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Recruitment Behavior, Orientation, and the Organization of Foraging in the Carpenter Ant *Camponotus pennsylvanicus* DeGeer (Hymenoptera: Formicidae)

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Summary. 1. The recruitment process of *Camponotus pennsylvanicus* initiates and regulates foraging activities. Scout ants recruit nestmates to new food sources with alerting motor displays. Workers subsequently leave the nest and follow a recruitment trail that appears to be composed of hindgut material and poison gland secretion (formic acid) to the food. Hindgut material functions as a long-lasting olfactory orientation cue between the food source and the nest, whereas poison gland secretion makes the recruitment trail highly attractive to stimulated ants. Hindgut trails may also have a recruitment effect.

2. Although hindgut material is an important orientation cue during foraging, because ants make repeated foraging runs they may also make use of visual cues.

3. Mass foraging is organized by the behavioral activities of recruiting ants. Starvation intensifies the recruitment displays of scouts, which releases a strong recruitment response in the colony. The behavior of individual recruiters during the organization of foraging facilitates at first a quick mobilization of nestmates to the food; subsequently recruiter behavior changes. These changes the facilitate food transport to the colony. The amount of food brought into the colony along with the decrease in recruitment behaviors may account for the waning and eventual termination of foraging activity. Only ants of a particular age bracket respond to recruitment signals and participate in foraging, and of this group only a small proportion of workers are consistently active in foraging.

4. When compared to other formicine species, the recruitment behavior of *Camponotus pennsylvanicus* appears to illustrate some features of chemical mass communication while still retaining characteristics of the group recruitment technique.

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Introduction

Ants of different species employ a variety of strategies to alert and orient nestmates to a new food source, nest site, or area of disturbance. These strategies typically involve motor displays and chemical substances discharged from various exocrine organs. Recruitment behavior differs from one species to another as does the relative importance of the motor and pheromonal components.

Recruitment techniques may be comparatively analyzed based on their relative level of sophistication. Wilson (1971) has noted that primitive recruitment systems involve tandem running, in which there is a dependence on tactile signals and surface pheromones. These signals permit the formation of a communicative bond between two individuals. In this technique odor trails, if present, serve only as orientation signals. Among the ants that illustrate tandem running are the myrmicine *Cardiocondyla venestula* (Wilson, 1959) and the ponerine *Bothroponera tesserinoda* (Maschwitz et al., 1974). The group recruitment technique, in which a recruiting ant guides a group of 5 to 20 workers to the target area, represents a higher level of organization. Trail pheromones provide only directional information and are unable to induce recruitment. Tactile signals are required to stimulate nestmates to follow trails. In the advanced system of chemical mass communication it is the amount of trail pheromone discharged by workers that controls the number of ants leaving the nest. The entire recruitment process can be carried out experimentally with extracts of trail pheromone. For example, in fire ants of the genus *Solenopsis*, the trail substance functions as an orientation and alerting signal (Wilson, 1962). Among the Formicinae, *Lasius fuliginosus* also utilizes this sophisticated recruitment technique (Hangartner, 1967). Möglich and Hölldobler (1975) have cited the recruitment behavior of *Formica fusca* as an intermediate that approaches mass communication.

The genus *Camponotus* is especially interesting for studying the evolution of recruitment behavior since a series of intermediates that show various degrees of advancement in communication techniques exists in different species. Tandem running has been documented in *Camponotus sericeus* (Hölldobler et al., 1974). In this species the recruited ant must maintain mechanical contact with its leader for recruitment to be successful. A trail substance that may be discharged from the hindgut of the leader serves only as an orientation signal. In *C. paria*, which appears to be a step above *C. sericeus*, this mechanical contact is not necessary as the follower orients along an ephemeral odor trail (Hingston, 1929; Wilson, 1971). Group recruitment has been described in *Camponotus socius* by Hölldobler (1971), in *C. compressus* by Hingston (1929), and in *C. beebei* by Wilson (1965). Of these group recruiting species *C. socius* has been examined in detail. In this species odor trails function solely as orientation cues. A leader ant is necessary to stimulate nestmates to follow a hindgut trail by a motor display and subsequently maintains the excitement of the group chemically (Hölldobler, 1971). Mass communication has not yet been documented in this genus.

Due to the variety of recruitment mechanisms in the genus *Camponotus*, further experimentation with other species may provide additional indirect evidence of the possible evolutionary pathway that has led to mass communication.

This paper describes the recruitment behavior and foraging activities of *Camponotus pennsylvanicus*, which seems to represent an intermediate stage between group recruitment and mass communication.

Materials and Methods

Camponotus pennsylvanicus nests in decaying wood and is commonly referred to as a "carpenter ant". Colonies were collected in the Amherst area, removed from their wood nests, and housed in laboratory nests constructed of 1/4″ plexiglass. Nests were connected to a rectangular foraging arena during recruitment experiments, or to a circular arena (diameter = 48 cm) during orientation experiments. Colonies were fed on a sucrose solution or honey-water, freshly killed *Periplaneta*, and a synthetic diet (Bhatkar and Whitcomb, 1970). Trail-laying and recruitment behaviors were analyzed from videotype recordings.

Orientation experiments were based on a method used to statistically evaluate empirical circular distributions (Batschelet, 1965). Using this method one may obtain a mean vector of orientation whose length r represents the dispersion of the directions of individual orientation runs about the mean direction. As r approaches 1, individual orientation runs become increasingly concentrated about the mean orientation vector. The Rayleigh test was used to evaluate the statistical significance of orientation data.

Food transfer was studied by labeling a sucrose solution with radioactive phosphorus (^{32}P as H_3PO_4 in acid-free water, New England Nuclear, Boston, Mass.). The labeled sucrose was prepared by adding 0.1 ml 1.0 M sucrose to 20 µCi ^{32}P in 0.1 ml water. Samples were placed in a PPO/toluene fluor and counted with a Beckman LS-150 liquid scintillation counter. Additional methods will be presented concurrently with individual experiments.

