

MASS RECRUITMENT TO NECTAR SOURCES
IN *PARAPONERA CLAVATA* : A FIELD STUDY

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SUMMARY

Paraponera clavata foragers employ a trail pheromone and activation within the nest to obtain mass recruitment to simulated nectar sources. Foragers leaving and returning to the nest normally follow the same path. The existence of a trail pheromone was inferred from a series of experiments in which different techniques were employed to disrupt main foraging routes. Individuals baited to simulated nectar sources were observed to drag their gasters in a distinctive fashion when returning to the main trail. The return of an individual from a bait site resulted in greatly increased foraging activity from the colony. A maximum of 352 individuals were recruited within an hour following presentation of the bait. Recruited individuals were able to find the bait site in the absence of the initial forager by following the path taken by the initial forager. Even under normal, unbaited, conditions ants leave colonies in a temporal sequence that suggests social facilitation.

RESUME

**Recrutement de masse vers des sources de nectar chez *Paraponera clavata* :
une étude de terrain**

Les fourragères de *Paraponera clavata* emploient une phéromone de piste et l'activation dans le nid pour obtenir un recrutement de masse vers des sources de nectar artificielles. Les fourragères allant et revenant au nid suivent normalement la même direction. L'existence d'une phéromone de piste découle d'une série d'expériences dans lesquelles différentes techniques furent employées afin de rompre les principales routes de fourragement. Des individus attirés vers des sources de nectar artificielles furent observés tirant leur abdomen d'une manière particulière en retournant à la piste principale. Le retour de l'individu du site de l'appât provoqua un grand accroissement de l'activité de fourragement de la colonie. Un maximum de 352 individus fut recruté dans l'heure suivant la présentation de l'appât. Des individus recrutés furent capables de trouver le site de l'appât en l'absence de la fourragère initiale en suivant la direction prise par cette dernière. Même dans des conditions normales, sans appât, les fourmis quittent les colonies dans une séquence temporelle qui suggère une facilitation sociale.

Ponerine ants include morphologically primitive ants ; studies of them have special value in understanding the evolution of recruitment systems. In the ponerines transitions from insectivory to other patterns of feeding are observed as well, making them important in understanding the relationships between the evolution of food preferences and recruitment systems. The purpose of this study was to quantify certain aspects of the recruitment system of the giant tropical ant, *Paraponera clavata*.

P. clavata is characteristic of lowland tropical forests of the New World and has been studied in Brazil (MANN, 1916), Ecuador (HERMANN, 1975 ; YOUNG and HERMANN, 1980), Panama (JANZEN and CARROLL, 1983), and Costa Rica (YOUNG and HERMANN, 1980 ; present study). Previous reports have focused on foraging behavior (YOUNG and HERMANN, 1980) and activity cycles (HERMANN, 1975 ; McCLUSKEY and BROWN, 1972). JANZEN and CARROLL (1983) give a brief account of the natural history of the species and describe nest structure and population size. *P. clavata* nests are found at the base of trees and foragers move primarily in the canopy of the nest tree and adjacent trees that are reached via canopy connections or trails on the ground (YOUNG and HERMANN, 1980). A variety of food items are collected including nectar, insect prey, carrion, and plant material. This species departs from the typical ponerine condition of entomophagy in that the majority of successful foragers return with large drops of nectar carried between the mandibles (YOUNG and HERMANN, 1980 ; personal observations). Other ponerines known to exploit liquid food include the closely related *Ectatomma ruidum* (VALENZUELA and LACHAUD, 1982) and *Odontomachus* (EVANS and LESTON, 1971).

Several excellent recent studies have reported on recruitment in ponerine ants (HÖLLDOBLER and TRANIELLO, 1980 *a, b* ; HÖLLDOBLER, 1983 ; MOGLICH, 1973), calling, and trail pheromones (HÖLLDOBLER, 1978). MASCHWITZ and MUHLENBERG (1975) documented a complex recruitment mechanism in predatory ants in the genus *Leptogenys*. Recently LACHAUD (1984) documented a group predatory strategy in *Ectatomma ruidum*. Our paper reports the existence of a trail pheromone and mass recruitment in the context of recruitment to liquid food in *Paraponera clavata*.

MATERIALS AND METHODS

Field site

This study was conducted at La Selva Station, The Organisation for Tropical Studies Heredia, Costa Rica, during January, 1984. Preliminary observations were made at La Selva in May, 1979. The primary study area was the arboretum, an area in which the understory is cleared allowing easy access to nests. A total of fourteen nests were located and studied ; the presence of a fifteenth was postulated and its approximate location was determined. A detailed description of the study site, an analysis of tree-nest associations, and a map of nest locations will be published elsewhere (BENNETT and BREED, in press).

