1976

Recruitment behavior, orientation, and the organization of foraging in the carpenter ant Camponotus pennsylvanicus DeGeer (Hymenoptera: Formicidae).

James Francis Anthony Traniello
University of Massachusetts Amherst

Traniello, James Francis Anthony, "Recruitment behavior, orientation, and the organization of foraging in the carpenter ant Camponotus pennsylvanicus DeGeer (Hymenoptera: Formicidae)." (1976). *Masters Theses 1911 - February 2014*. 3029.
Retrieved from https://scholarworks.umass.edu/theses/3029

RECRUITMENT BEHAVIOR, ORIENTATION, AND THE ORGANIZATION OF FORAGING IN THE CARPENTER ANT CAMPONOTUS PENNSYLVANICUS DEGEER (HYMENOPTERA : FORMICIDAE)

A thesis presented

by

James Francis Anthony Traniello

Submitted to the Graduate School
of the University of Massachusetts
in partial fullfillment of the requirements
for the degree of

MASTER OF SCIENCE

in

ENTOMOLOGY

August, 1976.

RECRUITMENT BEHAVIOR, ORIENTATION, AND THE ORGANIZATION OF FORAGING IN THE CARPENTER ANT CAMPONOTUS PENNSYLVANICUS DEGEER (HYMENOPTERA : FORMICIDAE)

A thesis presented

by

James Francis Anthony Traniello

Approved as to style and content by:

Dr. Henry H. Hagedorn, *Chairperson of Committee*

Dr. Alastair M. Stuart, *Member of Committee*

Dr. Ronald J. Prokopy, *Member of Committee*

Dr. John G. Stoffolano, Jr., *Acting Head of Department*

ACKNOWLEDGMENTS

It is indeed difficult to achnowledge all the people who have kindly devoted their time and energy in assisting me with this thesis. However, several people have been particularly instrumental and I would like to mention them here. My most sincere appreciation for their cooperation is given to:

Elliot Allis, for his help in the building of laboratory nests.

Walter Kaczor and Edward Tobin, for their assistance in the collection of ants. I apologize to Walt for the mandibles in the scrotum.

Thomas Flanagan for his interest, ideas, and stimulating discussion.

Dr. Marguerite Bohm for her consultation and criticism.

Dr. Edward Goldstein for his many fine comments and criticisms of my work.

Dr. Alistair Stuart for his cooperation, comments, and especially for his faith in my capabilities as an ethologist.

Dr. Ron Prokopy for serving as a member of my committee.

Drs. R.L. Jeanne and S. Duncan for their inspiration during my undergraduate education.

My deepest thanks go to Dr. Henry Hagedorn for his interest in my research and for allowing me to conduct behavioral research in a hormone physiology lab. I am also appreciative of his funding my work, and for having taken me under his protective wing when I was having difficulty gaining direction in the sciences.

I would also like to thank Dina Alison Brown for typing the manuscript and for her gracious company.

PREFACE

This thesis is divided into two major sections. In section one, a review of the literature pertinent to the thesis is presented. This section is intended to provide the reader with a background of information in the areas of communication, ecology, and physiology. The literature review includes a somewhat historical perspective and a detailed account of current work in the area. Unfortunately, one can never completely keep up with the literature, and some very recent studies have been omitted. However, this should in no way detract from the review as it is representative of the state of the art at this time.

Section two consists entirely of original research. In this research I have attempted to elucidate the behavioral mechanisms involved in the foraging activities of the ant _Camponotus pennsylvanicus_, while attempting to maintain a physiological, ethological, evolutionary, and ecological perspective. While this combined approach may appear schizoid, I feel that it ismost desireable.

While thisstudy is essentially eclectic, I believe that a good portion of the work will prove to be original in design and approach. I sincerely hope that the reader finds this study both edifying and entertaining.

This thesis is dedicated to my father, James Traniello, and to my grandfather, Francesco Fantasia.

CONTENTS

Section One: Literature Review

Chapter I: Recruitment Behavior

Chapter II: Orientation

Chapter III: Recruitment to Food and the Organization of Mass Foraging

Section Two: Research Results

Experiments and Results

I. Orientation during foraging

II. Recruitment to food

III. The organization of mass foraging

CHAPTER I

RECRUITMENT BEHAVIOR

Introduction

It is of great importance to the survival of an insect society to be able to quickly and efficiently mobilize individuals within the colony to a particular place where work is required. This process of nestmate mobilization is termed recruitment (Wilson 1971). The activity at the target area may involve nest moving, the exploitation of a food source, or the dispatching of an intruder. A variety of communication systems occur in different ant species to meet these needs. These systems may be ranked according to their relative level of sophistication as determined by the principal mode of communication involved. First to be considered in this discussion are relatively elementary forms of recruitment involving visual attraction and simple chemical communication.

Visual Attraction

A primitive form of recruitment which involves visual attraction has been noted in Formica lugubris by Stäger (1931, cited in Wilson 1971) and in F. nigricans by Sturdza (1942, cited in Wilson 1971). When workers of these species locate prey they run in erratic circles around the potential meal. This behavior then serves as a visual signal to attract and excite other workers. This effect is termed kinopsis, or "Stäger's effect." Wilson (1962a) has observed this phenomenon in Daceton armigerum and noted that this process led to a more efficient killing of insect prey.

In considering Stäger's effect, let us first of all assume that volatile excitation does not occur, if we are at all to hold this visual effect to be operative. Even in consideration of this working hypothesis, it is still difficult to ascribe any intraspecfic significance to Stäger's effect based on the similarity between the signal which originally eminates from the prey and the signal of worker first encountering prey. Considering the similarity of the nature of these visual signals (i.e. movement), this "communication" seems identical to visual stimuli involved in predator/prey relationships which account for the initial attraction of the predator.

Simple Chemical Recruitment

Chemical recruitment involves a number of types of olfactory communication which range from the simple discharge of alarm pheromones to the evolutionary acme of chemical mass communication. Pheromone glands in ants are located principally in the gaster (the poison gland, Dufour's gland, the hindgut) and the head (the mandibular glands). The chemical identification of these glandular products has revealed a wide assortment of compounds whose function varies dependent upon context. The glandular secretions may function as attractants, excitants, orientation cues, or one substance may serve more than one function dependent upon concentration. For example, 4-methyl-3-heptanone, the mandibular gland alarm substance of Pogonomyrmex badius, not only excites nestmates in the immediate area of the point of discharge but also attracts other workers within approximately 10 centimeters (Wilson 1958). This attraction/alarm function of the pheromone causes prey to be quickly subdued. Although it is difficult to separate this elementary system of attraction and alarm from true recruitment processes, a distinction may be made between the two. In the former, the communication has a directional component over only a short distance, is most effective as a nest defense or prey-trapping mechanism, and requires a strong stimulus to initiate the attraction of sister workers. The latter is not dependent upon strong alarming stimuli to elicit the subsequent assembly of nestmates. Other signals are used to accomplish this. The distinction, I feel, may only hold for the ants.

The Evolution of Recruitment Behavior

Chemical mass communication is considered to be the most sophisticated of the formicid recruitment techniques (Wilson 1971, Hölldobler 1975). The evolution of this highly efficient process was theoretically accompanied by a gradual decrease in the dependence of recruiting ants upon motor displays to alert nestmates. After being alerted by a specific action pattern of a recruiter, odor trails are provided by the recruiting ant to orient nestmates to the target area. As the necessity of alerting behavioral displays decreased, the function of the odor trail increased in it potency as an orientation cue and also provided intrinsic alerting stimuli. Assuming the plausibility of this evolutionary pattern, recruitment techniques will be considered with regard to this hypothetical model.

Tandem running. Wilson (1971) has pointed out that recruitment behavior involving tandem running is relatively primitive. This behavior has been documented in the ponerines *Bothroponera tesserinoda* and *Diacamma ceylonese* (Maschwitz, Hölldobler, and Möglich 1974), the myrmicines *Leptothorax acervorum* (Dobrzanski 1966) and *Cardiocondyla venestula* (Wilson 1959), and the formicine *Camponotus sericeus* (Hingston 1929, Hölldobler, Möglich, and Maschwitz 1974). Tandem running is used to recruit nestmates to newly found food and nest sites in all of the above ant species except *Leptothorax acervorum* which utilizes this technique to form tandem pairs which explore new territories (Dobrzanski 1966).

The communicative signals involved in tandem running are tactile and olfactory. In Cardiocondyla a tandem pair is formed when one ant finds a food particle too large to retrieve alone. Upon returning to the nest she encounters a nestmate and the pair subsequently maintain a communicative bond during the return to the food. The leader ant guides its follower to the food by a series of short runs during which the leader halts periodically and waits motionless until its follower regains antennal contact with the leader's gaster. The follower apparently orients along a short-lived odor trail; the leader orients to the food visually.

Communication by the tandem running technique has been examined in detail by Hölldobler, Möglich, and Maschwitz (1975) in Camponotus sericeus. In this ant tandem running is utilized to communicate both the location of new food sources and new nest sites. In C. sericeus tandem running essentially consists of a motor display given by the leader to a nestmate, mechanical contact between the pair, surface pheromones, and a trail of hindgut material. The nature of the motor display is dependent upon context. During recruitment to food the motor pattern consists of fast runs interrupted by self-grooming and "ritual" food offerings. The recruiting ant is subsequently approached by a small number of workers which attempt to maintain close antennal contact. Only one ant succeeds in maintaining this contact and arrives at the food with the recruiter. The formation of the pair is initiated when the recruiter pulls a nestmate by the mandibles and presents her gaster; movement begins when the follower touches the leader on the hindlegs or gaster. As the pair advance tactile contact is maintained between the head or antennae of the follower and the gaster or the hindlegs of the leader. This tactile stimulation provides the impetus to "drive" the leader forward. The follower orients along a hindgut trail. The ultimate success of the leader in recruiting a follower is highly variable.

During nest emigration the motor component which initiates tandem running is distinctly different. In this case the recruiter displays an "invitation behavior" to initiate the formation of a tandem pair. To release the follower behavior of a nestmate to a new nest site a recruiter faces a sister worker head on, grasps it by the mandibles, pulls it forward and, while turning its body 180° relative to the potential follower loosens its grip and presents its gaster. Tandem running begins when the leader is touched at the gaster or the hindlegs by the follower.

Maschwitz, Hölldobler, and Möglich (1974) have also analyzed tandem running _Bothroponera tesserinoda_, and have found a few noteworthy differences in comparison to the behavior of _C. sericeus_. In _B. tesserinoda_ either the head, thorax, or gaster may function as "leader dummies;" in _C. sericeus_ the gaster is preferred. Also, in _B. tesserinoda_ chemical orientation trails do not appear to be discharged by recruiting ants, and if the tandem pair is separated during the course of recruitment, both leader and follower search in circles until they find each other. Hindgut trails, are on the other hand, utilized as orientation cues for the follower in _C. sericeus_.

It should be noted that tandem running is regarded as being relatively primitive due to the dependence upon tactile stimuli. However, this technique does involve a number of elaborate behavioral patterns not found in species which utilize a recruitment system more dependent upon chemical cues, and must be regarded as having high adaptive value. It is possible that this behaviorally elaborate system has evolved in response to certain competition pressures and therefore has ecological significance as will be discussed later.

Group recruitment. Trail communication has evolved in some groups of ants from tandem running (Wilson 1971), and there exists a number of intermediate stages of recruitment between tandem running and more advanced communication systems. In particular, species in the genus *Camponotus* illustrate an evolutionary progression from tandem running to higher forms of recruitment. As mentioned earlier, tandem running is exhibited by *C. sericeus*. Hingston (1929) described intermediate forms of communication in *C. paria* and *C. compressus*. In *C. paria*, there does not exist the cohesive leader/follower tactile interaction; instead, the follower falls 5-10 centimeters behind and orients along a short-lived odor trail. The trail becomes increasingly important in *C. compressus*, as 10-20 workers follow single file behind a leader. Similar behavior occurs in *C. beebei* (Wilson 1965) and *C. socius*. The parameters involved in recruitment in *C. socius* have been examined in detail (Hölldobler 1971a).

