not therefore increased because of the surplus number of workers in the experimental sector. Ants I and II were not usually among this group of ants that suddenly left the nest, and even when they were, they were not at the head of the group. This excludes any suggestion that these ants may have been guiding the others.

The increased activity of the other ants in the experimental sector continued for a considerable time following the removal of the food source, whereas that of ants I and II virtually stopped.

## DISCUSSION

These massed exits by foragers into the experimental area, although infrequent, have also been very clearly observed on several occasions in addition to the experimental results reported here. This phenomenon can be provoked by using such varied food sources as bread, hard-boiled eggs, or living Coleoptera larvae from the fruit of the "chalum" tree (*Inga sp.*) which provides the shade needed for the coffee plantations and occurred on the experimental site. When scattering out on the experimental sector, the foragers did not follow a specific path, which in any case was never direct toward the food source. On the other hand the

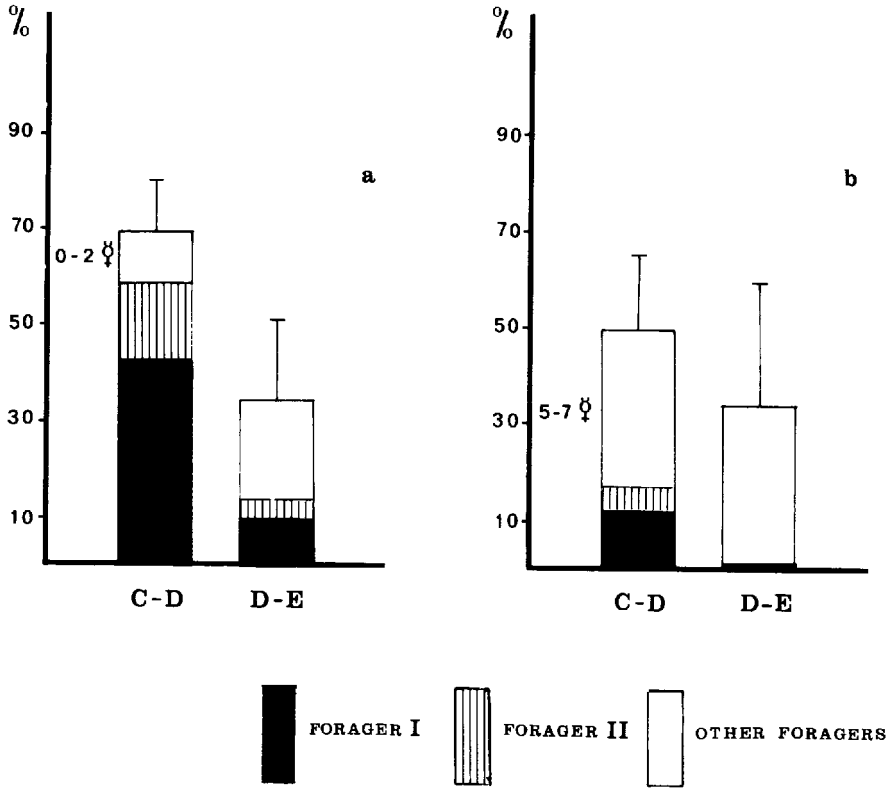


Fig. 3. Distribution of activity in the experimental sector (with food-source). The percentage of activity in this sector, compared to the total activity level is shown as a function of the different experimental periods. C-D: experimental period; D-E: post-experimental period. Foragers I and II are the first and second discoverers of the food-source. a) no recruitment (75% of observations). b) recruitment (25% of observations).

recruiter, when returning with prey, took an almost straight line back to within 2-3cm of the nest entrance. It seems difficult therefore, to explain the massed exit of the recruited workers on the basis of a chemical trail left either directly by the recruiter on its return to the nest, or indirectly by the contact of the prey with the substrate. Similarly, given the imprecision of the recruitment it seems unlikely that in the experimental conditions used (food source placed 50cm from the nest) there could have been an important intrinsic orientating effect of the source, even if one cannot totally neglect a small effect due to the food's odor. This factor however, becomes important as the distance from the nest to the food decreases. Additional observations using a food source (Coleoptera larvae) located 20-30cm from the nest entrance revealed improved foraging efficiency, with most foragers finding the food source by a fairly direct path. This improvement could well be explained in this case by an increase in the



precision of the olfactory localization, due to the proximity of the source.