Experimental methods

Foragers were marked with Testor's model airplane enamel when individual identification was necessary. For certain experiments, foragers leaving the nest were fed a concentrated sugar solution (50/50, v/v). In some cases, individual foragers were baited or carried away from the main foraging route and then fed. For all nests there was only one main foraging route up the trunk of the "home" tree. The bait was presented away from the main route, so that the ants detoured from their normal route. Baiting was accomplished by attracting the ant with a drop of sugar water at the tip of a dropper. The ant could be "led" with this bait to a site .5-1.5 m off the main trail. The existence of trail pheromones was tested by observational studies of returning baited ants for gaster dragging, marking paths of fed ants, observation of the route utilized by subsequent foragers, and physical disruption of traversed areas.

RESULTS

Foraging activity

At the La Selva station, *P. clavata* is active throughout the photocycle. Activity data was collected periodically from 0430 to 2000. Individuals were

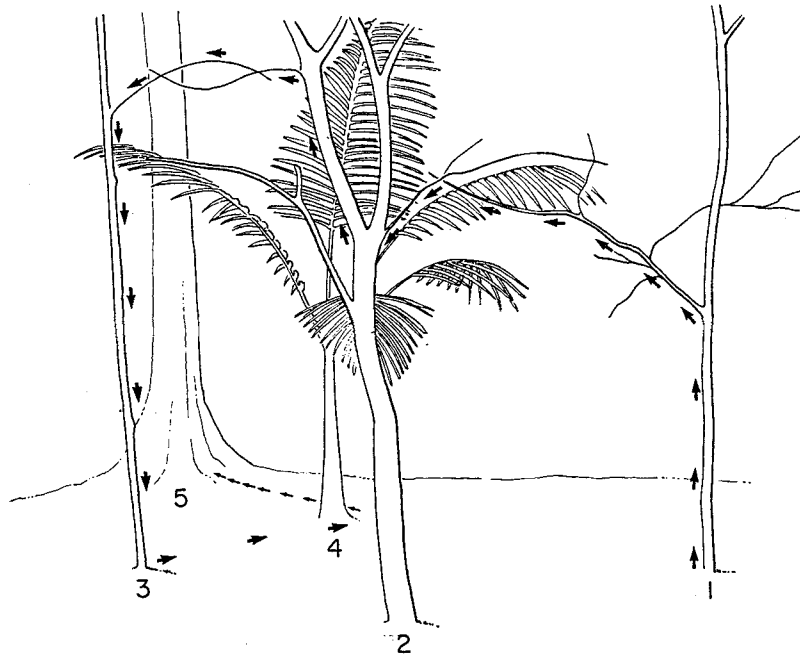


Fig. 1. — Foraging route of a typical nest; route is up the trunk of the nest tree, through the crowns of two adjacent trees, to the ground, and then up into the canopy of another tree.

Fig. 1. — Route de fourrage d'un nid typique; la route monte sur le tronc de l'arbre du nid, à travers les branches de deux arbres adjacents, sur le sol, et ensuite monte dans la canopée d'un autre arbre.

observed entering and leaving the nest continuously during this interval although activity was lowest between 1100 and 1400. Records of booty brought into the nest indicate that nectar and solid prey items were available during the entire observation period. Our observations of activity and booty are consistent with those of YOUNG and HERMANN (1980) at a nearby site.

Observations of the paths of foraging individuals indicate a high degree of fidelity to specific routes up the trunk of the home tree and into the canopy. Route fidelity is best illustrated by an example from one nest at the base of a small (6.4 cm dbh) *Pentaclethra macroloba* tree (fig. 1). 68 foragers were observed leaving and returning to this nest; none were seen to deviate from the illustrated path. Typically, there is a single trail leaving the nest; this trail does not branch until it enters the canopy.

Ants from this nest and other nests were typically observed on their foraging routes singly. Of over 1800 individuals observed leaving nests, no evidence of tandem running or other type of direct communication between individuals was seen. Extensive records were kept of temporal sequences of ants leaving colonies for statistical analysis. Figure 2 shows the frequency

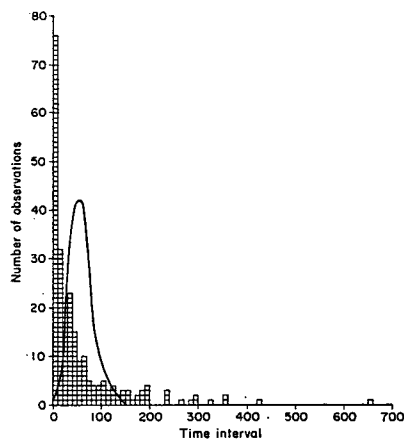


Fig. 2. — Histogram of time intervals between foragers leaving colonies. Smooth curve indicates Poisson expected distribution, based on a mean interval of 50.5 s.