Although Wilson first proposed that social responses in ants could be experimentally controlled by extracts of glandular secretions in 1959, a physiological approach to the analysis of recruitment behavior has been utilized by relatively few workers in the field. Since recruitment behavior is composed of a number of components, it is desirable to isolate each parameter and determine its relative role in the entire system. Such an analysis has been applied to recruitment in *C. socius*.

In *C. socius* recruiting ants lay a trail of hindgut material from newly discovered food sources to the nest. It must be noted that the hindgut substance, which functions solely as an orientation cue, cannot release recruitment. Since the trail itself contains no intrinsic excitatory information, recruiters must provide additional stimuli to successfully guide nestmates to the food.

Upon entering the nest the recruiter encounters nestmates head-on with a "waggle" motor display, which consists of vibratory movements of the head and thorax in the horizontal plane. This motor activity alerts nestmates which subsequently engage in brief food transfer with the recruiting ant and follow the recruiter (=leader) out of the nest. On the trail, the hindgut pheromone functions as an odor guide, while the leader discharges poison gland secretion to maintain the excitement of the group. Similar signals are involved in nest migration; non-responding individuals are carried to the new nest.

There is one parameter in the recruitment process of _C. socius_ which should be emphasized: the trail substance alone does not induce recruitment. Recruitment induction by trail pheromone alone is a higher level of communication; this system will be considered later in this review. Recruitment behavior in _C. socius_ is an excellent intermediate between _C. paria_ and the chemical mass communicators. The inability of the trail to elicit both excitement and orientation is compensated for by the behavioral activities and chemical discharges of the leader. The leader is necessary to the establishment and maintainance of the behavioral continuity of the group. Consequently, we would expect the existence of additional intermediates between _C. socius_ and other more advanced formicine species.

Möglich and Hölldobler (1975) have recently cited the recruitment behavior of _Formica fusca_ as such an intermediate. In _F. fusca_, neither the trail nor any combination of exocrine gland extracts are capable of eliciting recruitment. Again, the trail is of hindgut origin and functions only as an orientation cue, and nestmates must be previously stimulated to release trail following. However, a leader ant is not necessary to maintain group cohesiveness, and nestmates readily follow the recruiter's trail in the absense of the recruiter. The observed trend is toward a reduction in the complexity of motor activity and dependence upon "leaders" or experienced individuals in guiding nestmates to the target area. The elaboration of recruitment behavior to the stage of chemical mass communication is thus a process of simplification on one hand and increased stimulus coding on the other. As there is an elimination of specific interindividual motor activities, the functions of these activities are assumed by the trail pheromone itself.

Chemical Mass Communication. Chemical mass communication has thus far been documented in the myrmicine Solenopsis (Wilson 1962b) and the formicine Lasius fuliginosus (Hangartner 1967). This system is extremely well-defined in Solenopsis. When a worker is returning from a new food find, she moves at a relatively slow pace and, extruding her sting, discharges a potent trail pheromone from the Dufour's gland. The continuity of the sting trail is dependent upon the nutritional status of the recruiting ant. Therefore, the behavior of recruiting ants is also dependent upon the immediate conditions of the colony. Large, rich baits enhance the recruitment effect because the degree of sting extrusion is related to food quality and larger baits increase the number of trail-laying ants (and hence pheromone concentration) resulting from the accommodation of more ants at the food (Hangartner 1969). In this manner differential amounts of trail pheromone are discharged by foragers. It is the summation of each individual's contribution to the trail which regulates the number of workers leaving the nest. Wilson (1962b) referred to this feedback system as mass communication. To state it concisely, an increase in the number of trail-laying foragers increases pheromone concentration which in turn regulates the response of the colony. Thus the behavior of groups of individuals regulates the behavior of groups of other individuals.

It is possible to experimentally induce recruitment in Solenopsis by allowing Dufour's gland extract to diffuse from a glass rod placed near the nest entrance. Small amounts of extract induce trail following by dozens of individuals, while large quantities of pheromone may evoke the emigration of most of the nest inhabitants. Although some workers may show a vibratory behavior when encountering a nestmate, Wilson does not hold that this motion in any way constitutes a recruitment signal, as the trail pheromone alone can release full trail following behavior.

The Ecological Significance of Recruitment Systems

It is easy to imply the ecological significance of recruitment behavior in ants, but little has been documented experimentally. Ant species are in competition for food sources and nest sites present in their immediate habitat; foraging activities of ants are often temporally isolated (Hunt 1974), conflicts do occur and it is an advantage to be able to exploit a food find rapidly. Different ant species have evolved strategies to effectively cope with this type of competition pressure.

Wilson (1971) has loosely categorized the succession of ant species at a given bait as "opportunists," "extirpators," and "insinuators." Opportunists are adept at locating food, rapidly fill their crops and quickly return to their colonies to recruit nestmates. Next in the succession of species at the bait are the extirpators, which are aggressive in comparison to the timid opportunists. The opportunists flee as their competitors arrive but they have already consumed a portion of the spoils; but arriving early have insured colony survival at a minimal risk of workers in the ensuing competition between extirpator species for the remaining food. Extirpator species, such as Solenopsis are typically pugnacious.

While the mélé between extirpators is occurring, a third group of species may appear. These are the insinuators which rely on their comparatively small size and stealthy behavior to sucessfully acquire food without being noticed. These species, such as Cardiocondyla, recruit nestmates to the food by the tandem running technique; the tandem pair can pass through the extirpators unnoticed. Recall that tandem running is considered primitive, yet in the ecological context of this species it is highly adaptive. Were the insinuators to recruit nestmates with any greater efficiency they would most likely lose their anonymity and be dispatched by the more aggressive species.

The size of competing ant species apparently has little effect on their competitive character at a food source. Hunt (1974) has shown that the relatively small Tapinoma antarcticum can successfully repell their larger competitor Dorymyrmex antarticus. Although the ability of an ant to dispatch a larger competitor is related to its aggressiveness, efficient recruitment processes can allow a large number of workers to reach the target area in short order. It is important to explore the role of recruitment systems in competitive ecological patterns.

Wilson (1975) has documented an extremely interesting alarm/recruitment system and has postulated its adaptive significance. Solenopsis and Pheidole are closely related myrmicine species which have similar biotic requirements. Upon encountering a foreign ant, Pheidole sp. recruit nestmates to the area of intrusion. The recruitment mechanisms involved in nest defense, interestingly enough, are quite specific. The worker caste in Pheidole is dimorphic, consisting only of minor workers and large-headed major workers (soldiers). Typically, if a minor worker encounters an alien ant, she returns to the nest and recruits other minor workers by an odor trail. However, if the alien ant is of the genus Solenopsis, minor workers abscond from the battle area and return to the nest to recruit large-headed soldiers to dispatch the intruders. The recruitment system is thus enemy specific.

Wilson suggests the following explanation of the existence of this enemy-specific recruitment. Solenopsis forms large, aggressive colonies and is able to recruit nestmates rapidly and in large numbers by their precise odor trail. Since Pheidole rivals Solenopsis for the same resources, it is to the advantage of Pheidole to prevent a potential attack by responding immediately and in force to the presence of a fire ant scout. The threat alone of a fire ant attack warrants the temporary abandonment of the nest by the major workers to destroy the potential usurpers and search the area for additional scouts.

Alarm/recruitment systems may also be involved in intraspecific conflicts. Hölldobler (1976) has recently demonstrated that workers of Myrmecocystus mimicus recruit nestmates during territorial disputes with neighboring colonies. The opposing worker forces subsequently engage in ritualized tournaments involving walking in stilt-like fashion and antennal "drumming" on the opponent's gaster. Colony strength is thus assessed; the weaker colony is enslaved.

CHAPTER II

ORIENTATION

Olfactory Orientation

Trail pheromones and their anatomical source. Orientation by olfactory cues has long been suggested in the literature (Forel 1928, Hingston 1929). However, experimentation remained dormant until the more definitive work of MacGregor (1948) and Carthy (1950). Since then, chemical trails have been documented in many social Hymenoptera (see review by Blum 1974). Trails have been shown to be highly effective in organizing group behavior. The deposition of pheromonal material upon the trail is typically associated with specific trail-laying behavior.

Trail substances typically originate in the gaster and the principal anatomical structures responsible for their production are the hindgut (rectal sac), the poison gland, and the Dufour's gland (the accessory gland to the sting). The exception to this rule is the myrmicine Crematogaster, which lays a chemical trail from a tibial gland (Leuthold 1968, Fletcher and Brand 1968).

The potency of trail pheromones varies from species to species, as does the function of social substances produced in the exocrine glands. The functions of these substances include orientation cues, alarm, attraction, or recruitment signals; more than one glandular produce may be released dependent upon the system under consideration and the intended communicative function of the signal emitter.

The source of trail pheromone in ants varies between subfamilies. In the Myrmicinae, the trail substance originates in the Dufour's gland (Solenopsis) or the poison gland (Atta) (wilson 1962b Blum et al. 1964, Moser and Blum 1963, Blum 1966, Wilson 1963, Hölldobler and Wilson 1970); in the Formicinae and Dorylinae the hindgut (Blum and Wilson 1964, Hangartner 1969, Blum and Portocarrero 1964, Watkins 1964);

in the Dolichoderinae the anal gland (Wilson and Pavan, 1959); and in the Ponerinae the hindgut or the poison gland (Blum 1966

There is a wide range of information covering inter- and intra-specific trail following in ants. Trail pheromones of Solenopsis and Camponotus are fairly species specific, but many unrelated species may respond to each other's trails (Wilson 1962b, 1971, Barlin et al. 1976). Odor trails may also lack any specificity as has been demonstrated by Watkins (1964) in Neivamyrmex.

Considering the evolution of trail pheromones in different phyletic lines, it is interesting to note that in some cases the same organ serves the function of pheromone production in both poneroid and myrmecioid genera (the hindgut). This illustrates one point of convergence in the two complexes.

The ontogeny of trail organs in ants indicates that some of the reservoirs of glandular secretions have assumed their social functions secondarily, such as the poison gland which produces and stores defensive secretions, and the accessory gland of the sting, the Dufour's gland. In the Formicinae these organs are the sources of alarm pheromones and defensive secretions (Wilson and Regnier 1968, 1969, 1970).

The evolutionary origin of hindgut material as a trail pheromone in formicine ants has been speculated upon by Hölldobler (1975). In the Formicinae hindgut material is typically used as an orientation cue during the recruitment process. Many species of ants preferentially defecate at specific locations such as nest garbage dumps, nest periféry, and trunk trails. These preferred disposal areas could then serve as homing cues. This is indeed the case in a number of species, and this suggests that in the Formicinae trail communication behavior has evolved by a gradual ritualization of the defecation process. Thus Hölldobler speculates that hindgut material was primarily a homing cue which subsequently assumed a more specific role in orientation during recruitment. However, it has not been theorized how this orientation cue could evolve into a stimulating or alerting signal.

