RECRUITMENT TO FOOD IN THE ANT *CREMATOGASTER ASHMEADI*

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INTRODUCTION

The occurrence of mass-foraging of individuals in retrieving food is common in most social Hymenoptera. In ants crowds of foragers typically appear within a short time at a food source after it has been detected by the first scout ant. The recruitment of nestmates to the food is achieved by a mechanism of communication that consists of a chain of several releasing stimuli. Various behavioral patterns and glands are involved in the different subfamilies and tribes of ants in the attainment of this goal (Blum and Ross 1965, Cavill and Robertson 1965, Maschwitz 1964, Regnier and Law 1968, Wilson 1963). The most widely studied element of the recruitment is trail-laying. Different, modified or even *de novo* evolved exocrine glands in various ant groups have become adapted to the production of specific trail pheromones. The basic "releaser stimuli" (definition: Wilson and Bossert 1963) of scent trails are in most cases reported to be "true attractants" (definition: Dethier *et al* 1960) which cause the ants to follow trails in either direction. But in addition to this leading quality Wilson (1962) claims a second releaser effect of the trail pheromone in *Solenopsis saevissima* which evokes alert and increased running activity. Apart from the effect of the trail pheromone Wilson (1962) describes a typical behavior of homing trail-laying *Solenopsis* workers when they contact nestmates on their way: "They may do no more than rush against the encountered worker for a fraction of a second before moving on again, but sometimes the reaction is stronger: they climb partly on top of the worker and, in some instances, shake their body lightly but vigorously, chiefly in a vertical plane." Following Wilson's interpretation this behavior functions solely "to bring the trail substance to the attention of the sister worker" and does not confer any information beyond the attractive effect of the trail substance.

In *Crematogaster ashmeadi* a similar behavior, possibly with simultaneous release of a pheromone, appears to have evolved into an important constituent of the recruitment to the food. Goetsch (1934) mentions "alarm" behavior of recruiting workers in *Crema-*

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togaster scutellaris that at least indicates the corresponding recruitment stimulus in that species. The subject of this paper is an analysis of the complex food recruitment behavior and its efficiency in *C. ashmeadi.*

MATERIAL AND METHODS

Crematogaster ashmeadi is an arboreal ant that dwells in dead hollow branches. Its range is the coastline from Virginia to Florida and the Eastern Gulf States (Creighton 1950). Our laboratory colonies were collected from red mangrove trees *(Rhizophora mangle)* on the Florida Keys and established in horizontally piled pieces of hollow mangrove branches on wooden frames measuring 20 × 25 cm. These colonies, polygynous in nature, were kept at room temperature in plastic trays 30 × 45 × 17 cm with the inside walls coated with talcum powder to prevent escape. Various shapes of 50-cm-long bridges were used to join the nest site with a food station located in another tray where water, honey and mashed shrimps or cockroaches were offered to the ants. To begin recruitment experiments the colonies were first starved for five days or longer, then a new food source was offered on a movable side bridge which was connected to the old pathway between the nest and the former feeding station. The patterns of movements and courses were analyzed by slow-motion cinematography (16 mm film, 64 frames per second).

THE RECRUITMENT BEHAVIOR OF A FOOD FINDER ANT AND THE RESPONSES OF OTHER WORKERS

On the pathway between nest site and feeding station of a *Crematogaster* laboratory colony, a basic back-and-forth traffic of workers continues even when no more food is available at the feeding place. Even in starved colonies the workers keep up running over the bridge. Most of them still strictly follow their well established trail pathway but a certain low percentage abandon the trail to explore neighboring areas. To begin food recruitment experiments, a 24-cm-long side bridge supplying a honey source at its end is connected to the main bridge of a starved colony. Usually within a few minutes the side bridge is discovered by a scout ant which starts searching the new area and quickly locates the food. In order to observe the recruitment behavior of one single explorer ant, the side bridge is removed and reconnected only for the passage of this particular ant. The explorer ant smells honey, diluted with water (1:1) already at a distance of about 4 cm. It may be attracted to