Fig. 2. — Histogramme des intervalles de temps entre les fourragères quittant les colonies. La courbe continue indique la distribution de Poisson attendue, basée sur un intervalle de moyenne de 50,5 secondes.

distribution of time intervals between ants leaving the nests. If ants left in a random manner with respect to each other, then the time intervals would be expected to have a Poisson distribution. The actual distribution differs dramatically ($p < .001$) from the expected distribution, with an excess of ants leaving within a few seconds of each other and an excess of long gaps. This supports the hypothesis that communication, which could be behavioral activation or pheromone release, is occurring within the nest, a point that is tested further below.



Fig. 3. — The main foraging route goes up the larger branch in this case (indicated by arrow). The ant on the other branch has been moved to a bait site there; after feeding it dragged its gaster and left a trail used by other ants.

Fig. 3. — La principale route de fourragement monte sur la plus grosse branche dans ce cas (flèche). La fourmi sur l'autre branche a été déplacée vers un appât; après s'être nourrie, elle tire son gastre en laissant une piste utilisée par d'autres fourmis.

Field demonstration of a trail pheromone

Single foragers were baited to a location at least 25 cm from the main trail. The baited ant was fed sugar water and marked at this location. For purposes of illustration one replicate will be described (*fig. 3*). In this replicate an ant leaving the nest was baited 40 cm from the main foraging route. When this ant had collected a maximum load, it returned to the main foraging route dragging the ventral surface of the distal portion of the gaster. In the 300 s between the time when this ant entered the nest with food and returned to the food site 19 ants left the nest, all of which left the main foraging path and followed the path used by the original animal when returning from the bait. As more ants came to the bait the path was modified slightly to allow more direct travel. Two striking features of this and other replicates were that the bait was found in the absence of the baited animal, indicating an absence of tandem running, and that recruited ants were able to distinguish the new trail laid to the bait from the main foraging trail.

Six replicates of this experiment were conducted. In each case, the baited ant dragged its gaster on the substrate between the bait and the main trail. Ants leaving the nest always followed this path to the bait.

Controls were conducted to test for possible confounding factors. Of particular concern was the possibility that the food itself was acting as an attractant. To test for this drops of bait were placed 10 cm from the main foraging route at several nests. The mean time to traverse 25 cm of trail adjacent to the bait was recorded for ants leaving (5.83 s, $s = 5.33$, $n = 23$) and returning to the nest (4.23 s, $s = 3.86$, $n = 30$; not significantly different from the unbaited condition, leaving: $\bar{x} = 5.41$ s, $s = 2.68$, $n = 17$; returning: $\bar{x} = 4.16$ s, $s = 2.21$, $n = 19$). No ant was observed to leave the trail or to engage in searching (looping) or other changed activity/patterns in the vicinity of the bait.

Three treatments were used to test for the existence of trail pheromones on the main foraging routes. Survey tape was tied around the trunks of nest trees to form a 2.54 cm barrier. In each of the fourteen nests observed, this resulted in temporary disruption of foraging activity. Ants exiting the nest stopped and moved erratically in the area adjacent to the tape or returned to the nest. Returning foragers were also disrupted although foragers with booty moved much faster and tended to run past the tape with only slight hesitation. In a single replicate, a sheet of clean white paper was used to encircle a branch along which a foraging route ran. In this case, 6 foragers were observed to encounter the paper; 5 were deterred and one succeeded in traversing the paper. After 24 hours the foraging route appeared to have been abandoned. The interpretation of the preceding experiments could be confounded by the presence of a foreign object on the trail. Thus, trails were also disrupted by scraping the substrate over which the trail proceeded. In five replicates, 40 foragers were observed at the disrupted areas. A similar result to that described for the paper and tape was observed; all foragers displayed disrupted locomotion and looping behavior. Again, foragers with booty were more successful in traversing the disturbed areas. The main trails in these replicates appeared to be quite broad: an area approximately 10 cm wide was disrupted but some individuals were able to follow the periphery of these areas.