Perception of the odor trail. Forel (1928) assumed that the "topochemical" sense of ants was located in the terminal segments of the antennae. However, trails were not known to exist during Forel's time and little attention was given to the perception of trails. Any analysis involving chemoreception must by necessity include the characteristics and nature of the pheromone itself, in addition to behavioral bioassays. Bossert and Wilson (1962) and Hangartner (1967) have elaborated upon the physical and behavioral aspects of chemical communication. Although the trail pheromone is deposited as a liquid upon the substrate, ants do not respond to the chemical in this state. Instead, they move up a molecular concentration gradient (a process known as osmotropotaxis) within a "vapor tunnel" created by the diffusion of the pheromone. By sweeping their antennae laterally, ants orient themselves within this semiellipsoidal vapor tunnel where the pheromone concentration is at or above the behavioral threshold. The vapor tunnel contains no directional information (Wilson 1971).

The ontogeny of trail-following behavior. Ants have a well-defined polyethism and during a worker's development, tasks may change temporally. Otto (1958) made an extensive study of caste polyethism in the wood ant Formica polyctena. His division of the temporal activities of workers is into two principal groups: 1) the Innendienst, or service inside the nest such as brood care, and 2) the Aussendienst, or service outside the nest such as foraging. There are physiological correlates with each group concerning ovarian development. Workers of the Innendienst have developed ovaries, whereas those of the Aussendienst have ovaries which are partially or totally resorbed.

It is obvious that during a worker's lifespan the programming of either the periferal orcentral nervous system changes. One postulate might be that a sensory maturation process is coincident with the observed changes in labor. If this assumption is accurate then one would expect to find a differential responsiveness to social substances based on age. Foraging behavior, therefore, may be "turned-on" as an animal's receptivity to trail pheromone develops.

There is little experimentation regarding the ontogeny of trail following in ants, and the small amount of data available is rather conflicting. Topoff (1972) compared the ability of callows and mature workers of _Neivamyrmex_ to follow extracts of their trail pheromone. Results showed that although callows do not participate in raids until they are several days old, they exhibit trail following ability comparable to or better than adults. Therefore, at least in _Neivamyrmex_, there is an early onset of pheromone responsiveness. Topoff attributes the callows abstention from raids to be due to an increase in chemical and tactile stimuli inside the nest.

Cammaerts-Tricot and Verhaeghe (1974) found quite a different situation in _Myrmica_ _rubra_. In this species, as workers age their poison sacs (the source of pheromone) increase in size and their ability to follow artificial trails becomes concordantly accurate.

The growth of exocrine glands during worker development is fairly well documented (Blum and Ross 1965, Moser and Blum 1963). However, glandular development can not directly be correlated with the ontogeny of a behavioral phenomena and there is a definite need for a wider range of experimentation in this area. The differences in responsiveness in the above mentioned species may, however, constitute distinct generic differences and may not actually represent any conflict. This explanation is more tenable if the behavioral differences between *Myrmica* and the nomadic *Neivamyrmex* are considered.

Visual Orientation

Visual acuity in ants is typically correlated with their epigaeic or hypogaeic nature (Wilson 1971). Exceptions lie in the legionary species such as *Eciton*, *Anomma*, *Dorylus*, and *Leptanella* which although epigaeic are blind. Subterranean genera such as *Acanthomyops*, *Carebara*, and *Liomyrmex* are eyeless, whereas above-grand foraging species (*Formica*, *Gesomyrmex*, *Gigantiops*) posess large eyes and their alertness attests to their keen vision. However, the visual capabilities of these larged-eyed species have not been evaluated physiologically.

Sun-compass orientation and orientation to polarized light. Sun-compass orientation was originally studied in desert ants by Santschi (1911) and Wehner and Menzel (1969). These species orient to home by reckoning the angle subtended by the sun and the nest and holding it constant as they return homeward. Ants also compensate for the movement of the sun over time; thus a time sense is correlated with their visual orientation. Furtheremore, Jander (1957) has demonstrated that this process of following the sun's movements is actually learned.

It is interesting to note that in *Cataglyphis* orientation is totally dependent upon this method as trails are not used (Wehner and Menzel 1969). Hölldobler (1971b) has found an interesting system in the harvester ant *Pogonomyrmex badius*. During homing, workers use both chemical and visual cues in orientation although chemical signals dominate. But the chemical cue used in homing is distinct from that of the recruitment trail. Recruiting ants lay an ephemeral recruitment trail from the poison gland, whereas the secretion of the Dufour's gland is longer lasting and is utilized as a homing cue.

Nocturnal ants have been shown to possess a moon-compass orientation, as this has been documented in *Monomorium* by Santschi (1923) and in *Formica* by Jander (1957). Ants are also able to orient to the plane of polarized light. This has been shown in *Myrmica* by Vowles (1950, 1954) and in *Tapinoma*, *Lasius*, and *Camponotus* by Carthy (1951), Jander (1957), and Jacobs-Jessen (1959).

CHAPTER III

RECRUITMENT TO FOOD AND THE ORGANIZATION OF MASS FORAGING

Introduction

Recruitment systems may be considered as alerting mechanisms which engage and regulate foraging activities. Workers which respond most often belong to a particular age bracket and, dependent upon the system, may be of a particular caste. Therefore, a prominent division of labor occurs in foraging activities and other processes (such as nest moving) which are initiated by a recruitment mechanism. It appears that individual and group labor requires either a motor or chemical induction or a combination of both. This induction mechanism, coupled with nutritional feedback devices and individual physiological states, regulates the foraging activities of the colony.

The Effects of Polyethism on Foraging

Attempts to analyze formicid foraging activities have been made by Dobrzanski (1958), Wallis (1962, 1964) and Sudd (1957). (For a good basic review of foraging and related activities see Sudd 1967). These experiments were concerned with answering basic questions about foraging behavior and among the aspects covered were the effects of starvation, food distribution, solicitation and acceptance during food transfer, and motor activities associated with recruitment. Dobrzanski (1958) noted that foraging grounds are partitioned in *Formica* spp. and that workers remained in a particular route. Working with several genera of ants, he divided species into two groups. The first group, which included *Formica*, foraged on permanent routes, the second group (*Myrmica*, *Tetramorium*, and *Leptothorax*) had no foraging routes but were thought to convey information about the presence and location of food. In other words, this latter group possessed quick recruitment systems. Dobrzanska's mistake, however, was to negate the presence of recruitment systems in *Formica* which,of course, do exist at least in _F_. _fusca_ (Möglich and Hölldobler 1975).

Rosengren (1971) and Horstmann (1973), working with _Formica_ furthered some of the concepts of Dobrzanski in regard to labor division and the partitioning of the foraging territory. Their results are especially important because they confirm Otto's (1958) observations of the presence of an Aussendienst and also establish that these ants have a visual memory and are capable of learning environmental configuration pertinent to their foraging route. This process results in a stable worker composition within foraging tracts and attests to a further division within the Aussendienst leading to "route fidelity" (Rosengren 1971).

Regulatory Mechanisms Involved in Foraging

As has been previously discussed, motor activities may be one method of initiating foraging. Early workers such as Goetsch (1934, cited in Szlep-Fessel 1970) described the excitatory bumping and antennal beating of _Monomorium_ recruiters. Szlep and Jacobi (1967) further described the displays of recruiting ants of this genus and also _Tapinoma_ and _Pheidole_ as accelerated antennal beatings, body oscillations, and head pushings. The collective term "oscillatory recruitment display" encompassed any mechanical pattern given by a recruiting ant. These authors also noted that these displays led to a coordination of nestmate activity which resulted in mass foraging. Further observations of mass foraging in _Pheidole_ led Szlep-Fessel (1970) to the conclusion that recruiter motor displays in conjunction with the scent trail are highly effective in mobilizing nestmates, and that the motor display is particularly important in recruiting soldiers. Recruitment stimuli lead to the rapid formation of a foraging force, the size of which is dependent upon the number of recruiters and the character of the recruitment performance. The recruiting stimuli decrease in effectiveness over time, and this waning of the releasing properties of motor displays eventually causes recruitment to be terminated. As permanent foraging becomes established the initial high level of recruitment gives way to the effects of polyethism and the number of foragers diminishes.

LITERATURE CITED

Barlin, M., M.S. Blum, and J.M. Brand. 1976. Species-specificity studies on the trail pheromone of the carpenter ant *Camponotus pennsylvanicus*. J. Ga. Ent. Soc. 11: 162-164.

Blum, M.S. 1966. The source and specificity of the trail pheromones of *Termitopone*, *Monomorium*, and *Huberia*, and their relation to those of some other ants. Proceedings of the Royal Entomological Society of London 41: 155-160.

_________, 1974. Pheromonal sociality in the Hymenoptera. In: Pheromones. M. Birch, ed. North-Holland Pub., Amsterdam. viii + 495 pp.

_________, and C.A. Portocarrero. 1964. Chemical releasers of social behavior IV. The hindgut as the source of the odor trail pheromone in the Neotropical army ant genus *Eciton*. Ann. Entomol. Soc. Am. 57: 793-794.

_________, and G.N. Ross. 1965. Chemical releasers of social behavior V. Source, specificity, and properties of the odor trail pheromone of *Tetramorium guineense* (F.) (Formicidae: Myrmicinae). J. Insect Physiol. 11: 857-868.

_________, and E.O. Wilson. 1964. The anatomical source of trail substances in formicine ants. Psyche, Cambridge, 71: 28-31.

_________, J.C. Moser, and A.D. Cordero. 1964. Chemical releasers of social behavior II. Source and specificity of the odor trail substances in four attine genera. Psyche, Cambridge 71: 1-7.

Bossert, W., and E.O. Wilson. 1963. The analysis of olfactory communication among animals. Journal of Theoretical Biology 5: 443-469.

Cammaerts-Tricot, M.-C., 1975. Ontogenesis of the defense reactions in the workers of *Myrmica rubra* L. Animal Behaviour 24: 124-129.

______________, and J.-C. Verhaeghe. 1974. Ontogenesis of trail pheromone production and trail following behaviour in the workers of *Myrmica rubra* L. Insectes Sociaux 21: 275-282.

Carthy, J.D. 1950. Odour trails of *Acanthomyops fuliginosus*. Nature, London 166: 154.

Carthy, J.D. 1951. The orientation of two species of British ants. Behaviour 3: 275-318.

Dobrzanska, J. 1958. Partition of foraging grounds and conveying information among ants. Acta Biologiae Experimentalis, Warsaw 18:55-67.

Dobrzanski, J. 1966. Contribution to the ethology of Leptothorax acervorum. Acta Biologiae Experimentalis, Warsaw 26: 71-78.

Fletcher, D.J.C., and J.M. Brand. 1968. Source of the trail pheromone and method of trail laying in the ant Crematogaster peringueyi. J. Insect Physiol. 14: 783-788.

Forel, A. 1928. The social world of ants compared with that of man. (tr. C.K. Ogden) Two volumes. G.P. Putnam & Sons Ltd., London. xlv + 551, xx + 445 pp.

Hangartner, W. 1967. Spezifität und Inaktivierung des Spurpheromons von Lasius fuliginosus Latr. und Orientierung der Arbeiterinnen im Duftfeld. Z. vergl. Physiologie 57: 103-136.

__________, 1969. Structure and variability of the individual odor trail in Solenopsis geminata. Z. vergl. Physiologie 62: 111-120.

Hingston, R.W.G. 1929. Instinct and Intelligence. MacMillan Co., N.Y. xv + 296 pp.

Hölldobler, B.K. 1971a. Recruitment behaviour in Camponotus socius. Z. vergl. Physiologie. 75: 123-142.

__________, 1971b. Homing in the harvester ant Pogonomyrmex badius. Science 171: 1149-1151.

__________, 1975. Communication in social Hymenoptera. In: How Animals Communicate (T. Sebeok, ed.). Indiana University Press, Bloomington.

__________, 1976. Tournaments and slavery in a desert ant. Science 192: 913-914.

__________, and E.O. Wilson. 1970. Recruitment trails in the harvester ant Pogonomyrmex badius. Psyche, Cambridge 77: 385-399.