Results

I. Orientation during Foraging

1. Trail-Laying Behavior and the Physical Nature of the Trail

Field observations indicated that, while foraging, workers of *C. pennsylvanicus* oriented to principal food resources by what apparently were olfactory trunk routes. Chemical orientation trails are known to occur in other species of *Camponotus* (Hölldobler, 1971; Hölldobler et al., 1974; Wilson, 1971), as well as in other formicine wood ants (Rosengren, 1971; Möglich and Hölldobler, 1975). Thus my first series of experiments was concerned with examining the nature of the chemical signals involved in orientation during foraging.

In the laboratory I simulated foraging conditions by connecting a colony of ants (approx. 400 ☿☿, alates, and brood, starved 5–10 days) to a foraging arena with a section of plastic tubing. A bait of 1 M sucrose or honey-water was placed in the foraging arena and scout ants were allowed to sample the food and return to the nest. After discovering the bait a scout would feed to partial or full repletion. Feeding was interrupted by self-grooming and circling the food. The scout would subsequently leave the sucrose and start off toward the nest dragging the tip of its gaster over the substrate. However, scouts would frequently return to the food, feed briefly, and start off toward the nest again. This behavior typically occurred two or three times before the ant finally returned to the nest. During the return trip, the gaster remained inclined with its tip pressed to the substrate. This posture is indicative of trail-laying.

In order to examine the physical nature of the trail, the same experimental design described above was used with a modification. The plastic tube leading from the nest to the arena was divided into two halves and a glass slide (75 × 25 mm) coated with soot and covered with a larger semicircular section of tubing was inserted between the two halves. This technique, previously used by Brun (1914) and Hangartner (1969), proved effective in determining the physical nature of the trail. As a scout returned to the nest through the tube, soot was removed from the glass where the ant's body touched the slide. The slides were then sprayed with an acrylic coating and used as negatives to make photographic enlargements.

Figure 1 shows the trail-laying posture of a worker and the structure of the trail. The thin lines composing the trail are apparently produced by a group of hairs ventral to the acidpore. In comparison with the control (normal walking posture) it can be seen that "footprint" areas are exaggerated, perhaps due to an increase in the number of tarsal segments that contact the substrate.

2. The Source of Trail Substance and Its Significance during Foraging

The preceding experiments suggest that ants lay chemical trails during their foraging activities. My next experiments attempted to answer questions concerning the origin and function of these trails.

Since trail-laying ants press the tip of the gaster to the substrate, it was logical to assume that the trail substance originated in an abdominal organ. The occurrence of trail pheromones in formicine ants is well documented (see review by Blum, 1974). In the gaster there are only three likely sources of trail substances: (1) the poison gland, (2) the Dufour's gland, and (3) the hindgut or rectal sac. In order to determine the source of trail pheromone, organs of each type were dissected from five worker ants and each group was homogenized in 0.1 ml benzene. To assay for the attractiveness of these extracts as trail substances, workers were given access to a sucrose bait and were allowed to establish foraging activites. After foraging was established, the tube leading to the foraging arena was divided and a glass plate on which an artificial 40-cm trail of 10 µl of each extract was drawn was inserted between the two halves. During the next 10 min, the response of foraging ants to each of the artificial trails was recorded. Results are shown in Table 1.

The response of foragers to poison gland extract was typically excitement. Dufour's gland extract was only mildly attractive during one trial. The response to hindgut material was strong: 71% of all foragers encountering the trail followed it at least half way. From these results I concluded that the hindgut is the source of trail pheromone. This is apparently typical of the Formicinae (Blum and Wilson, 1964).

3. Orientation during Foraging

The experiments thus far presented suggest that hindgut material functions at least as an orientation cue during foraging. This is the case in other formicine