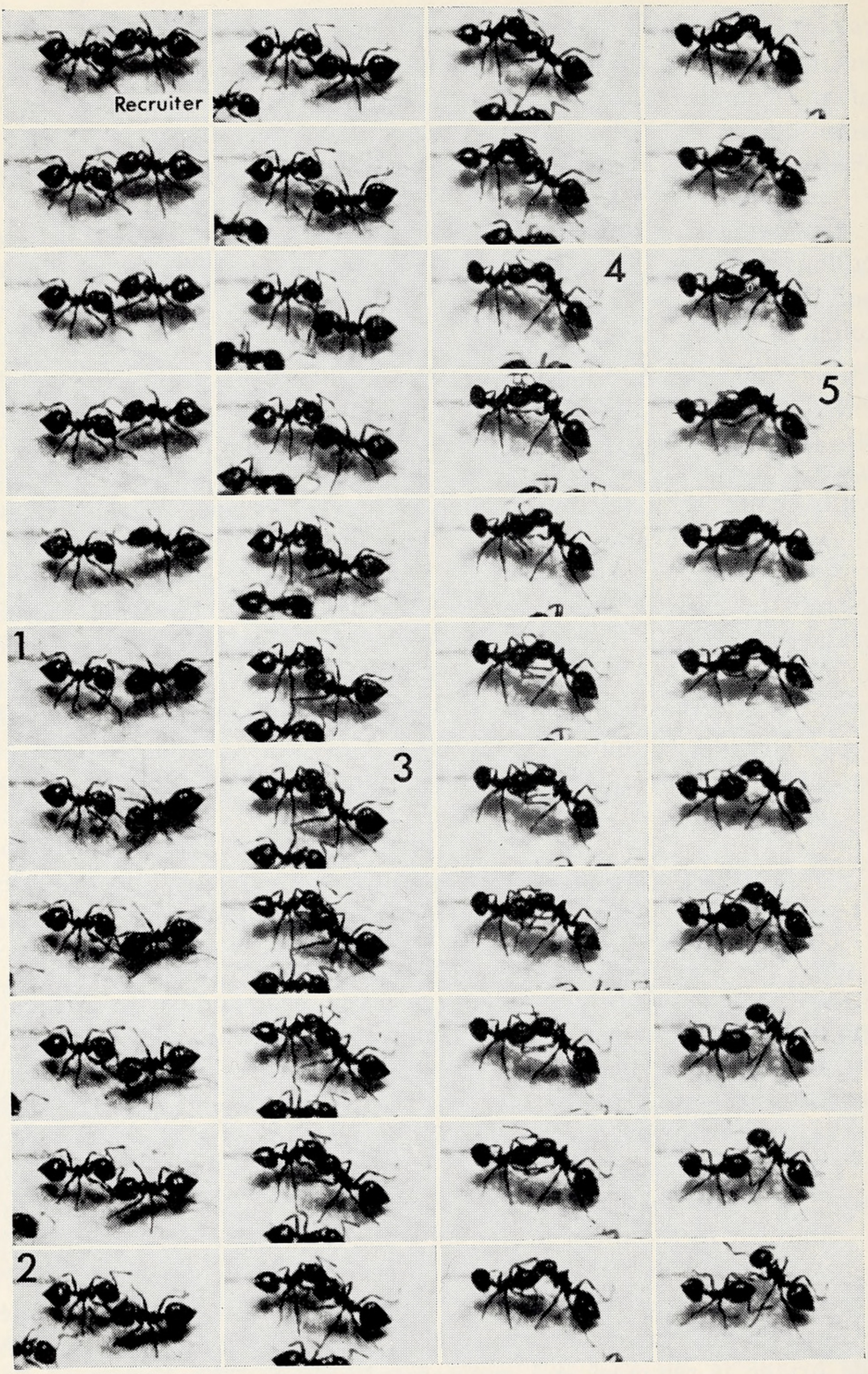

Fig. 1. Alerting performance of a recruiter ant. Numbers indicate the stroking movements towards the encountered worker. (From movie film, 64 frames per second).

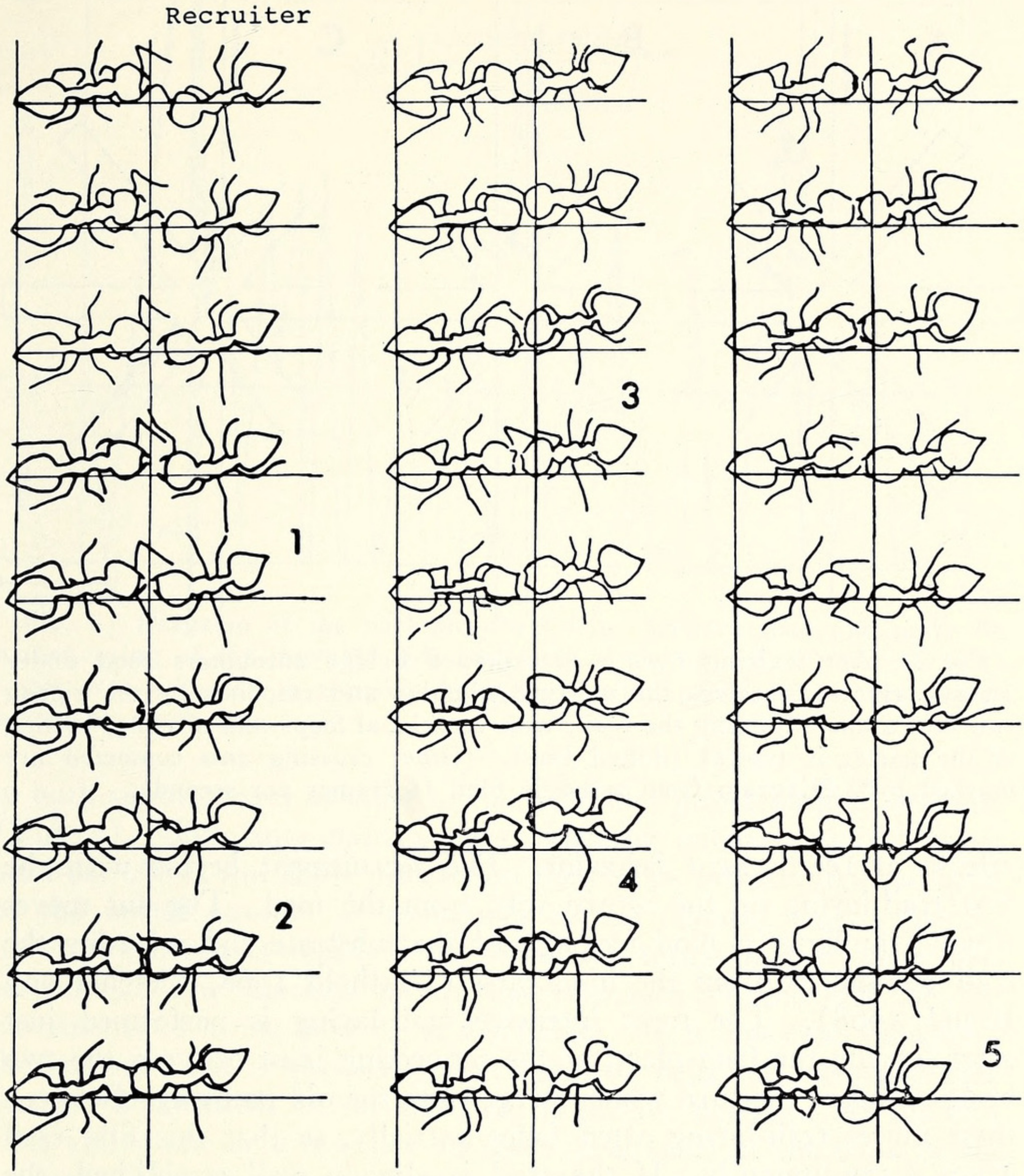

Fig. 2. Alerting performance of a recruiter ant. Numbers indicate the stroking movements towards the encountered worker. (From movie film, 64 frames per second).