__________, M. Möglich, and U. Maschwitz. 1974. Communication by tandem running in the ant Camponotus sericeus. J. comp. Physiol. 90: 105-127.

Horstmann, K. 1973. Untersuchen zur Arbeitsteilung unter den Aussendienstarbeiterinnen der Waldameise *Formica polyctena* Foerster. Z. Tierpsychologie *32*: 532-543.

Hunt, J.H. 1974. Temporal activity patterns in two competing ant species. Psyche, Cambridge *81*: 237-242.

Jacobs-Jessen, U.F. 1959. Zur Orientierung der Hummeln und einiger anderer Hymenopteren. Z. vergl. Physiologie *41*: 597-641.

Jander, R. 1957. Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa* L.). Z. vergl. Physiologie *40*: 162-238.

Leuthold, R.H. 1968. A tibial gland scent trail and trail-laying behavior in the ant *Crematogaster ashmeadi* Mayr. Psyche, Cambridge *75*: 223-248.

Maschwitz, U., B. Hölldobler, and M. Möglich. 1974. Tandemlaufen als Rekrutierungsverhalten bei *Bothroponera tesserinoda* (Formicidae:Ponerinae). Z. Tierpsychologie *35*: 113-123.

Möglich, M. and B. Hölldobler. 1975. Communication during emigration and foraging in the ant *Formica fusca*. J. comp. Physiol. *101*: 275-288.

Moser, J.C., and M.S. Blum. 1963. Trail-marking substance of the Texas leaf-cutting ant: source and potency. Science *140*: 1228.

Otto, D. 1958. Uber die Arbeitsteilung im Staate von *Formica rufa rufo-praetensis minor* Gossw. und ihre *verhaltenphysiologischen Grundlagen*: Ein Beitrag zur Biologie der Roten Waldameise. Wissenschaftliche Abhandlungen der Deutschen Akademie Landwirtschaftswissenschaften zu Berlin *30*: 1-169.

Rosengren, R. 1971. Route fidelity, visual memory, and recruitment behavior in foraging food ants of the genus *Formica*. Acta zool. Fenn. *133*: 3-106.

Santschi, F. 1911. Observations et remarques critiques sur le mecanisme de l'orientation chez les fourmis. Revue Suisse de Zoologie *19*: 303-338.

Szlep-Fessel, R. 1970. The regulatory mechanisms in mass foraging and recruitment of soldiers in *Pheidole*. Insectes Sociaux *17*: 233-244.

Szlep, R., and T. Jacobi. 1967. The mechanism of recruitment to mass foraging in colonies of *Monomorium venustrum* Smith, *M. subopacum* ssp. *phoenicum* Em., *Tapinoma israelis*

For. and *T. simothi* v. *phoenicum*. Insectes Sociaux 14: 25-40.

Stäger, R. 1931. Uber das Mitteilungsvermogen der Waldameise beim Auffinden und Transport eines Beutesstückes. Zeitschrift fur Wissenschaftliche Insektenbiologie 26: 125-137.

Sturdza, S.A. 1942. Beobachtungen über die stimulierende Wirkung lebhaft beweiglicher Ameisen auf träge Ameisen. Bulletin de la Section Scientifique de L'Academie Roumaine 24: 543-546.

Sudd, J.H. 1957. Communication and recruitment in Pharaoh's ant, *Monomorium pharaonis* L. Animal Behaviour 5: 104-109.

__________, 1967. *An Introduction to the Behaviour of Ants*. St. Martin's Press. viii + 200 pp.

Topoff, H., M. Bosches, and W. Trakimas. 1972. A comparison of trail following between callow and adult workers of the army ant *Neivamyrmex nigrescens* (Formicidae: Dorylinae). Animal Behavior 20: 261-266.

Vowles, D.M. 1950. The sensitivity of ants to polarized light. Nature, London, 165: 282-283.

__________, 1954. The orientation of ants. I. The substitution of stimuli. II. Orientation to light, gravity, and polarized light. J. exp. Biol. 31: 341-375.

Wallis, D.I. 1962. Behaviour patterns of the ant *Formica fusca.* Animal Behaviour 3: 1-13.

__________, 1964. The foraging behaviour of the ant *Formica fusca*. Behaviour 23: 149-175.

Watkins, J.F. 1964. Laboratory experiments on the trail following of army ants of the genus *Neivamyrmex* (Formicidae: Dorylinae). Journal of the Kansas Entomological Society, 37: 22-28.

Wehner, R., and R. Menzel. 1969. Homing in the ant *Cataglyphis bicolor*. Science 164: 192.

Wilson, E.O. 1958. A chemical releaser of alarm and digging behavior in the ant *Pogonomyrmex badius* (Latreille). Psyche, Cambridge 66: 29-34.

__________, 1959. Communication by tandem running in the ant genus *Cardiocondyla*. Psyche, Cambridge, 66: 29-34.

__________, 1962a. Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. Bulleting of the Museum of Comparitive Zoology, Harvard, 127: 403-422.

__________, 1962b. Chemical communication among workers of the fire ant Solenopsis saevissima (Fr. Smith). 1. The organization of mass foraging. 2. An information analysis of the odour trail. 3. The experimental induction of social responses. Animal Behaviour 10: 134-164.

__________, 1965. Trail sharing in ants. Psyche, Cambridge 72: 2-7.

__________, 1971. The Insect Societies. Belknap Press of Harvard University. x + 548pp.

__________, 1975. Enemy specification in the alarm/recruitment system of an ant. Science 190: 798.

__________, and T. Eisner. 1957. Quantitative studies on liquid food transmission in ants. Insectes Sociaux 4: 157-166.

__________, and M. Pavan. 1959. Glandular sources and specificity of some chemical releasers of social behavior in dolichoderine ants. Psyche, Cambridge 66: 70-76.

__________, and F.E. Regnier. 1968. The alarm/defense system of Acanthomyops claviger. J. Insect Physiol. 14: 955-970.

__________, and ____________. 1969. The alarm/defense system of Lasius aliennus. J. Insect Physiol. 15: 893-898.

__________, and ____________. 1971. The evolution of the alarm/defense system in the formicine ants. American Naturalist 105: 279-289.

RECRUITMENT BEHAVIOR, ORIENTATION, AND THE ORGANIZATION OF FORAGING IN THE CARPENTER ANT CAMPONOTUS PENNSYLVANICUS DEGEER (HYMENOPTERA:FORMICIDAE) *

by

James F.A. Traniello †

Department of Entomology, University of Massachusetts,
Amherst, Massachusetts. 01002

---

* Paper No. 2048, Massachusetts Agricultural Experiment Station. This research supported (in part) from Experiment Station Project No. 357.

† Current address: Department of Biology, Harvard University, Cambridge, Massachusetts. 02138

ABSTRACT

Scout ants of Camponotus pennsylvanicus recruit nestmates to new food sources with alterting motor displays. Workers subsequently leave the nest and follow a recruitment trail composed of hindgut material and formic acid to the food. Hindgut material, which is also deposited on the trail by foraging ants, functions as a long-lasting olfactory orientation cue between the food source and the nest, whereas formic acid makes the recruitment trail highly attractive to stimulated ants. Hindgut trails, which may also have a mild recruitment effect, are important orientation cues during foraging. Foragers may also make use of visual cues. Mass foraging is regulated by the motor displays of recruiting ants. Starvation increases the recruitment response of the colony by intensifying the behavioral displays of recruiting ants. As increasing amounts of food are transported to the colony, the number of foragers diminishes. The majority of foraging is conducted by a relatively small number of ants of a certain age group. 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.

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 which 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 5-20 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 which 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 *Solenopsis* the potent trail substance functions both as an orientation and alerting signal (Wilson, 1962). In 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 which approaches mass communication.

The genus *Camponotus* is especially interesting for studying the evolution of recruitment behavior since a series of intermediates which show various degrees of advancement in communication techniques exist 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 discharged from the hindgut of the leader permits the following ant to orient olfactorily. However, the leader must halt periodically so that its follower can regain mechanical contact. 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 (Hőlldobler, 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 which 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 videotape recordings.

Orientation experiments were based on a method used to 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 labelling a sucrose solution with radioactive phosphorus (P^{32} as H_3PO_4 in acid-free water, New England Nuclear, Boston, Mass.). Samples were placed in a PPO/toluene fluor and counted with a Beckman LS-150 liquid scintillation counter. Additional methods will be presented concurrent with individual experiments.

EXPERIMENTS AND 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 (Fig. 1a). 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 2 or 3 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 2 halves and a glass slide (75 mm x 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 2 shows the trail-laying posture of a worker and the structure of the trail. The thin lines composing the trail are produced by a group of perianal hairs. In comparison with the control (normal walking posture) it can be seen that "footprint" areas are exaggerated. This is most likely produced by an increase in the number of tarsal segments which grip the substrate in order to maintain contact with the gaster tip.

2. <u>The source of trail substance and its significance during foraging</u>.

The above 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 3 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 .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 activities. The nest arrangement used is shown in Figure 1a. 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 10μl of each extract was drawn. During the next 10 minutes, 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, as 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 as at least an orientation cue during foraging. This is the case in other formicine ants (Hölldobler, 1971; Möglich and Hölldobler, 1975). There is additional evidence to indicate that this is also true in Camponotus pennsylvanicus, as the following experiments suggest.

A colony of ants was connected to a circular foraging arena. Ants entered the center of the arena through a piece of tubing (Fig. 1b). 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 minutes. 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 10μl of hindgut extract (5 hindguts in .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 minutes the directions taken by individual foragers were recorded by noting the positions of ants as they crossed over the 3 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 3 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. 4). Since visual cues were eliminated by conducting the foraging runs in dim red light, it is apparent that ants on foraging routes orient by means of olfactory cues provided by hindgut contents which are deposited on the trail by foraging ants.

The above experiments were only concerned with olfaction; they do not exclude the possibility that visual cues, if present, are also used. Other ants species are known to utilize visual cues to various degree during foraging (Hölldobler, 1970; Wehner and Menzel, 1969; Jander, 1957). 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 minutes 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 minutes 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. 5). 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. These ants oriented randomly in the arena.

4. Conclusions

From these experiments I concluded that foraging ants follow trails of hindgut contents. Hindgut material is an important orientation cue during foraging, but as ants make repeated foraging runs they may also make use of visual cues. The possibility that hindgut material also serves the function of a recruitment signal will be considered in the next section.

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 5-10 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 Moglich 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 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 5 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 labelling 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 minutes, after which each ant was assayed for radioactivity. From the data presented in Fig. 6 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 minutes 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.

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 which is chemically coded in the trail itself. 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. Thus recruitment may proceed in the absence of a leader ant. Alerted nestmates readily follow the recruitment trail and arrive at the target area. The various interactions between the initial recruiter and the colony are summarized in Table 2.

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 laid 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 the recruitment trail is composed of hindgut material and poison gland secretion, formic acid (Hölldobler, 1971). A distinct 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 .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 five minutes 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 trails was recorded within the first 5 minutes following the return of the scout. To summarize the two conditions of these experiments, the alerting displays of a recruiter were provided only in the second series. Results are given in Tables 3 and 4.

These results demonstrate two important points. First of all, from Table 3 it can be inferred that hindgut material is a strong olfactory signal which is readily followed in the absence of alerting displays. This suggests that trail pheromone itself may constitute a recruitment signal. Secondly,

Table 4 indicates that dependent upon context, trails are responded to differently. In particular, a comparison between Tables 3 and 4 suggests that a trail of hindgut material and poison gland secretion is more attractive to ants which have been previously stimulated by a recruitment display. Ants not previously alerted respond to the same trail differently. Many ants encountering a hindgut/poison gland trail in this situation did not respond positively, but ran off with open mandibles or returned quickly to the nest. Similarly, the response to a hindgut trail decreased if ants were 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.