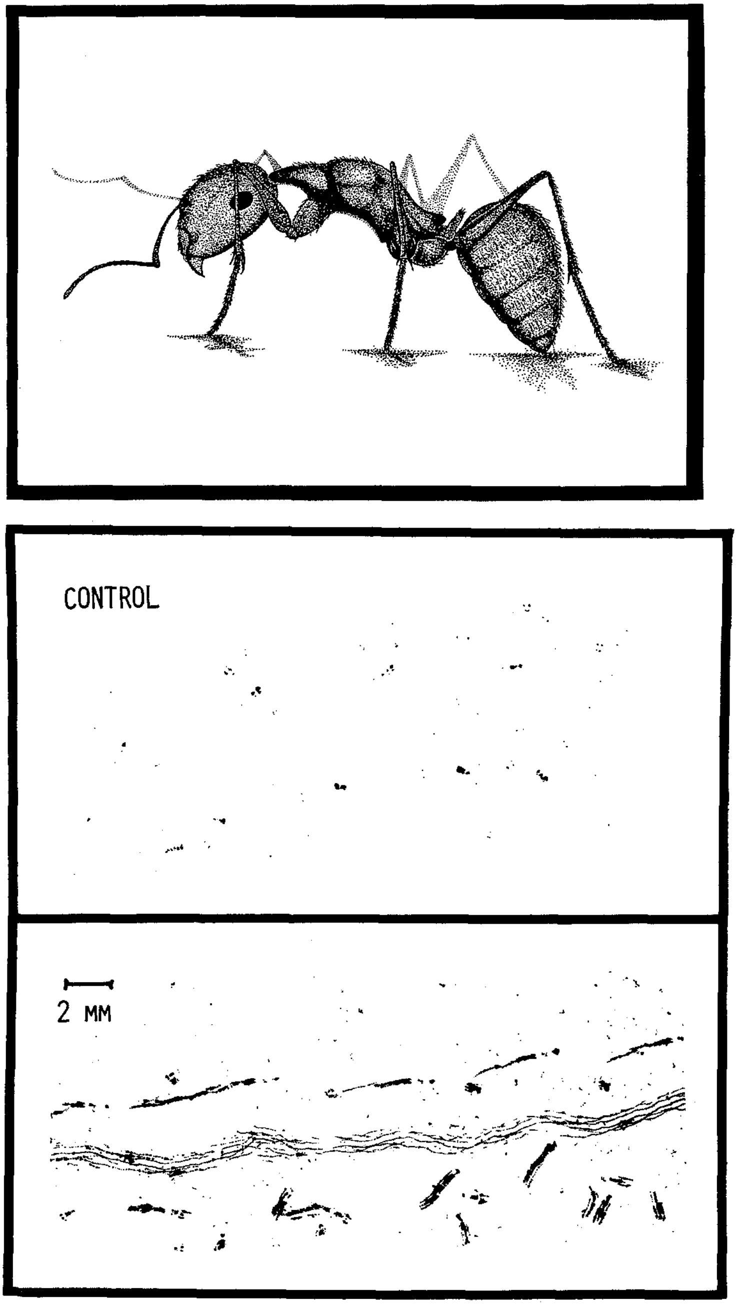

Fig. 1. Worker of *Camponotus pennsylvanicus* in trail-laying posture, with photographs made from smoked glass slides showing normal walking posture (control) and the nature of the trail. Drawing from videotape recording

Table 1. The following response of foraging ants to artificial trails of different organ extracts; five replicates

	Dufour's gland	Poison gland	Hindgut	Benzene control
No. of encounters with trail	89	128	129	106
Average following response (in cm, ±S.D.)	9.7±8.1	6.0±1.7	24.5±3.2	3.0±1.4
% following entire trail (40 cm)	10.1	3.1	30.2	0
% following 19–39 cm	18.0	8.6	41.1	1.9
% following < 19 cm	19.1	20.3	18.6	32.1
% showing no response	52.8	68.0	10.1	66.0

ants (Hölldobler, 1971; Möglich and Hölldobler, 1975). There is additional evidence to indicate that this is also true in *Camponotus pennsylvanicus*. Based on methods described by Möglich and Hölldobler (1975) I conducted the following orientation experiments.

A colony of ants was connected to a circular foraging arena. Ants entered the center of the arena through a piece of tubing. The floor of the arena consisted of a cardboard disk divided into 10° sectors. Concentric circles with radii of 5, 10, and 20 cm were drawn on each disk. The disk could easily be removed and replaced. Food was placed at the periphery of one of the sectors and ants were allowed to forage for 45 min. During this time the colony established its foraging activity, and workers oriented to the food by trails laid from the center of the arena to the food. Following this period the bottom of the arena was replaced with a fresh disk on which a trail of 10 µl of hindgut extract (five hindguts in 0.1 ml distilled water) was drawn out to a food source at the periphery. A control trail of distilled water was drawn out in the opposite direction. During the next 45 min the directions taken by individual foragers were recorded by noting the positions of ants as they crossed over the three concentric circles. To control for any attraction due to food odors a second sucrose solution covered by a wire screen and therefore inaccessible to the ants was placed 180° opposite the accessible sucrose solution. To exclude visual cues the experiment was conducted under dim red light.

Figure 2 shows that foragers used the directional information provided by the artificial hindgut trail to orient to the food. To further establish that hindgut material is an important orientation cue the food bait and the hindgut trail were rotated 90° and the response of the foragers again recorded. These results again show that the mean vector of the individual foraging runs is in the direction of the hindgut trail (Fig. 3). Since visual cues were eliminated, it is apparent that ants on foraging routes orient by means of olfactory cues provided by hindgut contents that are deposited on the trail by foraging ants.

The preceding experiments were only concerned with olfaction; they do not exclude the possibility that visual cues, if present, are also used. Other

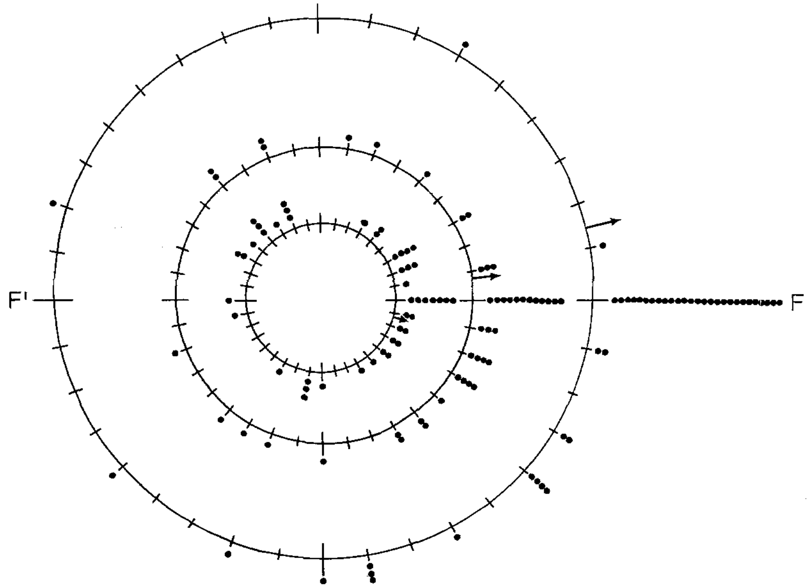

Fig. 2. Orientation of foragers in the circular arena to a hindgut trail. The mean direction of all foraging runs is represented by an arrow whose length is a measure of the dispersion about the mean direction $r^5=0.39$ ($0.01>P>0.001$), $r^{10}=0.60$ ($P<0.001$), and $r^{20}=0.79$ ($P<0.001$) ●, 1 ant; *F*, food source; *F'*, inaccessible food source