Mass recruitment

A series of experiments were conducted in which recruitment to baits was detailed and analyzed. In each case the original marked forager returned at least once to the bait site. Marked foragers spent a mean of 284.5 s ($s = 174.1$; $n = 11$; range = 59 s to 669 s) in the nest between the first feeding and the return to the bait site. Subsequent to the first trip 8 of the 13 marked ants returned two or more times (mean time spent in nest = 426.4 s, $s = 443.2$), ($n = 17$ trips, range = 1 — 5) to the bait site. *Figure 4* (open bars)

shows the regular timing of these trips. The remaining five individuals returned only a second time or not at all. The larger mean for subsequent trips reflects the inclusion of one individual that remained in the nest 1 922 s and another 1 067 s. Returning foragers were marked at three nests to determine if time spent within the nest for unbaited individuals was within the same range as spent inside the nest by baited foragers. Of the 28 returning foragers so marked none emerged within the 700 second time range observed for baited foragers. Two emerged and proceeded into the canopy after much longer times inside the nest (2 749 s ; 1 868 s). Two other individuals briefly emerged from the nest but returned to the nest without leaving the vicinity of the nest entrance.

The first stage of recruitment consists of a small number ($\bar{x} = 7.57$, $sd = 6.27$, $n = 7$, range = 1—18) of ants responding only to the initial nest visit by the baited ant. The responding ants return to the nest, and in some instances lay more trail or lay trail on a more direct route to the main trail. Recruitment of a large number of ants occurs after the initial ant returns to the nest a second time. Returning recruits also contribute to this effect (*fig. 4*).

Recruitment was also analyzed by measuring the rate of ants leaving the nest. After the return of the original forager to the nest, dramatic increase in the numbers of foragers emerging was noted. The number of these new recruited individuals arriving at the bait was recorded for a one hour block of time subsequent to the return of the initial baited animal to the nest (*fig. 4*). As each recruit arrived it was marked to distinguish between new and returning recruits. The pattern in each case was for the number of new recruits emerging from the nest to peak between 25 and 35 minutes after the baiting began and then to fall off. In most cases this decline was large relative to the peak numbers of new recruits leaving the nest (nests 6, 9, and 12) but in nest 1 (*fig. 4*) the rate of recruitment remained more stable through the 1 h observation period. In nests 12, 9 and 1 recruits often returned for subsequent loads, yielding rather large aggregations of foragers at the bait site. In one case (nest 6), there was a high rate of initial recruitment. Ants that returned to the nest with food tended not to come to the feeding site for a second feeding bout. Thus ants were spending greater periods of time in the nest. In this case the size of the foraging aggregation at the bait site was considerably smaller. One nest with a very small population was located (nest 13, *fig. 4*), and it was possible to individually mark almost all of the foragers in this nest. 10 foragers were identified. These made a total of 20 visits to the site in an one hour observation period. The mean time spent by foragers in this nest (187.1 s, $s = 81.1$, $n = 9$) was not significantly different from the mean time in nest determined for larger nests ($t = 1.478$, $p = n.s.$). The total number of recruited ants for each nest was determined by summing the number of unmarked ants leaving the nest over the observation period. 352 recruits

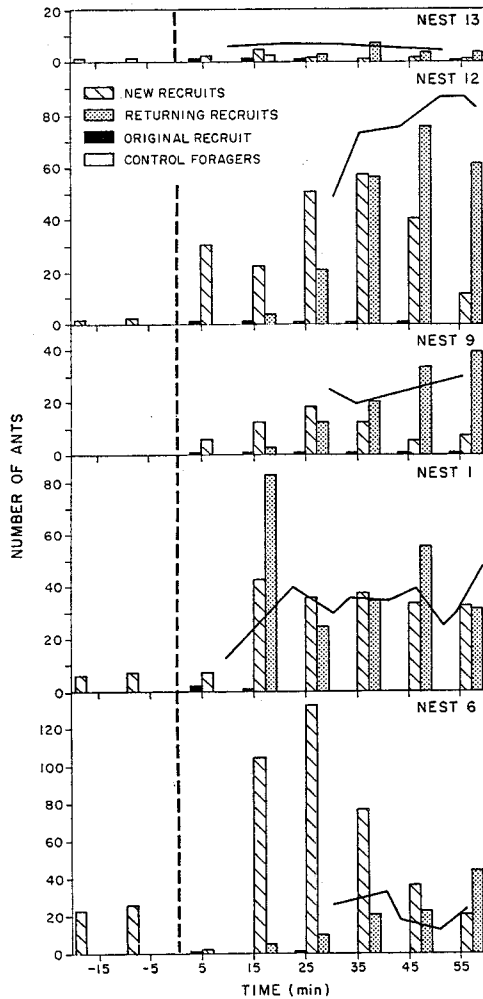


Fig. 4. — Pattern of recruitment in five nests. Time of baiting the first forager is indicated by the dashed line. As a control, the rate of ants leaving the colony prior to baiting is indicated (open bars to the left of the dashed line). A single forager was fed (solid bar) at time 0. The hatched bars indicate recruits. Some recruits came to the feeding site a second time (stippled bars). The number of recruits at the bait at any one time is indicated by the solid line in each graph.