These results seem to imply that although the hindgut pheromone alone is highly attractive, 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 follow a trail of hindgut material plus a glandular secretion. Since the contents of Dufour's gland and poison gland have been identified as n-undecane and formic acid respectively (Ayre and Blum, 1971), I drew out .5μl of undecane or formic acid with a microsyringe over the 50 cm trail. Only those ants which 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. The results of this experiment are presented in Table 5.

This experiment shows 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 release 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 trail was also highly attractive to alerted ants, it seems likely that this is the composition of the recruitment trail.

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 were 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. 7). 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 effects, a colony of 250 workers were separated in the same nest by means of a double wire mesh screen (Fig. 1c). 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 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 both involved in the regulation of foraging. Motor displays are predominant during the first and second return trips to the nest (Fig. 8). 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 ($\leq$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 an 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 which has previously been a recruiter solicits food from a forager which 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. Divison 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). 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 1 month period. During each trial the number of foraging trips made by individual workers and the consistency of their participation in foraging was recorded. Based on the records of individual foragers the following relative foraging index (RFI) was developed:

$$\mathrm{RFI} = \frac{N}{EN}\,(100)\;(C)$$

where N is the number of trips made by an individual forager, EN is the summation of all foraging trips made by all foragers, 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 Fig. 9 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 which 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 .197 ± .063 mm, range .1-.35 mm). An intermediate group of workers engaged in comparatively little foraging.

4. Conclusions

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 then 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 shut-off of foraging activity. Only ants of a particular age bracket consistently respond to recruitment signals and participate in foraging.

DISCUSSION

The recruitment process of Camponotus pennsylvanicus initiates and regulates foraging activities. Scout ants return from newly discovered food sources dragging their abdominal tips over the ground laying chemical trails. Inside the nest the scout engages in fast running, ritual food offering, and encounters nestmates head-on with waggle motor displays. Nestmates of a certain age group alerted by the recruitment activity of the scout leave the nest and follow the previously laid trail; the scout does not "guide" the recruited group to the food. Recruited ants subsequently return to the nest to perform their own displays and lay down additional trail material. Although the trail is an important olfactory orientation signal, experienced foragers may also use visual cues and eventually recognize the environmental configuration around their foraging route. A nutritional feedback mechanism coupled with a "decay" of the recruitment activities of foraging ants, regulates foraging activities.

Foraging trails are composed of accretions of hindgut material, whereas the initial recruitment trail is apparently composed of hindgut material and poison gland secretion. The latter trail functions as an orientation cue and an excitatory signal which is highly attractive to ants previously alerted by recruitment displays. Since poison gland secretion (formic acid) is highly volatile, it quickly evaporates leaving a long-lasting hindgut orientation trail. It seems that fresh recruitment trails of hindgut contents and poison gland secretion are necessary to divert ants from existing hindgut trials to new food sources. A similar situation occurs in Camponotus socius, as ants on recruitment trails cross older hindgut trails without distraction (Hölldobler, 1971).

There are two aspects of this study which should be emphasized. First of all, 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 which 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 which 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 which may serve as more than just an orientation cue. Recently, Barlin et al. (1976) have chromatographically identified the hindgut pheromone, which is specific for C. pennsylvanicus, as a single peak. Again, the role of hindgut material is different in C. socius as 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,1970; et al.). 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 _C. socius_ or _Formica fusca_. Hölldobler (1975) 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.

ACKNOWLEDGMENTS

I wish to express my most sincere appreciation to Dr. H.H. Hagedorn, Dr. A.M. Stuart, and Dr. E.L. Goldstein for their assistance in this research. I would also like to thank Ms. Dina A. Brown for her assistance in preparing the manuscript.

REFERENCES

Ayre, G. L., and M. S. Blum. 1971. Attraction and alarm of ants (Camponotus spp. - Hymenoptera:Formicidae) by pheromones. Physiol. Zool. 44:77-83.

Barlin, M. R., M. S. Blum, and J. M. Brand. 1976. Species-specificity studies on the trail pheromone of the carpenter ant Camponotus pennsylvanicus. J. Georgia Ent. Soc. 11:162-164.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. AIBS Monograph, American Institute of Biological Sciences.

Bhatkar, A., and W. H. Whitcomb. 1970. Artificial diet for rearing various species of ants. Florida Entomologist 53:229-231.

Blum, M. S. 1974. Pheromonal sociality in the Hymenoptera. In: Pheromones. M. Birch, Ed. North Holland Publishing Co., Amsterdam, xi + 495 pp.

__________, and E. O.Wilson 1964. The anatomical source of trail substances in formicine ants. Psyche 71:28-31.

Brun, R. 1914. Die Raumorientierung der Ameisen und das Orientierungsproblem im allgemeinen. Gustav Fischer, Jena. viii + 234 pp.

Buckingham, E. N. 1911. Division of labor among ants. Proceedings of the American Academy of Arts and Sciences 46:425-507.

Hangartner, W. 1967. Spezifitat und Inaktivierung des Spurpheromons von _Lasius fuliginosus_ Latr. und Orientierung der Arbeiterinnen im Duftfeld. Z. vergl. Physiol. 57:103-136.

____________. 1969. Trail-laying in the subterranean ant _Acanthomyops claviger_. J. Insect Physiol. 15: 1-4.

Hingston, R. W. G. 1929. Instinct and Intelligence. Macmillan, New York.

Hölldobler, B. K. 1970. Homing in the harvester ant _Pogonomyrmex badius_. Science 161:1149-1150.

____________ 1971. Recruitment behavior in _Camponotus socius_. Z. vergl. Physiologie 75:123-142.

____________. 1975. Communication in social Hymenoptera. _In:_ How animals communicate (T. Sebeok, ed.). Bloomington, Indiana, University Press.

____________, M. Möglich, and U. Maschwitz. 1974. Communication by tandem running in the ant _Camponotus sericeus_. J. comp. Physiol. 90:105-127.

Maschwitz, U., B. Hölldobler, and M. Möglich. 1974. Tandemlaufen als Rekrutierungsverhalten bei _Bothroponera tesserinoda_ (Formicidae:Ponerinae). Zeitschrift fur Tierpsychologie 35:113-123.

Möglich, M., and B. Hölldobler. 1975. Communication and orientation during foraging and emigration in the ant _Formica fusca_. J. comp. Physiol. 101:275-288.

Jander, R. 1957. Die optische Richtungorientierung der Roten Waldameise (_Formica rufa_ W.). Z. vergl. Physiologie 40:162-238.

Otto, D. 1958. Über die Arbeitsteilung im Staate von Formica rufa rufo-pratensis minor Gössw. und ihre verhaltensphysiologischen Grundlagen: Ein Beitrag zur Biologie der Roten Waldameise. Wissenschaftliche Abhandlungen der Deutschen Akademie der Landwirtschaftswissenschaften zu Berlin 30:1-169.

Rossengren, R. 1971. Route fidelity, visual memory and recruitment behavior in foraging wood ants of the genus Formica (Hymenoptera:Formicidae). Acta zool. Fenn. 133:3-106.

Szlep-Fessel, R. 1970. The regulatory mechanisms in mass foraging and recruitment of soldiers in Pheidole. Insects Sociaux 17:233-244.

Szlep, R., and T. Jacobi. 1967. The mechanism of recruitment to mass foraging in colonies of Monomorium venustum Smith, M. subopacum ssp. phoenicium Em., Tapinoma israelis For. and T. simothi v. phoenicium Em. Insects Sociaux 14:25-40.

Voss, C. 1967. Uber das Formensehen der roten Waldameise (Formica rufa-Gruppe). Z. vergl. Physiologie 55:225-254.

Wehner, R., and R. Menzel. 1969. Homing in the ant Cataglyphis bicolor. Science 164:192-194.

Wilson, E. O. 1959. Communication by tandem running in the ant genus Cardiocondyla. Psyche 66:29-34.

___________. 1962. Chemical communication among workers of the fire ant Solenopsis saevissima (Fr. Smith). 1. The organization of mass-foraging. 2. An information analysis of the odour trail. 3. The experimental induction of social responses. Anim. Behav. 10:134-164.

___________. 1965. Trail-sharing in ants. Psyche 72: 2-7.

___________. 1971. The Insect Societies. Belknap Press, Harvard University, Cambridge, Massachusetts, 548 pp.

___________, and T. Eisner. 1957. Quantitative studies on liquid food transmission in ants. Insectes Sociaux 4: 157-166.

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

Table 2.

The interactions between a scout ant and nestmates upon the return of the scout to the nest.

Number of Observations	Scout remains in nest; nestmates leave ahead of scout	Recruited ants proceed behind scout	Recruited ants overtake scout	Scout quickly returns to food in advance of nestmates
30	18	2	5	5

Table 3.

The following response of ants to 50 cm. artificial trails drawn out from the nest entrance. A positive response is equivalent to trail following for at least 10 cm. Responses were recorded during a 5 minute period. In this situation a hindgut trail is readily followed in the absence of recruitment displays. 10 replicates.

	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

Table 4.

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

	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.)	40.3	32.1	47.1

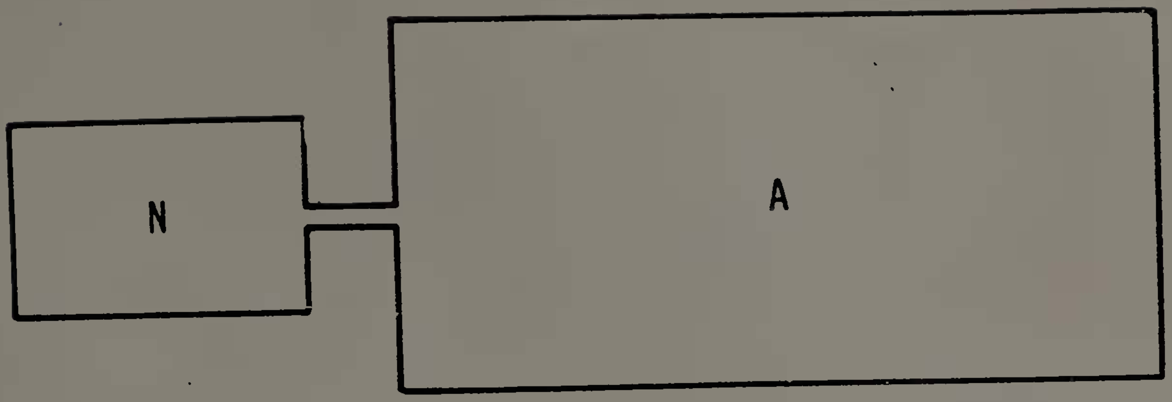
Table 5.