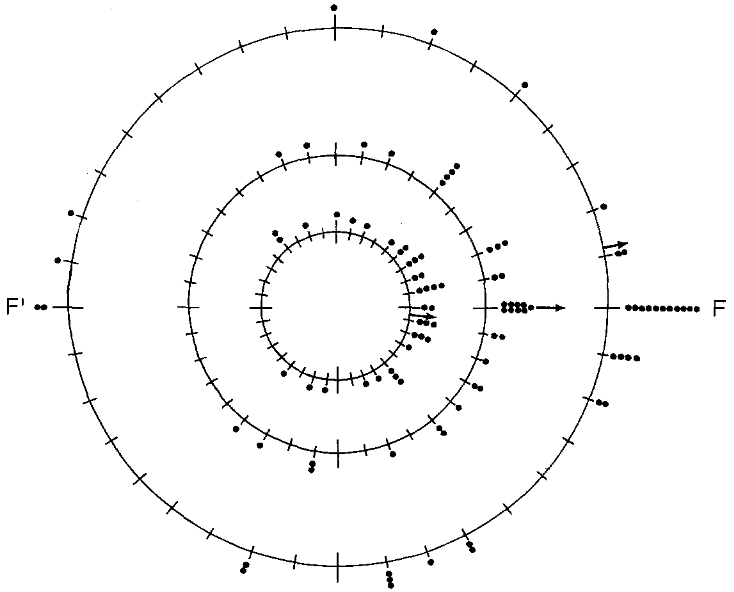

Fig. 3. Orientation of foragers in the circular arena after a 90° rotation of the hindgut trail. $r^5=0.57$, $r^{10}=0.63$, $r^{20}=0.52$. All results are significant ($p<0.001$). For further explanation see Figure 2, Materials and Methods, and text

ant species are known to utilize visual cues to various degrees during foraging (Jander, 1957; Wehner and Menzel, 1969; Hölldobler, 1970; Hölldobler et al, 1974; Möglich and Hölldobler, 1975). Furthermore, some species are apparently capable of facultatively changing their mode of orientation depending upon the presence or absence of visual cues. Since *Camponotus pennsylvanicus* is active during daylight hours as well as at night and foragers make repeated trips to food sources along well-defined routes (unpublished data), it seemed likely that visual cues might also be involved in orientation. I tested this hypothesis in the following manner.

Ants were allowed to forage at a sucrose bait in the circular arena. On the bottom of the arena a hindgut trail was drawn out in one sector. Also, on the arena wall a visual cue (an alternating black and white pattern) was provided over the food-containing sector. During the first 45 min of the experiment all ants arriving at the food were marked with a drop of paint. Most ants made more than one trip to the food during this period. The arena bottom was then replaced with a clean disk; the visual cue remained in place. During the next 15 min the individual runs of foragers were recorded. The results indicate that marked or "experienced" foragers continued to orient in the direction of the food in the absence of olfactory cues (Fig. 4a). In order to negate the possibility that the ants were spontaneously orienting to the black and white pattern, as might be suggested from the work of Voss (1967), a naive colony was tested. Data from the naive colony (Fig. 4b) indicates that these ants oriented randomly in the arena.

II. Recruitment to Food

1. Recruitment Behavior

In order to analyze the recruitment process of *Camponotus pennsylvanicus,* it was necessary to remove colonies of ants from their wood nests. Therefore, specific recruitment displays were viewed only in the laboratory. Colonies were starved for 5 to 10 days before recruitment experiments were conducted.

As stated earlier, scout ants return from newly discovered food sources dragging their abdominal tips over the substrate. Upon entering the nest, the scout encountered nestmates head-on with a waggle motor display. This behavior, previously described by Hölldobler (1971) and Möglich and Hölldobler (1975), consists of vibratory movements of the head and thorax in the horizontal plane. This behavior is an important alerting display during the recruitment performance of a scout ant. Waggle motor displays were interspersed with brief food offerings and self-grooming. Another integral part of recruitment behavior is the fast run, which consists of a sequence of waggle displays delivered to individuals in different groups within the nest. In this way a scout recruited a large number of nestmates during a single return trip to the nest.

Waggle displays were observed to occur either before or after food exchange occurred. The majority of displays were observed immediately after the scout returned to the nest, but in a number of cases food exchange occurred first