the food and feed for a few seconds up to 5 minutes. After feeding it often turns straight back with the abdomen more or less swollen. Sometimes it circles around the food area several times before returning or even returns before touching the food at all, excited solely by the smell. (The latter behavior most frequently occurred after the colony had been starved a long time, viz. ten days or longer.) In all possible cases the food source induces the active recruitment behavior of the explorer ant. Hence uptake of food is not needed for the

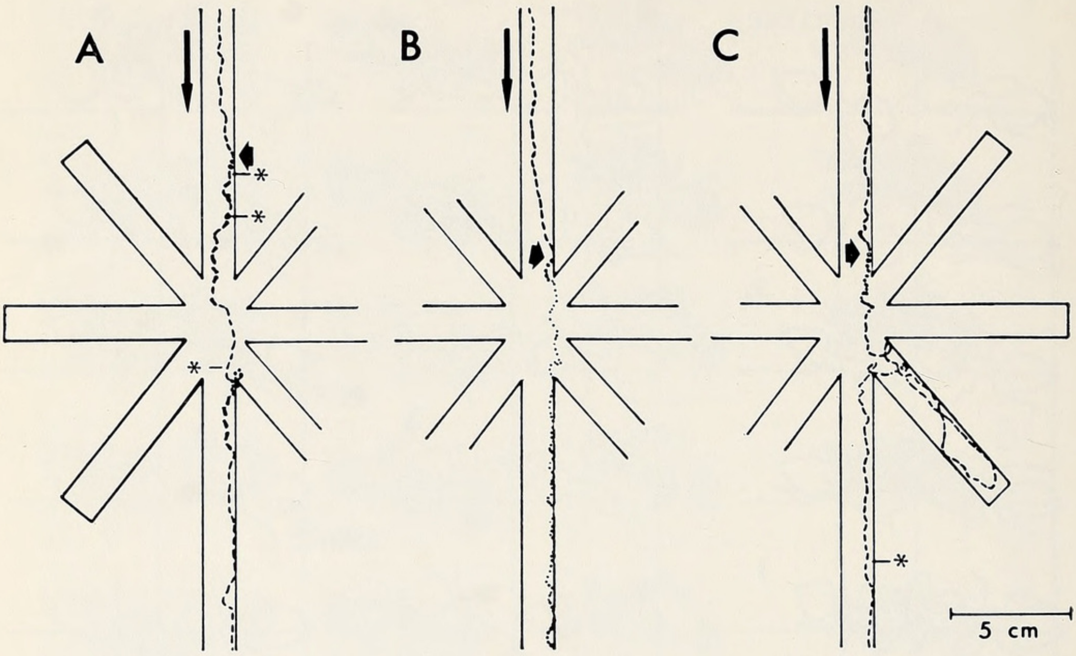

Fig. 3. Ant walking over a star-shaped bridge encounters food finder (heavy arrow), receives the alerting stimulus and responds by the zigzag run into areas adjoining the trail, with occasional loops and circling, raising of the gaster is typical (dotted line). (Other crossing ants contacted are marked by*. Diagram from a movie film, 16 frames per second).

release of recruitment behavior. The recruitment begins with the first trail-laying on the return way from the food. The ant moves slowly, shuffling its hind feet against the substrate and releasing the trail pheromone from the hind tarsi (Leuthold 1968, Fletcher and Brand 1968). The most intensive trail-laying is performed just after leaving the food place, at the connecting joint between the two bridges and at the turn which merges into the old pathway. Between these places trail-laying often fades partially, so that this first trail arises discontinuously. If the trail is already well established, the food finder ant usually lays a weak trail or no trail at all on the old pathway. It rushes nestwards obviously activated and excited. When it encounters other workers on the trail it performs a new alerting behavior which is an individual recruiting signal. The food finder ant actively faces the encountered nestmate and standing more or less still it shakes its head vigorously towards the other's face. This fast vibration of about 12 strokes per second lasts from 1/6 second to 1 second; then the two ants separate. More details of this alert behavior are resolved by slow motion cinematography (Figs. 1 and 2). The alerting ant flings its head from a slightly ducked, nearly opposite position towards the head of the encountered worker, usual-

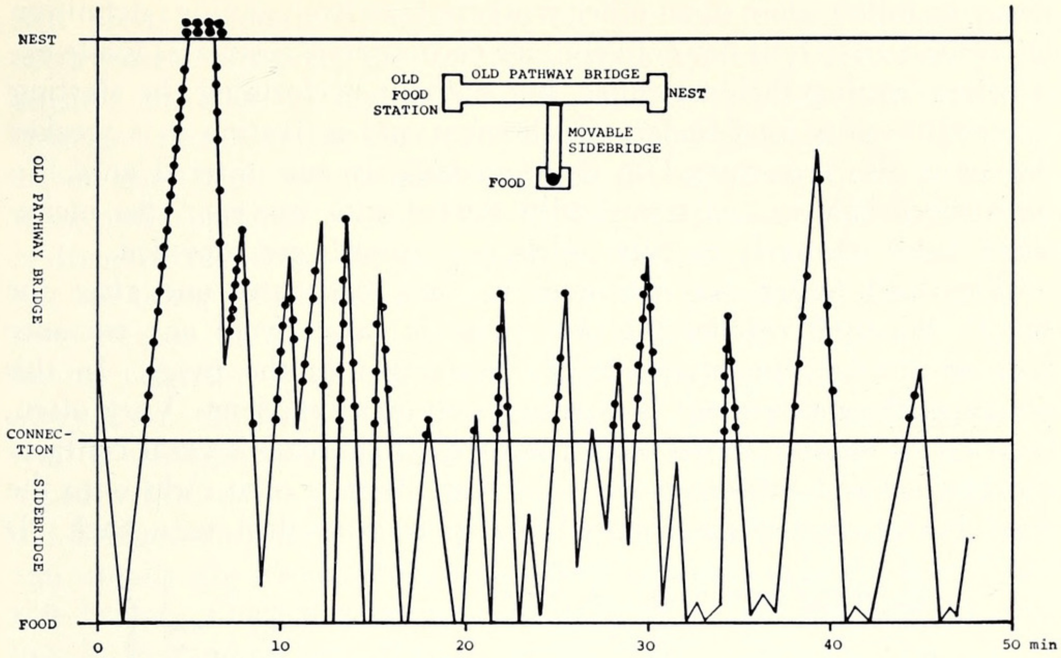

Fig. 4. Diagram of the back-and-forth trips between food and nest. By maneuvering of the movable side bridge only the food finder but no newcomer was admitted to the side bridge. Alerting performances are represented by black dots.