Response of recruited ants to trails of hindgut material and synthetic glandular products. A fed scout was allowed to return to the nest and recruit nestmates. Recruits proceeded along a Y-shaped trail consisting of a short 4cm section of hindgut material alone and two longer trails which diverged at an angle of 90°. At the point where the 4cm hindgut trail diverged recruits had a choice of following either branch of the trail. The artificial trails of either branch (Trails 1 and 2) were varied and the response of recruits recorded. The mean number of ants following at least half way on either trail was significantly different (.02<p<.05) only for a trail composed of hindgut material and formic acid; 10 replicates. NS = no significant difference.*

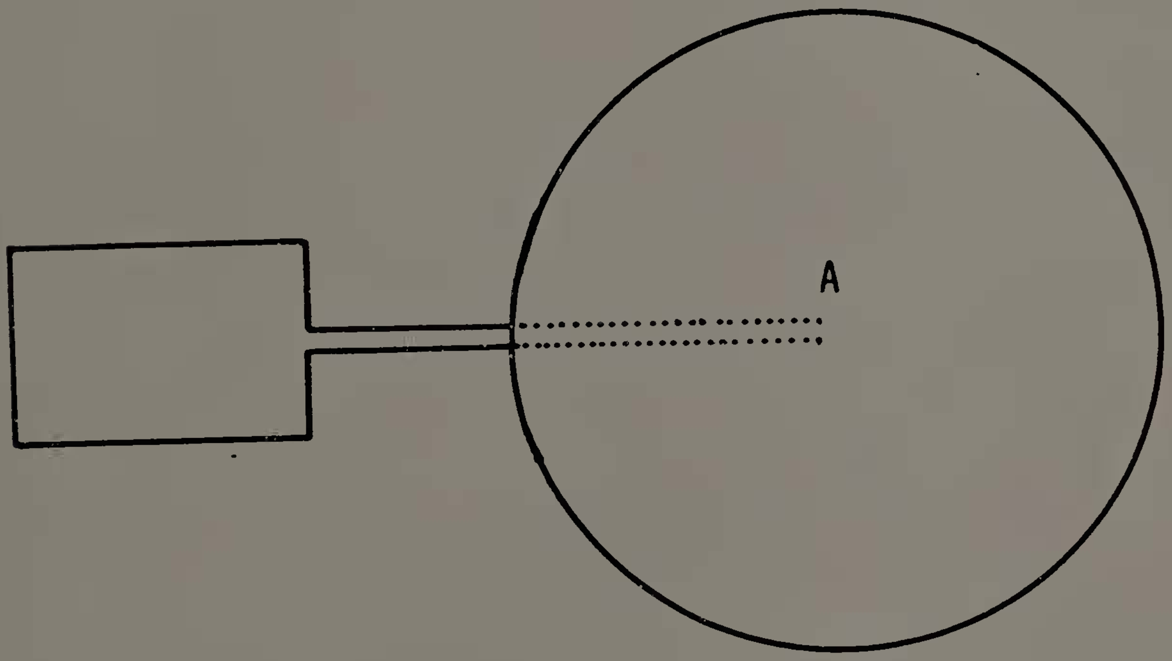
	MEAN NO. OF ANTS ON EACH TRAIL	RANGE
TRAIL 1 (HINDGUT)	5.5 (NS)	1-13
TRAIL 2 (HINDGUT)	5.6	1-16
TRAIL 1 (HINDGUT)	3.5 (NS)	0-15
TRAIL 2 (HINDGUT + UNDECANE)	2.5	0-15
TRAIL 1 (HINDGUT)	2.4 *	0-7
TRAIL 2 (HINDGUT + HCOOH)	10.5	1-24

Figure 1. Laboratory nests. a) Nest connected to foraging arena used in recruitment experiments. b) Nest connected to circular arena used in orientation experiments. c) Nest used to keep two groups of workers from same colony in different starvation regimes, separated by two wire mesh screens. N = nest, A = arena, G = gates used to route scouts to different nests, F = location of food in nest type c.

a)



b)



c)

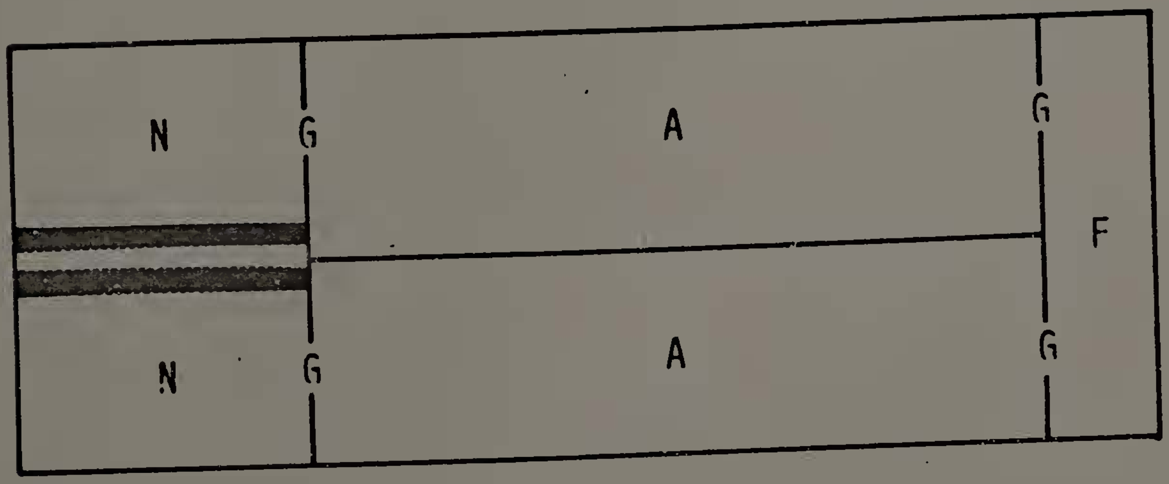
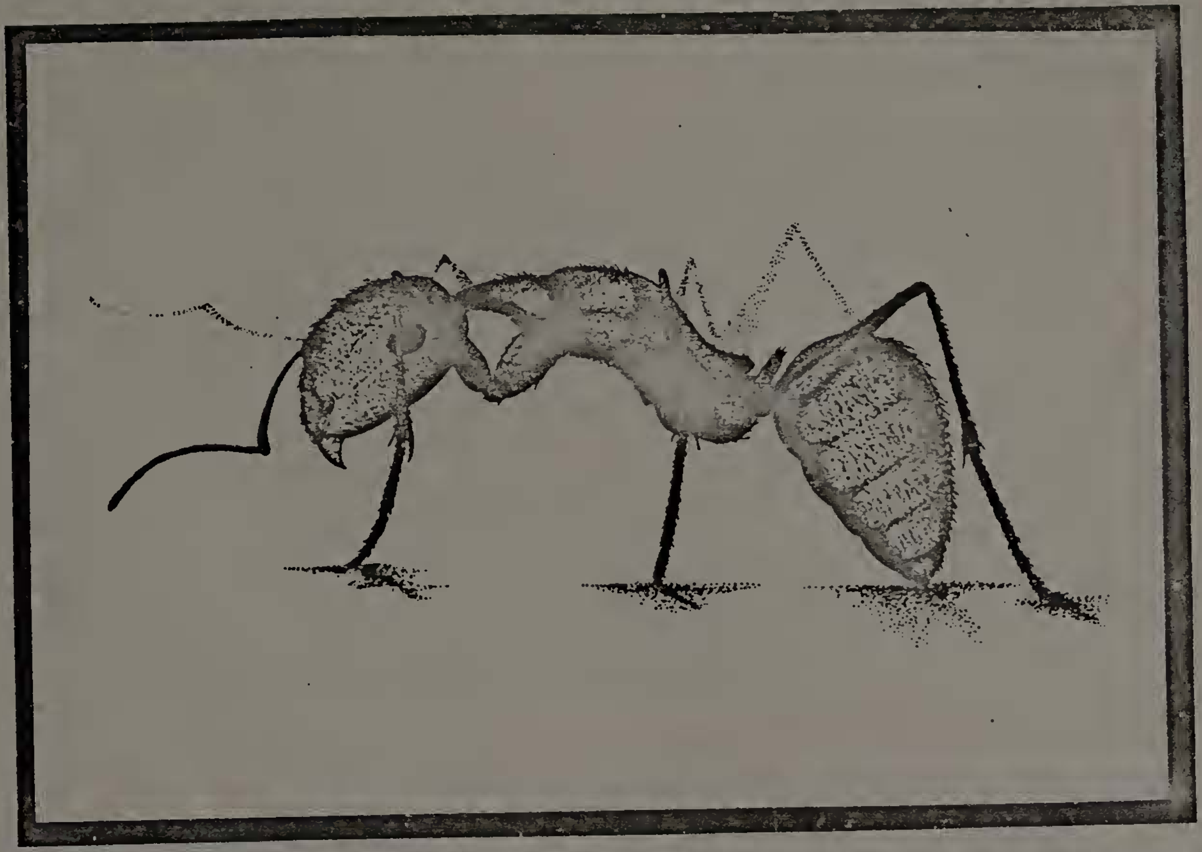


Figure 2. Worker of Camponotus pennsylvanicus in trail-laying posture, with photographs made from smoked glass slides showing normal walking posture (control) and the nature of the trail. Drawing from videotape recording.



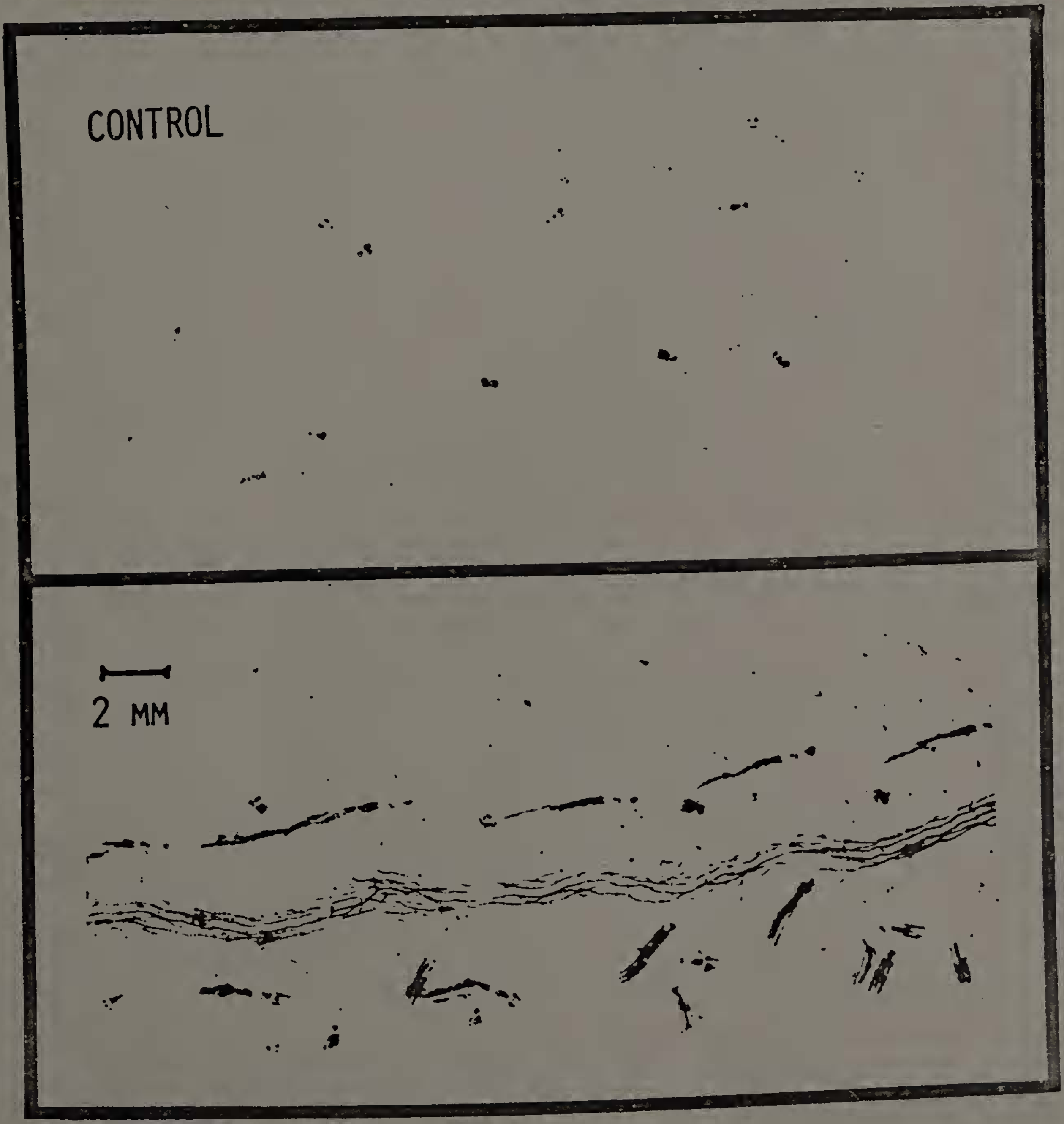

CONTROL
2 MM

Figure 3. Orientation of foragers in the circular arena to a hindgut trail. An artificial trail of 10 microliters of hindgut material was drawn from the center entrance of the arena to a food source (F) at the periphery of one sector. An inaccessible food source (F') was placed at the end of a distilled water trail drawn out from the center in the opposite direction. Postions of individual foragers were recorded as they crossed concentric circles with radii of 5, 10, and 20 cm. The mean direction of all foraging runs is represented by an arrow whose length r is a measure of the dispersion about the mean direction. r^{5}*=.39,* r^{10}*=.60, and* r^{20}*=.79. All results are highly significant.* ● = *2 ants,* ○ = *1 ant.*