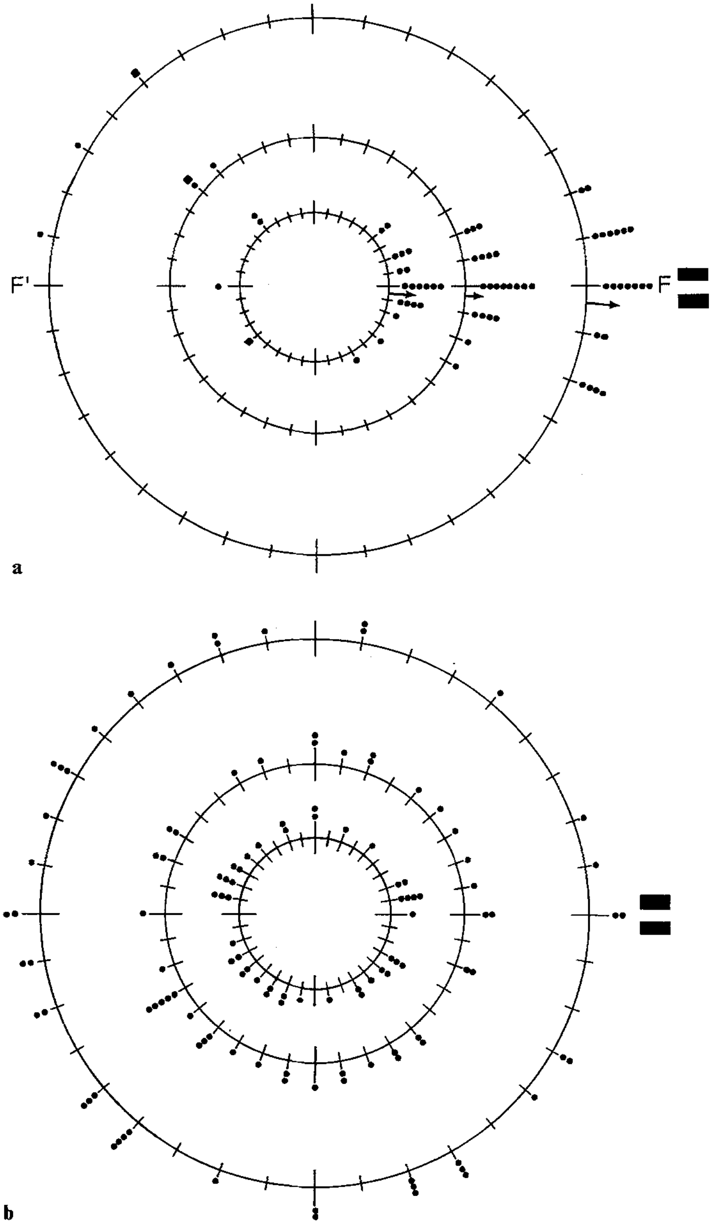

Fig. 4. a Orientation of foragers in circular arena to visual cue after removal of hindgut trail. $r^5 = 0.64$, $r^{10} = 0.45$, and $r^{20} = 0.75$. All results are significant ($p < 0.001$). ●, 1 ant; ■, unmarked ("inexperienced") ant; ▬, visual cue. **b** Spontaneous orientation of naive colony of ants in circular arena to visual cue. $r^5 = 0.07$, $r^{10} = 0.22$, $r^{20} = 0.23$. The results are insignificant ($p > 0.05$) and the orientation is random

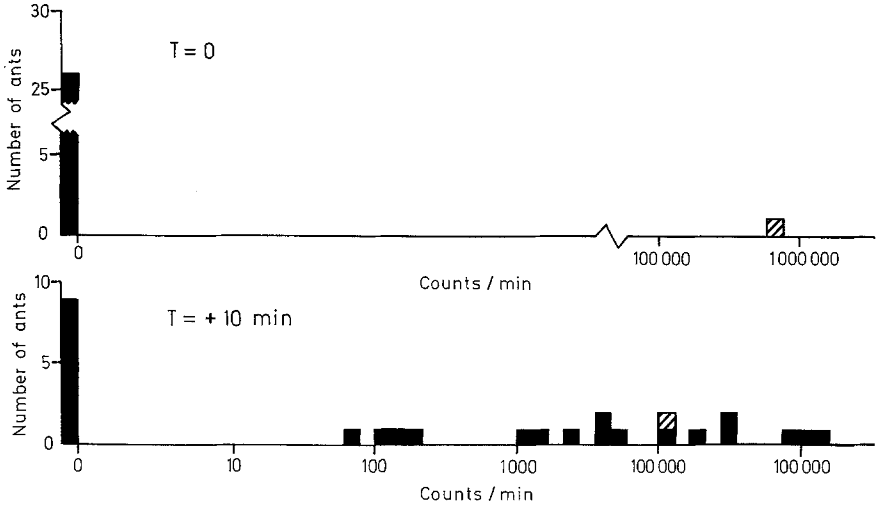

Fig. 5. Food transfer from scout to nestmates. The upper histogram represents an approximation of the number of transferable counts in the scout's crop before her return to the colony. The lower histogram shows the distribution of radioactive liquid to nestmates during a 10-min period. Only ants with at least double the amount of background radiation are represented in this figure. ■ , food recipients; ▨ , scout

and was then followed by fast running. If food transfer preceded motor displays, a recruiter immediately encountered a nestmate head-on with open mandibles exposing a droplet of food upon entering the nest. In this case the recruiter apparently emptied her crop contents before performing recruitment displays.

Nestmates reacted to a recruiting ant by becoming alert and showing trail-seeking behavior. Some nestmates became alert without being contacted directly. Food transfer was accompanied by vigorous antennation and a "boxing" motion of the recipients' forelegs to the head of the donor. The recruiter soon became surrounded by nestmates attempting to partake in the food sharing. Up to five nestmates were observed soliciting food from a single recruiter simultaneously. During such a food transfer the recruiter was observed to remain motionless as she voided her crop contents. The recruiter would eventually terminate the food exchange and subsequently engage in a recruitment performance or return to the food to feed again.

The extent of the transfer of liquid food from the recruiter was examined by labeling a sucrose solution with radioactive phosphorus, a widely used technique (see for example Wilson and Eisner, 1957). An artificial nest of 27 workers was isolated in an attempt to simulate the conditions in the first nest cell entered by a recruiting ant. A single scout was allowed to discover and feed at the labeled food and return to the colony. After the return of the scout, ants were allowed to exchange food for 10 min, after which each ant was assayed for radioactivity. From the data presented in Figure 5 it can be inferred that a scout may transfer up to 98% of her liquid intake upon returning to the colony. The initial liquid intake of the scout was conservatively estimated at

8 µl. Within the 10 min following the arrival of the scout, food was rapidly distributed to 62% of workers in the nest.

2. Analysis of the Recruitment Process and the Nature of the Recruitment Trail

Presumably the evolutionary trend in the development of advanced recruitment techniques is toward a decrease in the necessity of tactile communication and an increase in the excitatory and orienting information that is chemically coded in the trail itself (Hölldobler, 1977). A characteristic of the recruitment behavior of *Camponotus pennsylvanicus* is that a leader ant is not necessary to guide the recruited group to the food. Alerted nestmates readily follow the recruitment trail and arrive at the target area. There were a number of different interactions between the initial recruiter and the colony. Of 30 observations, the scout remained in the nest either alerting nestmates or transferring liquid food while nestmates left the nest to follow the recruitment trail on 18 occasions. On five occasions each it was observed that the scout quickly returned to the food in advance of nestmates or the recruited nestmates overtook the scout while returning to the food. Only twice did recruited ants leave the nest and proceed behind the scout.