ly with simultaneous opening of its mandibles into a parallel attitude (Fig. 1). Both ants contact their vibrating antennae while facing head-on. After this short interaction the alerter retracts its head back to the initial position or sometimes to the opposite side. The behavioral pattern is repeated up to twelve times in a stronger performance. The motions of this performance remind one of the movements of a dog barking at a stranger. In a few cases, however, the recruiter ant is also seen to perform its behavior from a higher position downwards to the head of its passive partner. At the end of a volley one or a few last strokes are directed at the flank of the partner. Then the two separate and both ants keep on pursuing their course. The typical response of alerted ants to a strong alerting stimulus consists of raising their gasters after the first few strokes (Fig. 2, No. 4) of the recruiter's head. They most often spread their mandibles, sometimes during the whole performance. Both partners contact their antennae in a vibrating way. After separation, alerted ants usually follow their general direction on the bridge, slightly excited and performing a zigzag run, often moving in circles or small loops into areas adjoining the trail (Fig. 3). After a few seconds of this excited dashing, however, their behavior changes into accurate trail-following or seeking for the trail. They show an increased tendency to follow close upon other workers (tandem running: definition by Wilson 1959). They actively face encountered nestmates while excitedly vibrating their antennae, but without performing the alerting movements of a food finder. Excitement and activation in a weaker degree is also transmitted to these secondarily encountered ants. In both the primarily and secondarily alerted ants, however, the incitement fades relatively quickly unless new stimuli are provided.

The food finder ant continues to alert nestmates one after the other. When it reaches the nest twigs it passes from one entrance hole to another, sometimes briefly entering into the twigs. In this situation the recruitment is quantitatively most efficient. Very often, however, it returns in the direction of the food after several contacts on the road and before reaching the nest. It may turn right onto the food bridge or else pass beyond that place and then turn back. It

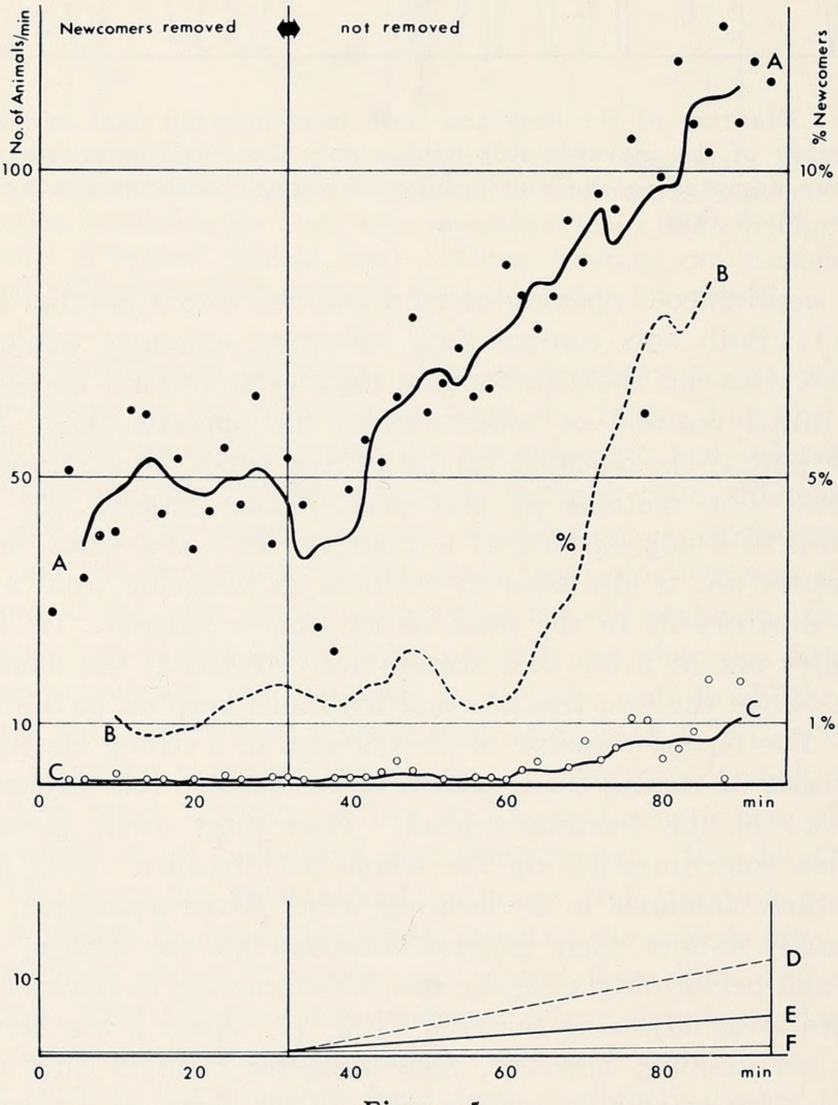

Figure 5.

still alerts encountered nestmates all the way along. After many occurrences, however, the act of alerting typically decreases in intensity. As soon as the food finder reaches the side turn again, it changes from a rather fast run into trail-laying behavior. The ant either goes back to the food and returns again or turns nestward when only partway on the food bridge. If the movable side bridge is disconnected from the main path so that only the first food finder but no other newcomer ant can cross the connection, the recruiter then repeats its back-and-forth travel indefinitely (Fig. 4). Trail-laying behavior is always more intensive when the ant is moving away from the food. After an average of three return passages the trail is strong enough to lead a newcomer with accuracy to the food (Leuthold 1968). At the turn and the connecting joint from the old bridge to the new one, however, the pheromone marks from one run usually are strong enough to deflect new ants onto the base of the side bridge. Once they set foot on the side bridge they find the food mostly by random searching.