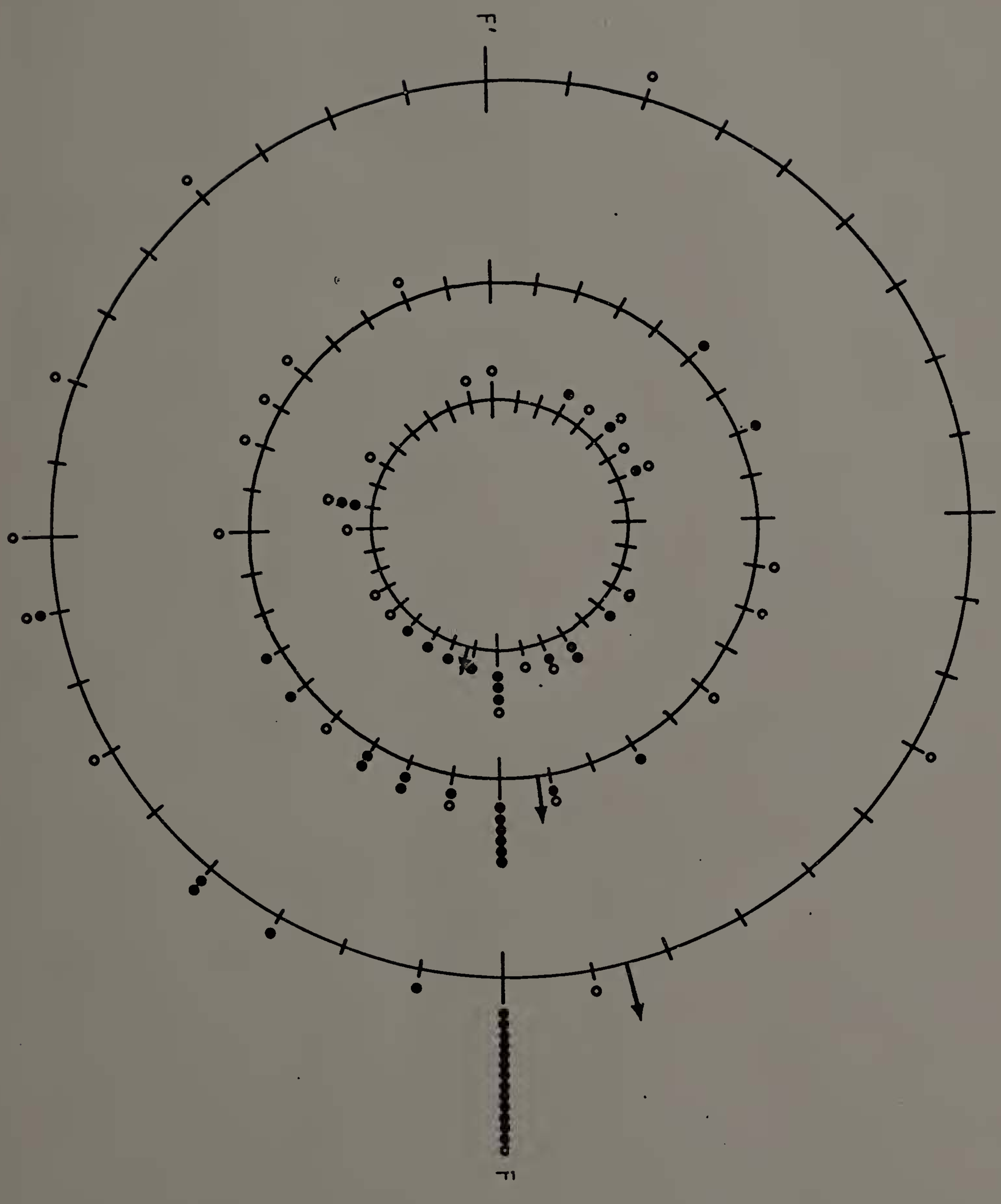

F'
F'

Figure 4. Orientation of foragers in the circular arena after a 90° rotation of the hindgut trail and food source. $r^{5}=.57$, $r^{10}=.63$, $r^{20}=.52$. All results are highly significant. F = food source; F' = inaccessible food source; ● = 2 ants; o = 1 ant. For further explaination see Fig. 3, methods, and text.

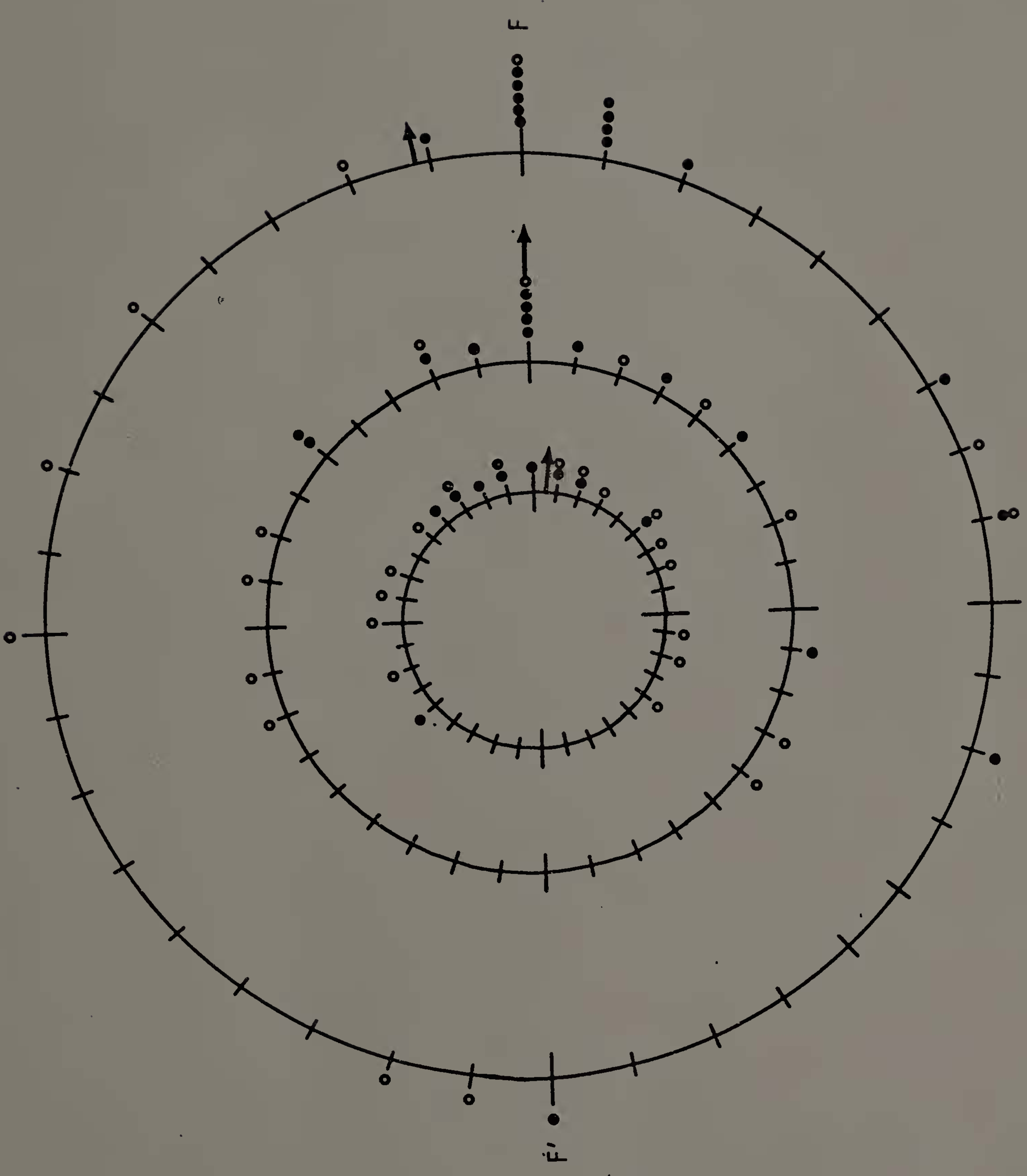

F
F'

Figure 5. Orientation of foragers in circular arena to visual cue after removal of hindgut trail. Ants were allowed to forage at food source F for 45 minutes along a hindgut trail. During this period all workers appearing at the food were marked. The bottom of the arena was then replaced with clean disk and the individual runs of the foragers recorded. r^5=.64, r^{10}=.45, and r^{20} =.75. All results are highly significant. F' = inaccessible food source; ● = 1 ant; ■ = unmarked ("inexperienced") ant; ▨ ▨ = visual cue.