Ants not directly stimulated by motor displays were also observed to show trail-seeking behavior. Many of these individuals would become excited and run into the foraging arena with open mandibles. These observations suggest that the recruitment trail layed by a scout may be distinct from the hindgut trail used for orientation during foraging. Such is the case in *Camponotus socius*, as hindgut material is used as an orientation signal between nest entrances and food sources, but circumstantial evidence strongly suggests that the recruitment trail is composed of hindgut material and poison gland secretion, formic acid (Hölldobler, 1971). A distinction between recruitment and orientation trails could also occur in *C. pennsylvanicus*. The following experiments attempted to analyze the nature of the recruitment trail.

Extracts of hindgut, Dufour's gland, and poison gland were prepared by homogenizing 10 organs of each type in 0.1 ml distilled water. Colonies were starved 7–10 days prior to this series of experiments. Artificial trails 50 cm long were then drawn out from the nest entrance and the following response of individual ants recorded under two different conditions. In the first set of experiments artificial trails of hindgut contents, hindgut contents plus Dufour's gland secretion, and hindgut contents plus poison gland secretion were drawn out on a sheet of paper covering the bottom of the arena. During the next 5 min the number of ants encountering the trail and showing a positive response (a following response of at least 10 cm) was recorded. A second set of experiments involved the same experimental design with one difference. In this set, a single scout ant was allowed to feed at a sucrose solution and return to the nest to encounter nestmates with a recruitment display. Following the return of the scout to the nest the bottom of the arena was replaced with a sheet of paper with one of the three types of trails. The response of ants to the

Table 2. The following response of ants to 50 cm artificial trails drawn out from the nest entrance

	Hindgut	Hindgut + Dufour's gland secretion	Hindgut + poison gland secretion
Number of encounters	237	211	141
Number of positive responses	162	136	78
Percent of positive responses	66%	65%	55%
Average following response (in cm)	43.2	40.8	37.8

A positive response is equivalent to trail following for at least 10 cm. Responses were recorded during a 5 min period. In this situation a hindgut trail is readily followed in the absence of recruitment displays. 10 replicates

Table 3. The following response of recruited ants to 50 cm artificial trails drawn from the nest entrance during the first 5 min after the return of a fed scout to the colony

	Hindgut	Hindgut + Dufour's gland secretion	Hindgut + poison gland secretion
Number of encounters	244	251	264
Number of positive responses	118	157	189
Percent of positive responses	49%	63%	72%
Average following response (in cm)	40.8	32.1	47.1

Under these conditions, a trail composed of hindgut contents and poison gland secretion is highly attractive to the excited ants. 10 replicates. For further explanation see Table 2 and text

trails was recorded within the first 5 min following the return of the scout. Results are presented in Tables 2 and 3.

The results demonstrate two important points. First of all, from Table 2 it can be inferred that hindgut material is a strong olfactory signal that is readily followed in the absence of alerting displays. This suggests that the trail pheromone itself may constitute a recruitment signal. Secondly, Tables 2 and 3 indicate that dependent upon context, trails are responded to differently. For example, if ants were previously stimulated by a recruitment display, the response to trails of hindgut contents and hindgut contents plus poison gland secretion is significantly different (χ^2:$p<0.001$), suggesting that previously stimulated ants require additional odor cues to increase the effectiveness of the recruitment trail. Also, a comparison between Tables 2 and 3 suggests that a trail of hindgut material and poison gland secretion is more attractive to ants that have been previously stimulated by a recruitment display ($0.001<p<0.01$). Ants not previously alerted respond to the same trail differently (Table 2). Many ants encountering a hindgut/poison gland trail in this situation did not respond positively, but ran off with open mandibles or quickly returned to the nest.

In fact, under these circumstances the addition of poison gland secretion to a hindgut trail significantly decreased the response ($0.01 < p < 0.02$). Similarly, a comparison between Tables 2 and 3 shows that the response to a hindgut trail decreased significantly ($p < 0.001$) if ants were previously alerted by a recruiter, suggesting the possibility that a hindgut trail under these circumstances is not a sufficiently accurate odor guide. Trails augmented with Dufour's gland secretion were slightly more attractive to stimulated ants, but could not produce an increased trail-following response.

The results seem to imply that although the hindgut pheromone alone is attractive to ants that have not previously been stimulated by a recruiting nestmate, recruitment trails may consist of rectal material plus poison gland secretion. The following experiment tested this possibility.

A scout ant was allowed to feed at a sucrose bait in the foraging arena. After the scout returned to the colony the bottom of the arena was replaced with a new paper on which a Y-shaped trail was drawn. After being alerted by the displays of the scout, ants leaving the nest first encountered a short (4 cm) segment of the trail consisting only of hindgut material. After this portion of the trail the two branches of the Y diverged at an angle of 90° (Trail 1 and Trail 2). At the point of divergence ants following the trail had the choice of continuing to follow a hindgut trail or to follow a trail of hindgut material plus a glandular secretion. Since the contents of the Dufour's gland and the poison gland have been identified as n-undecane and formic acid respectively (Ayre and Blum, 1971), I drew out 0.5 µl of undecane or formic acid with a microsyringe over one of the 50-cm long hindgut trails. Only those ants that followed the hindgut trail to the junction of the two diverging trails and continued to follow either branch of the trail at least half way were considered to have responded. Ten replicates were performed.