THE ORGANIZATION OF MASS-FORAGING

When a new food source is joined to the main passage bridge of a starved *Crematogaster* colony, as described in "Methods", the maximum number of foraging workers at the food is usually reached after 10 to 90 minutes. Many factors are involved in raising the degree of mass-foraging, as follows. On an old, regularly frequented trail there is a low percentage of workers deviating from the trail. This is an important aspect leading to the discovery of new food sources. The percentage of deviating workers is fairly constant over

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Fig. 5. Food recruitment experiment (arrangement: see "Methods"). In the first phase of 32 min all newcomers were removed from the food. In the second phase, however, foragers were allowed to return and recruit nestmates.

A. Number of passages in both ways per min on the main bridge between food bridge and nest.

B. Percentage of ants deviating from the main bridge to the food bridge.

C. Number of newcomers to the food per min (Circles: actual number. Curve: moving average as in A). The number of newcomers during a 2 min period was obtained by the number of ants going to the food minus the number of returners during the preceding 2 min period, supposing repeated foraging of each food finder.

D. Number of passages per minute towards the food during the recruitment phase, averaged to linear rise.

E. Diagram (C) averaged to linear rise.

F. Average number of newcomers calculated proportionally to the increase of passages in (A) makes only 25% of the actual number in (E).

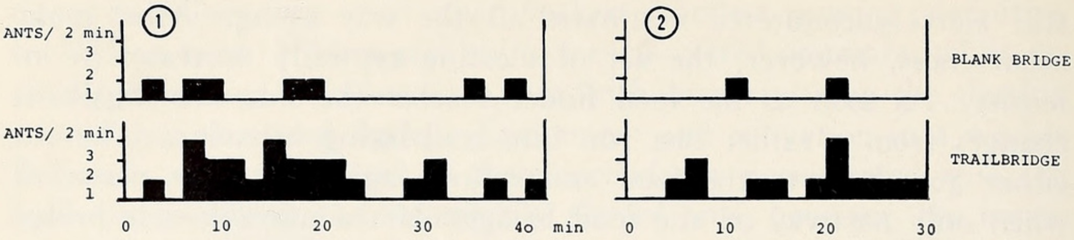

Fig. 6. Two experiments in which identical side bridges were joined to the main pathway, one bearing a trail, the other one blank. The deviation rate to the trail bridge is significantly higher than to the blank bridge (Student's test $p < 1\%$).

periods in the range of hours and comprises less than 6% of all by-passers unless the colony is extremely starved or has been recently disturbed. During the period of recruitment the number of deviations from the pathway rises dramatically. Only 15% of all newcomers during the recruitment phase in the experiment of Fig. 5 can be accounted for by basic deviation and as little as 5.3% in the adequate experiment shown in Table 1. Hence the existence of a recruitment message is obvious. One of the main factors of mass-recruitment caused by the alerting of the food finders is the increase in running activity of the colony measured by the number of workers passing over the main bridge (Fig. 5A, 7A, 9A, 10B). The sum of deviations calculated proportionally to the increased running activity, however, yields only 25% of the actual number of newcomers in the experiment of Fig. 5F and 28% in the experiment presented in Table 1. The increase of the deviation rate is represented in Fig. 5B. A second important factor for mass-recruitment is found to be the pheromone trail between main bridge and food which is built up in the beginning of the recruitment phase. To demonstrate the significance of a trail on a side bridge the following experimental situation was arranged: two identical side bridges, opposite each other, were joined to the main bridge, one bearing a good natural trail (from another ant colony), the other one blank. In a second experiment the arrangement of both bridges was interchanged in location. The basic deviation of ants onto the two kinds of bridges was counted during a period of 42 and 30 minutes respectively. All ants were removed from the bridges. In both experiments the number of newcomer ants was significantly higher (Student's test $p < 1\%$) on the trail bridge (Fig. 6. In the first experiment the deviation rate increased 3.7 times, in the second 7 times). Hence a trail on a side bridge is a powerful component that increases the deviation rate of ants from the old pathway. A trail has, however, only directing quality (true attractant: see "Introduction"). No alerting stimulus could be demonstrated by presenting the trail pheromone from crushed hind legs in front of a nest entrance. A new trail forking off from the old pathway gives the ant the choice to follow either the old or the new direction. The actual split ratio at such a fork, however, is not proportional to the strength of the trails. The old direction is characteristically always preferred. Deviations are still