Fig. 4. — Patron de recrutement de cinq nids. Le temps pour appâter la première fourrageuse est indiqué par la ligne en tirets. Le nombre de fourmis quittant la colonie avant le piégeage est indiqué en contrôle (en blanc, à gauche de la ligne en tirets). Une seule fourrageuse a été nourrie au temps 0 (barres pleines). Les barres hachurées indiquent les individus recrutés. Le nombre d'individus recrutés à l'appât pour la première fois est indiqué par la ligne continue sur chaque graphique.

were recorded from nest 6, 221 from nest 12, 197 from nest 1, 49 from nest 9, and 10 from nest 13.

DISCUSSION

Our major finding is that the mass recruitment system of *P. clavata* provides an effective mechanism for bringing large numbers of ants to rich liquid food sources. Statistical analysis of exits from unbaited colonies indicates that ants leave the nest in non-random temporal sequence. This suggests the hypothesis that social facilitation is taking place within the nest

and that foragers may be primed to leave by incoming foragers with booty. Our observations, however, show a more subtle system of recruitment than the group foraging and "tandem running" reported by YOUNG and HERMANN (1980) at other sites. In fact, we did not observe any behavior that could be classified as tandem running; in this respect our report differs from previous reports on this species.

Mass recruitment in *P. clavata* involves two components. First, a trail is laid from the food source to the main foraging path. The recruiting ant drags its gaster over the substrate and moves slowly, in a manner similar to other trail laying ants (WILSON, 1971). Second, ants within the nest are activated by an unknown mechanism to leave the nest and search for the new food source. Responses to rich baits are quite dramatic, but it should be emphasized again that even under unbaited conditions the ants do not leave the nest in a random temporal sequence. HERMANN (1973) reported "preforage aggregations" in *P. clavata*. He interpreted these as preparation for group raiding. We found no evidence for group predation in this species. Perhaps HERMAN (1973) observed groups of ants leaving to forage on flowers that produce nectar during restricted times. YOUNG and HERMANN (1980) referred to non-random sequences of departures from the colony as tandem running. We observed no tandem running in this species (HÖLLDOBLER and TRANIELLO, 1980 a).

The presence of a foraging system which mixes primitive solitary insectivorous foraging with the use of trail pheromones and mass recruitment to nectar sources provides special insight into the evolutionary lability of recruitment systems. This system is similar to that employed by ponerines that raid termite colonies (HÖLLDOBLER and TRANIELLO, 1980 b). In each case the use of a trail pheromone enhances exploitation of a large, stationary food source. This system allows for recruitment of more individuals more rapidly than tandem running (HÖLLDOBLER, 1977). This system of mass recruitment bears striking similarity to mass recruitment systems in higher ants (JAFFE and HOWSE, 1979 ; HÖLLDOBLER, 1971 ; HÖLLDOBLER and WILSON, 1977).

Field observation of *P. clavata* demonstrated trail laying behavior remarkably similar to that described in other ants. Main foraging routes, perhaps similar to trunk trails in other ants (HÖLLDOBLER and LUMSDEN, 1980) are apparently maintained through the use of chemical cues. Observations of foraging behavior in vegetation indicate that foragers in the canopy search in a solitary fashion away from the main trail for insect prey and nectar sources (YOUNG and HERMANN, 1980 ; JANZEN and CARROLL, 1983).

Some interesting and as yet unanswered questions concerning recruitment in *P. clavata* include the mechanism by which recruits are able to identify the location at which the trail to the new food source diverges from the main trail. The possibility exists that two pheromones are used, one for trunk trail and one for recruitment to new food sources (e.g. HÖLLDOBLER and WILSON, 1977). This suggestion remains to be tested. Second, highly concentrated

food rewards were used as baits in these experiments. The relationships among food quality, distance of the food from the nest, and the level of activation achieved are important in understanding a mass recruitment system (TRANIELLO, 1983). Finally, the mechanism by which the returning forager stimulates ants to leave the nest seeking a specific food source remains to be characterized (MOGLICH, 1973 ; MOGLICH and HOLDOBLER, 1975).

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