The results of this experiment indicate that there is no difference in the degree of attractiveness between either two hindgut trails (mean number of ants on Trail 1: 5.5, range 1–13; mean number of ants on Trail 2: 5.6, range 1–16) or between a hindgut trail (Trail 1) and a trail of hindgut material and undecane (Trail 2). In this latter case the mean number of ants on Trail 1 was 3.5 (range 0–15) while the mean number of ants on Trail 2 was 2.5 (range 0–15). However, when one branch of the trail was augmented with formic acid it was preferred by the recruited workers. The mean number of ants following the hindgut trail was 2.4 (range 0–7) while the mean number of ants which followed the hindgut/formic acid trail was 10.4 (range 1–24). This difference in response is significant (Student's t test, $0.02 < p < 0.05$).

This experiment illustrates that trails composed of hindgut contents and formic acid (poison gland secretion) are definitely preferred in a choice situation. Trails of hindgut material and undecane produced alarm and reduced the trail following on either trail. A trail of formic acid alone excited ants in the area of discharge and released a short-lived trail following. A trail of hindgut material and formic acid was effective in causing recruited ants to diverge from a hindgut trail. Since a hindgut/poison gland secretion trail was also highly attractive to alerted ants, it seems likely that this is the composition of the recruitment trail.

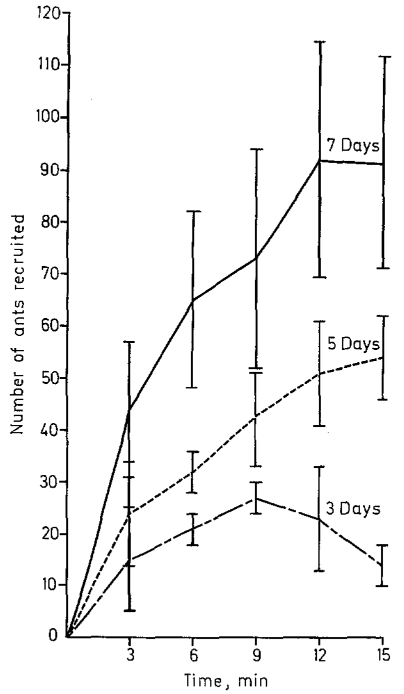

Fig. 6. The recruitment response of a colony after three, five, and seven days starvation periods. Each point is the sum of three replicates

III. The Organization of Mass Foraging

From observing the recruitment process it appears that foraging activities are organized by the behavior of recruiting ants and possibly by the odor trails themselves. Recruited ants arrive at the food source, feed, and return to the nest where they perform their own recruitment displays. As more nestmates are recruited, more food is brought into the colony and mass foraging eventually gives way to individual foraging. The next set of experiments was designed to define the parameters involved in this mechanism.

1. The Effects of Colony Nutrition

By starving colonies for 3, 5, and 7 days, respectively, it was possible to show that the nutritional status of the colony has an effect on the recruitment response (Fig. 6). This effect could be due to an increase in the response of the colony to a recruiting ant, or to the intensification of the behavioral displays of the recruiter. To separate these effect, a colony of 250 workers was separated in the same nest by means of a double wire mesh screen. One half of the colony was fed in excess, while the other half was starved for 10–15 days. A scout ant from the starved half of the colony was then allowed to find food (a drop of sucrose). However, the scout was then routed to return to the well-fed nestmates. Inside the nest the scout performed a recruitment display. Nestmates

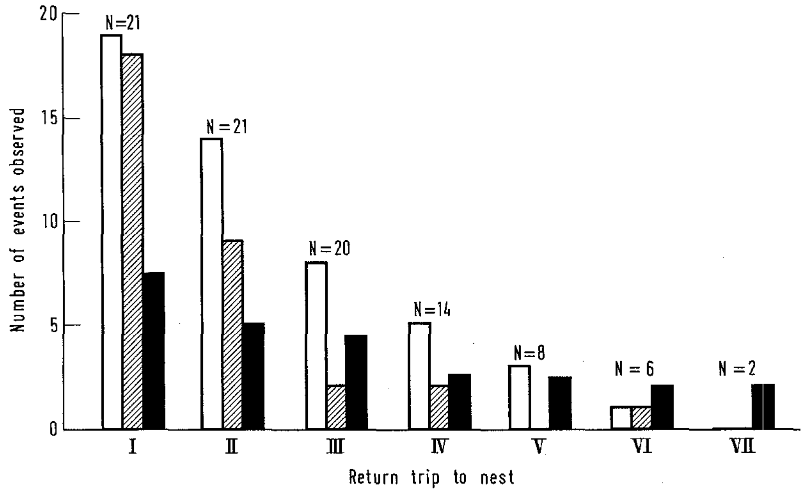

Fig. 7. Changes in recruiter behavior during the organization of foraging. ▨ , fast runs; □ , waggle displays; ■ , mean number of ants engaging in food transfer with recruiter. *N*, number of observations

in the vicinity of the recruiter became alert and left the nest, only to ignore the sugar water and return. This indicates that increased recruitment responses are due to the increased activity levels of recruiting ants. There is also an interesting sideline to this experiment. During the recruitment performance of a starved recruiter in the fed half-colony, food offerings were often totally ignored, but contacted nestmates still left the nest. This suggests that food transfer does not have a regulatory role in the recruitment process.

2. Changes in Recruiter Behavior during the Organization of Foraging

Recruiting ants were typically observed to make several trips from the food source to the nest. However, the nature of their behavior and interaction with nestmates differed markedly during the course of foraging. The criteria used to determine behavioral changes were the components of a recruitment display: fast runs, waggle displays, and the number of workers receiving regurgitated food from the recruiter. By focusing on the behavior of a single recruiting ant during foraging it can be shown that both recruiter behavior and the amount of food transported to the nest are involved in the regulation of foraging. Motor displays are predominant during the first and second return trips to the nest (Fig. 7). During subsequent return trips motor displays gradually drop out of the behavioral repertoire of the recruiter. However, the recruiter may also serve other functions dependent upon the nutritional status of the colony. For example, if a colony is starved for a relatively short time (<3 days) and then offered food, a recruiter does not exhibit intense motor activity and readily becomes a forager. In this case the recruiter functions as a food transporter, although recruitment proceeds at a low level. Longer starvation periods (>5 days) induce and increased recruitment response as recruiting ants exhibit more intense motor displays. The colony quickly responds to the food alarm and the build-up of workers at the food source is maximal. After alerting nestmates the recruiter may then continue to excite foragers by encountering workers on the trail with brief waggle displays. The recruiter may also become involved in the secondary transport of food by becoming a member of a "food transport chain". In this instance an ant that has previously been a recruiter solicits food from a forager that has fed directly at the food source and transports this food to the nest. This is typically observed when crowding occurs at the food. This behavioral plasticity allows a quick and efficient exploitation of food sources.