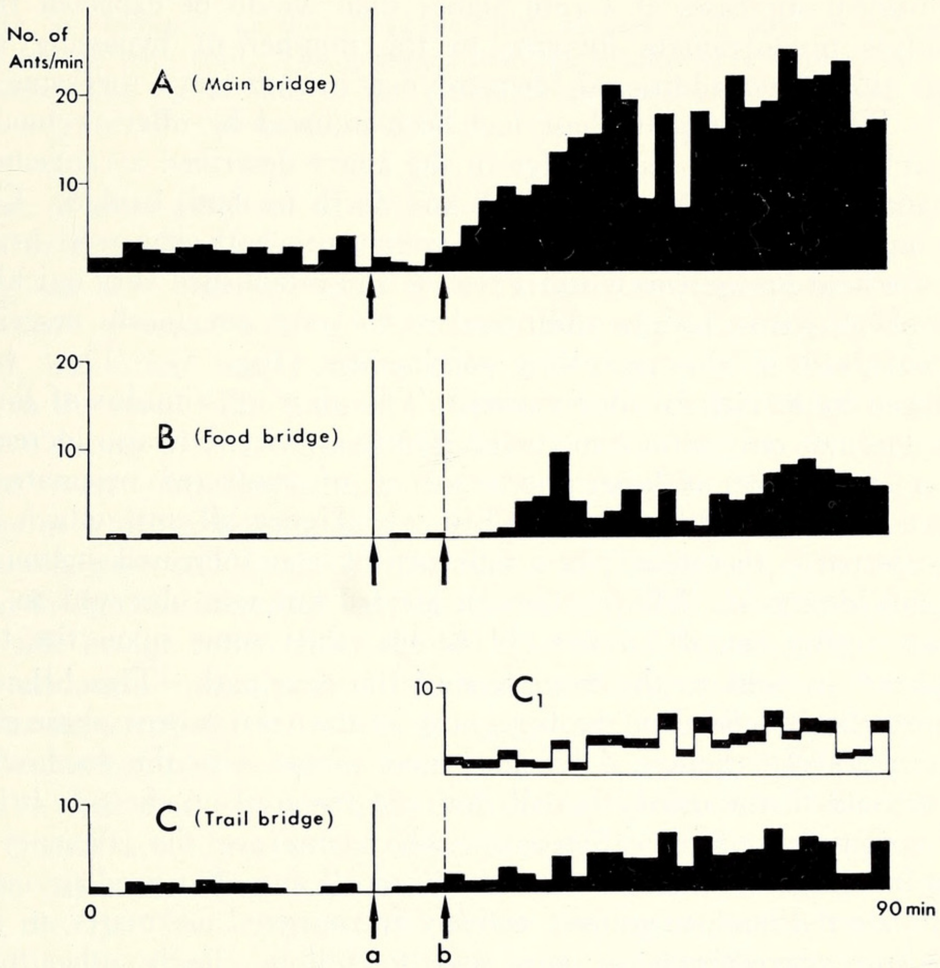

Fig. 7. Food recruitment in a small colony. A food bridge and an adequate bridge without food but bearing a trail were joined opposite each other to the main bridge. Until time "a" (arrow) all ants were removed from the bridges. At time "b" the first recruiter ant arrived on the main bridge.

A. Activity on the main bridge. Passages both ways counted in 2 min intervals.

B. Number of ants passing towards the food.

C. Number of ants going onto the trail bridge.

C_1. The white columns show the calculated amount of ants which would go onto the trail bridge during the recruitment phase if it were proportional to the total increase of activity in A. The black tops give the actual numbers from C.

exceptional even though significantly higher in number than on a side turn without a trail.

There are other factors in addition to increased colony activity and trail-laying that enhance the efficiency of the recruitment to mass-foraging. Some evidence for their existence is supplied by the fact that the number of newcomers on a trail side bridge during recruitment increases at a rate higher than would be expected from a simple proportionate increase to the number of bypassing ants (Fig. 7C. Two additional identical experiments gave the same result). The recruitment phase had been induced by offering food at the end of the blank side bridge in the above described arrangement. All ants were allowed to go back and forth on both bridges. Considering the actual number of ants going onto both, the trail bridge and the food bridge (on which a trail is also established very quickly), it is obvious that factors additional to the ones previously described are involved in the recruiting mechanism (Fig. 7). They were analyzed by behavioral observations. The alerting stimulus of finder ants does not only induce increased colony activity, but also increases, for a short time at least, the tendency of contacted nestmates to deviate from the old pathway (Fig. 3). Hence all ants which had been alerted in the vicinity of a side turn have an increased inclination to explore onto it. Many times an alerted ant was observed to run a fast zigzag course on the old bridge, then come upon the turn and head straight to the extremity of the new path. This behavior is especially beneficial at the beginning of the recruitment phase since it increases the chance of bringing new pioneers to the food while the activity in the colony is still low and the trail on the side bridge still incomplete. Other properties which improve the efficiency of mass-foraging consist of the tendencies of all ants, but predominantly of the alerted ones, to contact actively encountered nestmates, to join gathering aggregations of ants and to follow closely other nestmates. These mechanisms gain importance as soon as a few foragers return from the food bridge to the main bridge where they usually go very slowly and accumulate, so that newcomers are easily attracted to the area. The influence of the attractive effect of returning ants has also been observed on a dead-end trail on a side bridge without food. In the experiment all newcomers were removed from the side bridge during the first 30 minutes, whereas in a following period of 36 minutes the scouts were allowed to return from the excursion. The activity of the colony stayed at a constant basic level during the whole experiment. The rate of newcomers, however, was seen to increase during the second period because of the overall attractive

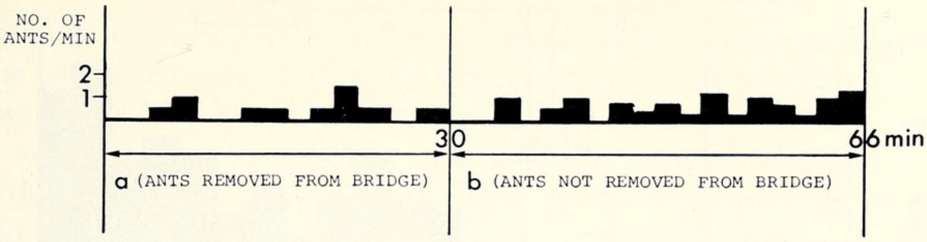

Fig. 8. Influence of the attractive effect of gathering ants on a foodless side bridge with trail. The passages onto the bridge were counted in 2 min periods. The significance of the difference between phase "a" and "b" is $5\% > p > 1\%$ (Student's test).

effect of ants gathered at the joint (Fig. 8). Sometimes groups of two or three ants went together onto the side bridge. Tandem running has been observed to be an important factor speeding the establishment of mass-foraging. A forager ant, while turning back to the food, was often closely followed by a newcomer who was promptly led to the food. The influence of properties such as tandem running, active facing of encountered individuals and attraction to the crowd gains even more importance for the mass-recruitment during the stage in which a more or less continuous stream of ants starts flowing between nest and food. While this traffic builds to and from the food bridge, an increased rate of new ants follow the stream towards the side bridge rather than the old direction (Fig. 9). By considering all possible components involved in the recruitment, the causes of an exponential rise to mass-foraging can be analyzed step by step. A description of the rise of mass-foraging is presented below.