The recruitment by *E. ruidum* foragers following the discovery of the food source is composed in two stages:

1) Following the recruiter's return to the nest, certain foragers appear to be activated to leave the nest in search of the food source, apparently stimulated by some (mechanical or chemical ?) action by the recruiter.

As shown in Figure 2, these foragers are not taken from those foragers active in the non-experimental sectors, because the activity level therein was unchanged either in the C-D or in the D-E periods. Given the fact that in normal conditions there is no marked change in the rate of foragers leaving the nest during the hours corresponding to the observational period, there would inevitably be a change in activity levels in these sectors if the recruitment was based on a redistribution of the foragers among the different sectors of the foraging area. It would in fact appear that the activation of foragers is operant only on those individuals that are specialized in the same spatial region as the recruiter. This is in perfect agreement with what we know on the foraging strategies used by *E. ruidum* (Lachaud et al., 1984) in which each forager remains faithful to a particular portion of the colony's foraging area, at least over a several-day period.

This hypothesis was partially confirmed for two nests in which a fraction of the workers were identified, and their foraging sites known. We were thus able to verify that certain workers known to have their foraging sites in the experimental sector were among the recruited foragers, and conversely that none of the recruited foragers was known to be specialized in any of the three non-experimental sectors. These observations are presented anecdotally, because only the individual identification of all the workers (which is only practically possible in the laboratory) could provide an accurate answer to this question.

2) Once the recruited ants have left the nest in the direction of their usual foraging area, they spread out in search of the food-source. No use is apparently made of a chemical trail for guidance, and the recruiter does not act as a leader. In this case, only the odor of the food appears to have an orientating effect, and then only if it is in the immediate vicinity of the nest entrance. Trials in which food was placed one meter from the nest entrance resulted in no recruitment.

This recruitment by selective activation constitutes a first step toward mass recruitment, which is distinguished from group recruitment primarily in the absence of a leader among the recruited foragers. Such mass recruitment, while common among more highly evolved species (see reviews by Wilson, 1971 and Passera, 1984), has never until now been reported for the Ponerinae. The closest suggestion of its existence was made in the case of *Odontomachus chelifer* (Fowler, 1980) to explain the establishment of foraging groups, but the absence of individual identification did not allow the conclusion that there was no leader. This lack of

leadership by the recruiter in *E. ruidum* is however certain, even though the details of the selective invitation behavior by the recruiter and the content of the transmitted information remain to be elucidated.

This ability, though rare, to use an opportunistic strategy when confronted with the pressure of certain environmental factors, bears witness to a high level of behavioral plasticity. This is well known for the more highly evolved species of the *Pogonomyrmex* and *Veromessor* genera (Bernstein, 1975; Hölldobler, 1976), but the only equivalent in the Ponerinae was reported for *Megaponera foetens* (Lévieux, 1966; Longhurst and Howse, 1979). This plasticity allows *E. ruidum* to easily adapt its foraging strategy according to the characteristics of the food-source. The widening of the behavioral responses' repertoire available to the species thus confirms the highly evolved level of the *Ectatomma* genus within the Ponerinae subfamily (Fresneau et al., 1984; Lauchaud et al., 1985).

#### ACKNOWLEDGMENTS

This research was supported in part by the C.N.R.S. (R.C.P. n 645) and by the B.I.D.—C.O.N.A.C.Y.T (Mexique). I am very grateful to G. Goodall for the English translation.

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