3. Division of Labor during Foraging

Observations indicated that not all ants stimulated by recruitment displays actively engage in foraging. Polyethical differences may account for this differential response. Buckingham (1911) studied the division of labor in *Camponotus herculeanus pictus* (= *C. noveboracensis*) and attempted to correlate age with worker tasks. Polyethism has been documented in *Formica polyctena* and some physiological correlates have been defined (Otto, 1958). Also, Möglich and Hölldobler (1974) found a strong division of labor during nest moving in *Camponotus sericeus* and *Formica sanguinea*. In these species a relatively small number of "transportation specialists" are most active during nest moving. It is possible that similar factors are involved in *C. pennsylvanicus*. I examined worker polyethism during foraging in the following manner.

Each ant in a colony of 102 workers was color-coded with paint to permit individual recognition. Eight recruitment trials were then carried out over a one-month period. During each trial the number of foraging trips made by individual workers as well as the consistency of their participation in foraging was recorded. Based on the records of individual foragers the following foraging index (FI) was developed from a similar index used by Möglich and Hölldobler (1974):

$$FI = \frac{N \cdot C}{\Sigma N} \cdot 100$$

where N is the total number of trips made by an individual forager, ΣN is the summation of all foraging trips made by all foragers during the course of the experiments, and C is the number of trials during which an individual participated in foraging. At the end of the experiment all workers were dissected and the condition of the ovaries recorded. From Figure 8 it can be seen that there is a distinct division of labor during foraging. Only 14 workers consistently responded and performed 68% of all foraging. All of these workers had oocytes that were in a state of partial or total resorption, as evidenced by the presence of yolk remnants within individual oocytes. In contrast, of 37 innendienst workers, 76% had developed oocytes (average length of ultimate oocyte 0.197 ± 0.063 mm, range 0.1–0.35 mm). An intermediate group of workers engaged in comparatively little foraging.

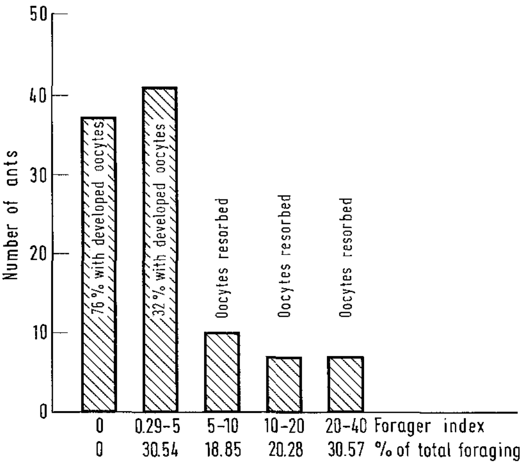

Fig. 8. Histogram showing the division of labor during foraging. The forager index (FI) of each group of workers is given with the % of total foraging performed by that group and the state of the ovaries of workers. For further explanation see text

Discussion

Two aspects of this study should be emphasized. First, a leader ant is not necessary to maintain the behavioral cohesiveness of the recruited group. This is in contrast to the behavior of other group-recruiting ant species. In *Camponotus socius* the leader keeps the recruited group excited by discharging poison gland material. In *C. pennsylvanicus* a similar trail is apparently laid by a scout on her first return trip to the nest. Secondly, in *C. pennsylvanicus,* hindgut trails are followed by workers that apparently have not received prior motor stimulation. However, it is difficult to determine whether this phenomenon actually constitutes a recruitment effect. It could be that those ants that leave the nest in this situation are of a particular age at which they are most responsive to the hindgut pheromone. Nevertheless, it does appear that hindgut material is a strong olfactory signal that may serve as more than just an orientation cue. Recently, Barlin et al. (1976) chromatographically identified the hindgut pheromone as a single peak. Again, the role of hindgut material is different in *C. socius,* because ants must be previously alerted by a motor display to respond to a hindgut trail.

Many species of ants require tactile contact as an alerting signal during recruitment (Szlep and Jacobi, 1967; Szlep-Fessel et al., 1970). In *Camponotus pennsylvanicus* motor displays are obviously an integral part of the recruitment process, but these displays do not appear to be entirely essential due to the attractiveness of pheromone trails. However, those ants previously alerted by recruitment displays do prefer a hindgut contents/poison gland secretion trail to a trail of hindgut contents alone. It must be noted that hindgut trails, although not preferred in a choice situation, are also followed to a lesser extent by alerted ants.

Considering the evolution of chemical mass communication in the formicine ants, these results suggest that the recruitment behavior of *C. pennsylvanicus* is of a higher organizational level than that of *C. socius* or *Formica fusca.* Hölldobler (1976) has suggested that hindgut material has become involved in the recruitment communication of formicine ants through a ritualization of the defecation process. Convergently, hindgut material has also attained a communicative function in some ponerine and doryline ants, perhaps in a similar fashion. During evolution the importance of hindgut material apparently increased from a cue used in home range orientation to a stimulating signal involved in recruitment. In *C. pennsylvanicus* it appears that hindgut material has some stimulatory properties and thus the recruitment behavior of this species approaches mass communication, while still retaining some characteristics of the group recruitment technique.

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