The first few explorer ants find the new food area independently by chance according to the basic probability of deviation from the main pathway. They are usually attracted to the food by the smell for the last few centimeters. After feeding or only touching or smelling the food, and often after a small orientation trip around the food, the first food finder turns back laying a trail. The trail is most efficient, as already mentioned, near the food, at the connection joining the food bridge to the old main bridge and on the turn merging into the old road. This first trace of a new scent trail alone somewhat increases the deviation rate of bypassers. The food finder on the old pathways also presents an alerting signal to encountered ants. Such signals transmitted in the closest vicinity of the side turn increase once more the probability that stimulated ants will scout onto the new bridge (Fig. 3). Even though the new trail is weak and fragmentary, a relatively increased number of newcomers arrive on the base of the food bridge, and find the way to the food. The alert-

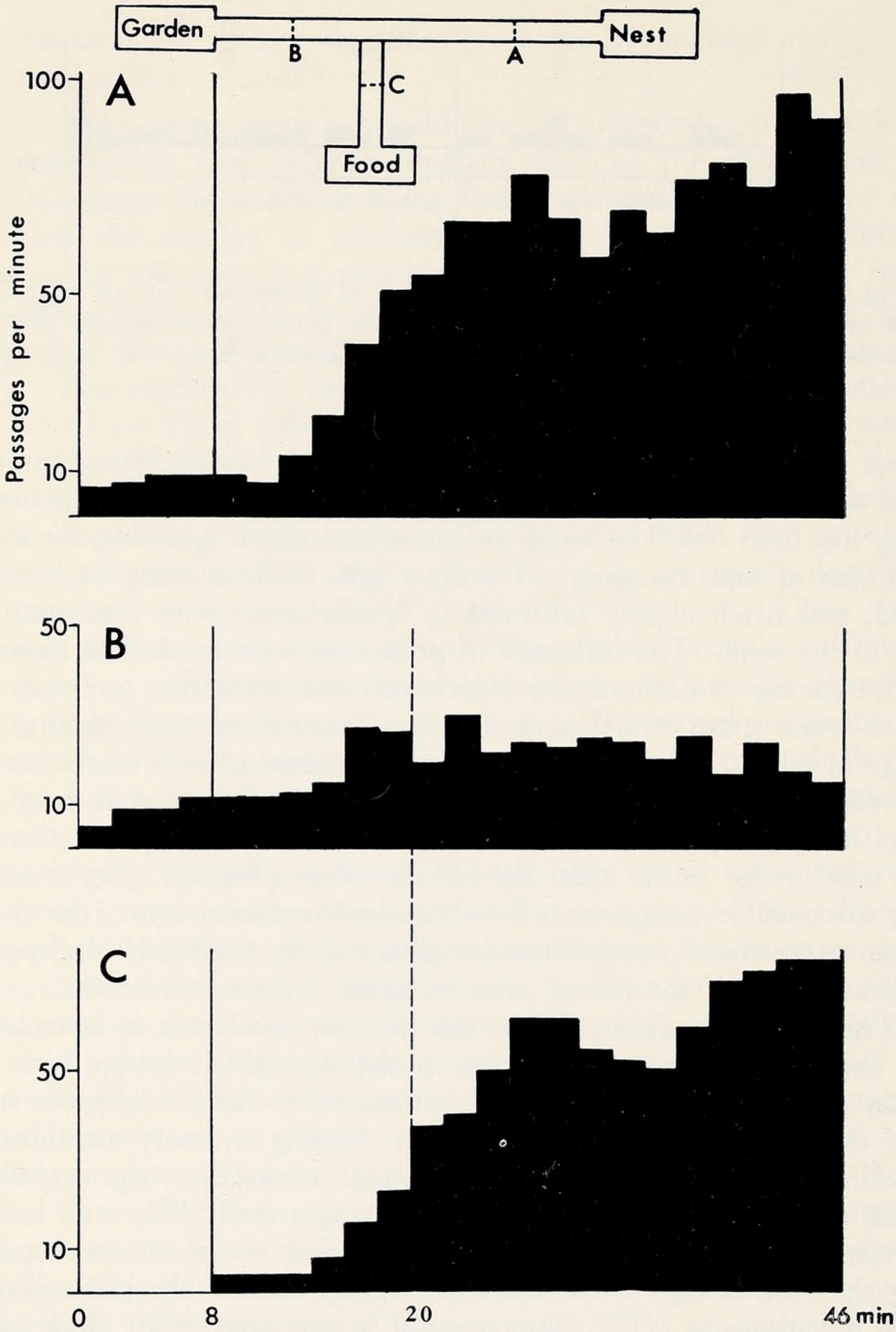

Fig. 9. Mass-recruitment experiment in a large colony. The back-and-forth passages of ants were counted in periods of 2 min at 3 different places: On the main bridge between nest and the side turn (A) and the "garden" (old feeding station) (B) and third on the food bridge (C). The food bridge was connected after 8 min. The alerting stimuli predominantly affect increase in running activity on the old trail (B) during the first period. Only after 20 min (dashed line) relatively more ants turn towards the food (C). This means that the alerting stimulus alone gives no information about the location of the food.

ing stimuli released on the pathway temporarily increase the activity of the recruited ants but their effect fades if the stimuli are not renewed (see "Behavior"). This is the case when the recruiter turns back again to the food before reaching the nest. If, however, the alerting behavior is performed in front of the nest entrance or even within the nest twigs, the colony activity increases significantly (Fig. 10). Excited workers leave the nest in large numbers and start running over the bridge. In the meantime other foragers which had found the access to the food come back onto the main bridge. They strengthen the new trail. The returning ants often accumulate at the joint from the new bridge to the old pathway because of intensive trail-laying. More new ants again are attracted towards this cluster and follow the fresh trail. All returning foragers in this stage alert encountering ants. The excitement and colony activity increase exponentially since the more recruiters on the path the stronger the recruitment effect becomes. All ants who find the food directly turn

Table 1. Food recruitment experiment. (Arrangement see: "Methods").

	Phase without recruitment. (All ants were removed from side bridge).		Phase of recruitment	
	54 min	per 1 min	68 min	per 1 min
Running frequency on the main bridge (passing ants both ways)	162	3	1096	16
Actual number of newcomers* to the side bridge	7	0.13	167	2.46
Calculated number of newcomers, supposed without any recruitment stimulus	7	0.13	8.8 or 5.3% of the actual number	0.13
Calculated number of newcomers proportional to the increase of running frequency on the main bridge	7	0.13	47 or 28% of the actual number	0.69

*Supposing repeated foraging of each food finder, the number of newcomers during a 2 min period was obtained by the number of ants going to the food minus the number of returners during the preceding 2 min period.

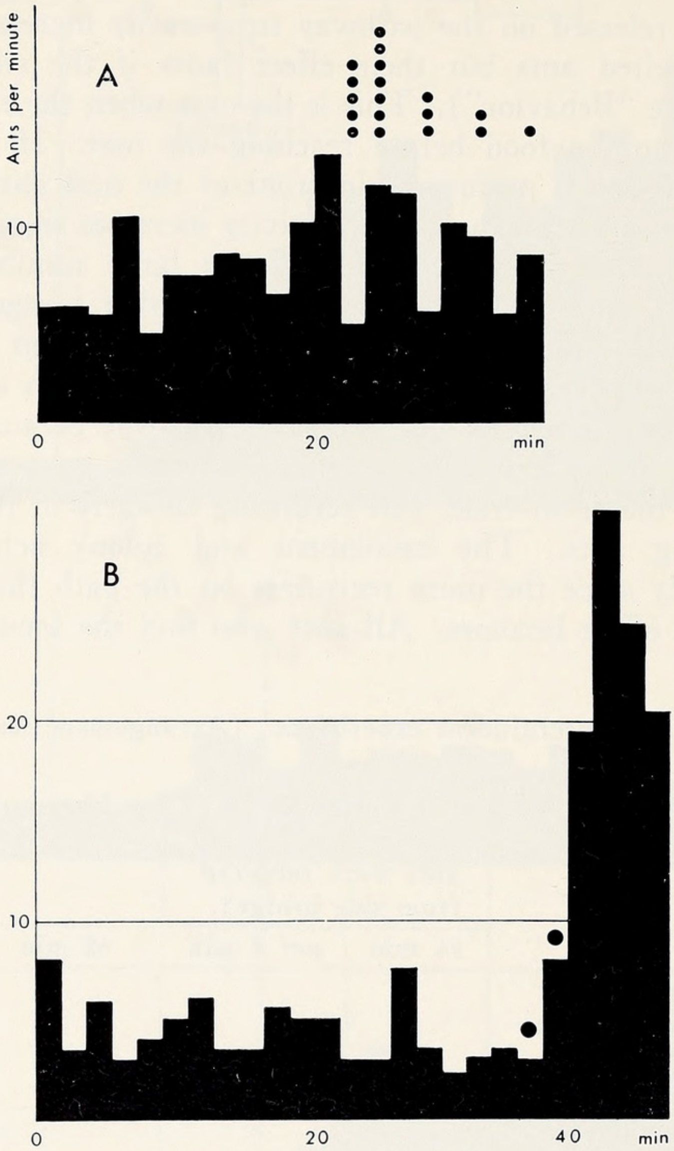

Fig. 10. Influence of the alerting behavior of one single food finder ant. A. The alerting performances occurring only on the pathway (small dots). B. The alerting performances occurring at the entrances of the nest logs (large dots). The ants walking over the main bridge were counted in 2 min periods.

back to that place. By means of the high tendency of tandem running and attraction to agglomerations in the alerted colony, large numbers of newcomers follow to the goal. The stream of running ants which at first develops on the main bridge now more and more deflects to the food bridge by the accumulative efficiency of all properties of recruitment. In summary, the multiple effects leading to buildup at the food source are:

(1) Increased running activity of workers due to the as yet unidentified alerting stimuli.

(2) Increased deviation rate from the old pathway caused by the new trail.

(3) Increased deviation rate by means of the alerting stimuli.

(4) Direct orientation of newcomers to the food through the new trail.

(5) Direct returns to the food by repeated foragers.

(6) Tandem running, active facing of encountered ants and attraction to agglomerations, three properties which are increased by the alerting stimuli and the consequent general excitement of the colony.

The activity of recruitment behavior decreases rapidly as soon as the peak of newcomer ants is reached and most of the colony has begun to participate in foraging. The full stream of foragers continues to flow until either the food source is exhausted or the colony becomes satiated with the particular kind of food present at the source.

SUMMARY

(1) Two active patterns of recruitment to the food are performed by food finder ants: trail-laying directed at the colony as a whole, and the alerting of individual nestmates.

(2) The sequential responses to those two recruitment stimuli are: a) increase of running activity in the colony by means of the alert stimuli; b) increase of the deviation rate from the old pathway as the result of both the alert stimuli and the new trail; c) improved trail-following or searching on either the old pathway or the new trail a few seconds after the perception of the alerting stimuli.

(3) Several stereotyped behavior patterns favor mass-recruitment. These include: a) the repeated back-and-forth passages of pioneer recruiters between the old running area; b) the repeated feeding by foragers; c) the tendency of all workers to follow close upon a leader ant (tandem running), to join agglomerations of ants, and to face and contact crossing ants. These behavioral effects are augmented by the alerting stimuli of food finders.

(4) The relative importance of the components and the quantitative control of mass-foraging are discussed.

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