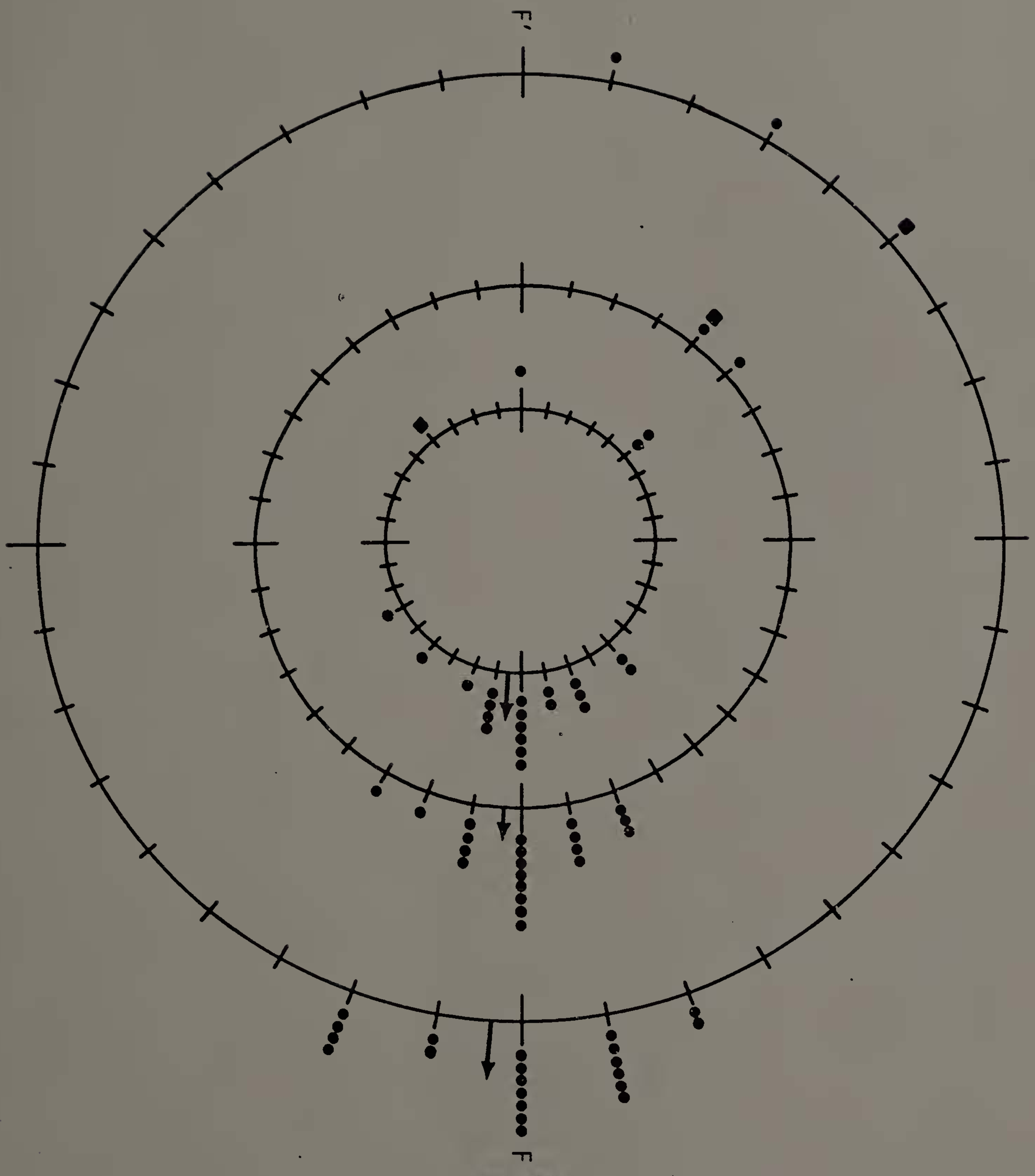
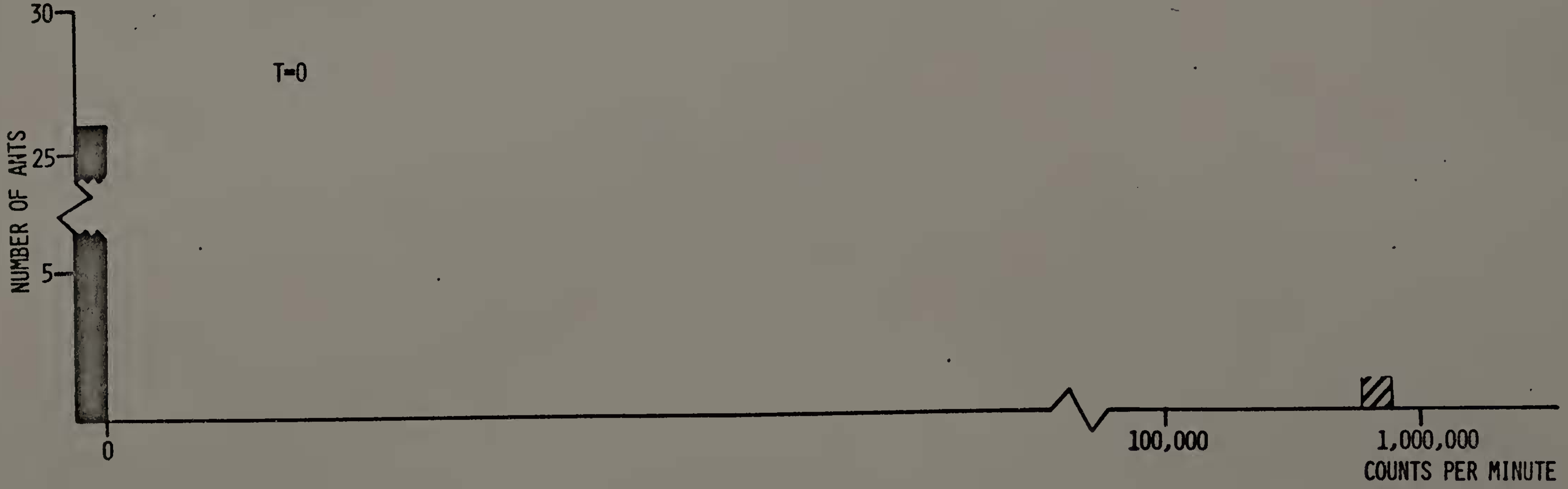

F′
F

Figure 6. Food transfer from scout to nestmates. A single scout was allowed to feed at a P^{32}-labeled sucrose bait and return to a small colony to engage in food transfer with nestmates. After 10 minutes individual ants were assayed for radioactivity. 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 the 10 minute period. Only ants with at least double the amount of background radiation are represented in this figure. ■ *=. food recipients;* ▨ *= scout.*


T=0
NUMBER OF ANTS
30
25
5
0
100,000
1,000,000
COUNTS PER MINUTE

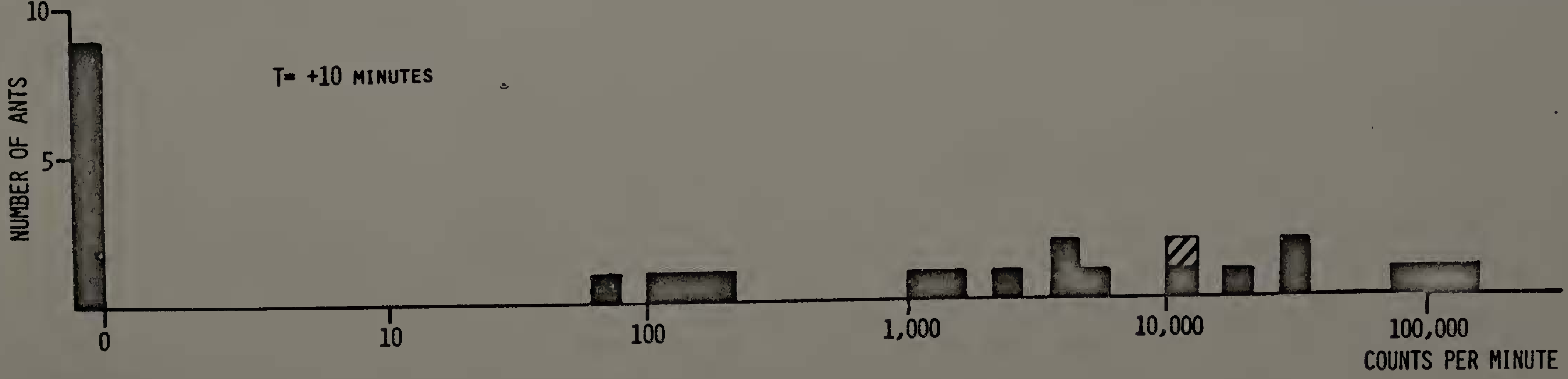

T= +10 MINUTES
NUMBER OF ANTS
10
5
0
10
100
1,000
10,000
100,000
COUNTS PER MINUTE

Figure 7. The recruitment response of a colony after 3, 5, and 7 day starvation periods. Each point is the sum of 3 replicates. – ——— – ———= 3 days; - - - - - - - - - - = 5 days, ———————————— = 7 days.

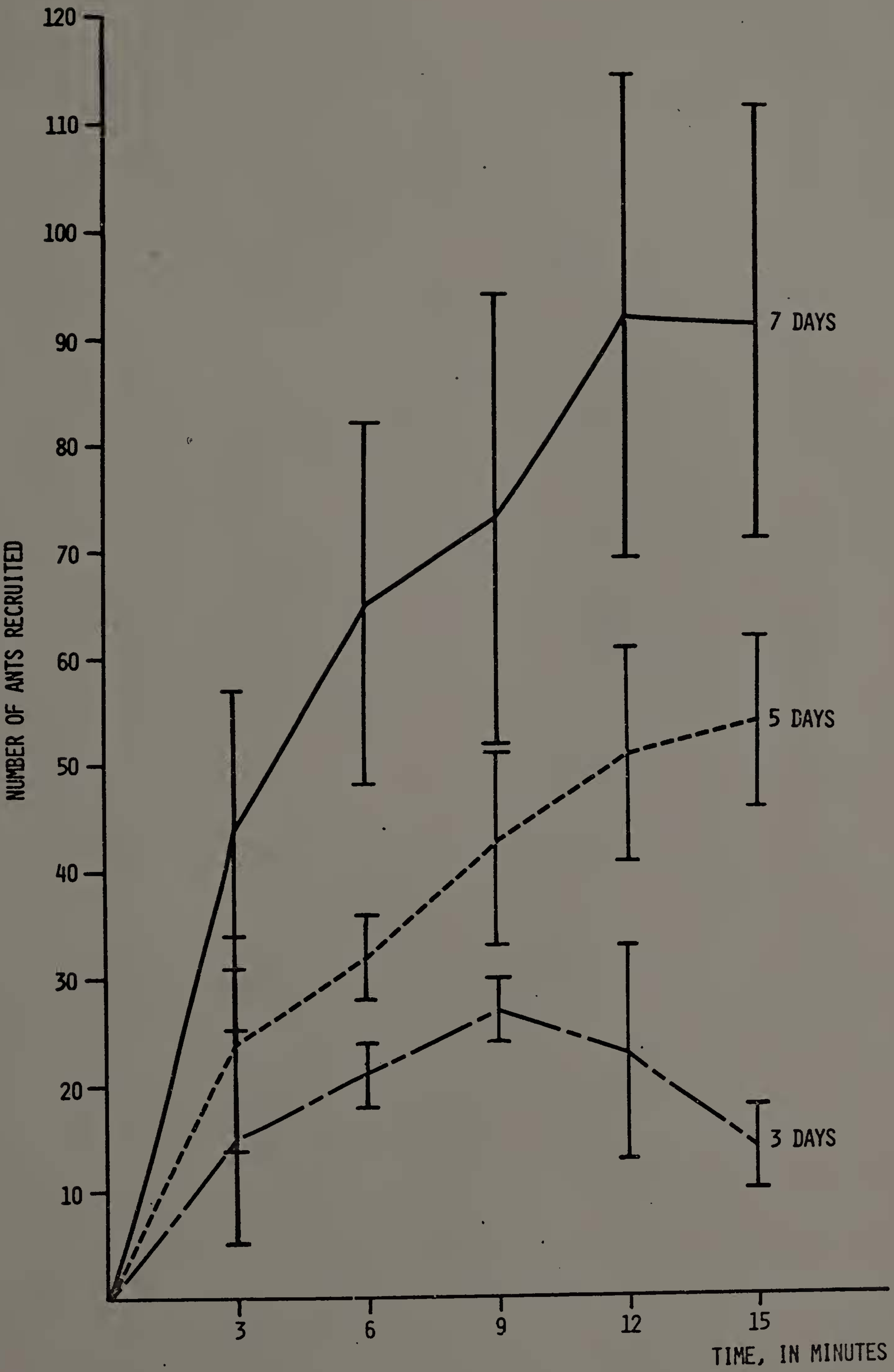

120
110
100
90
80
70
60
50
40
30
20
10
NUMBER OF ANTS RECRUITED
3
6
9
12
15
TIME, IN MINUTES
7 DAYS
5 DAYS
3 DAYS

Figure 8. Changes in recruiter behavior during the organization of foraging. The recruitment behavior and frequency of food transfer with nestmates of scout ants was observed as they made successive trips to the food and returned to the nest. The motor components of a recruitment display gradually drop out of the recruiter's beahvior. Foraging typically ended before a recruiter could make six trips to the food. ☐ = fast runs; ▨ = waggle displays; ■ = mean number of ants engaging in food transfer with recruiter. N = number of observations.

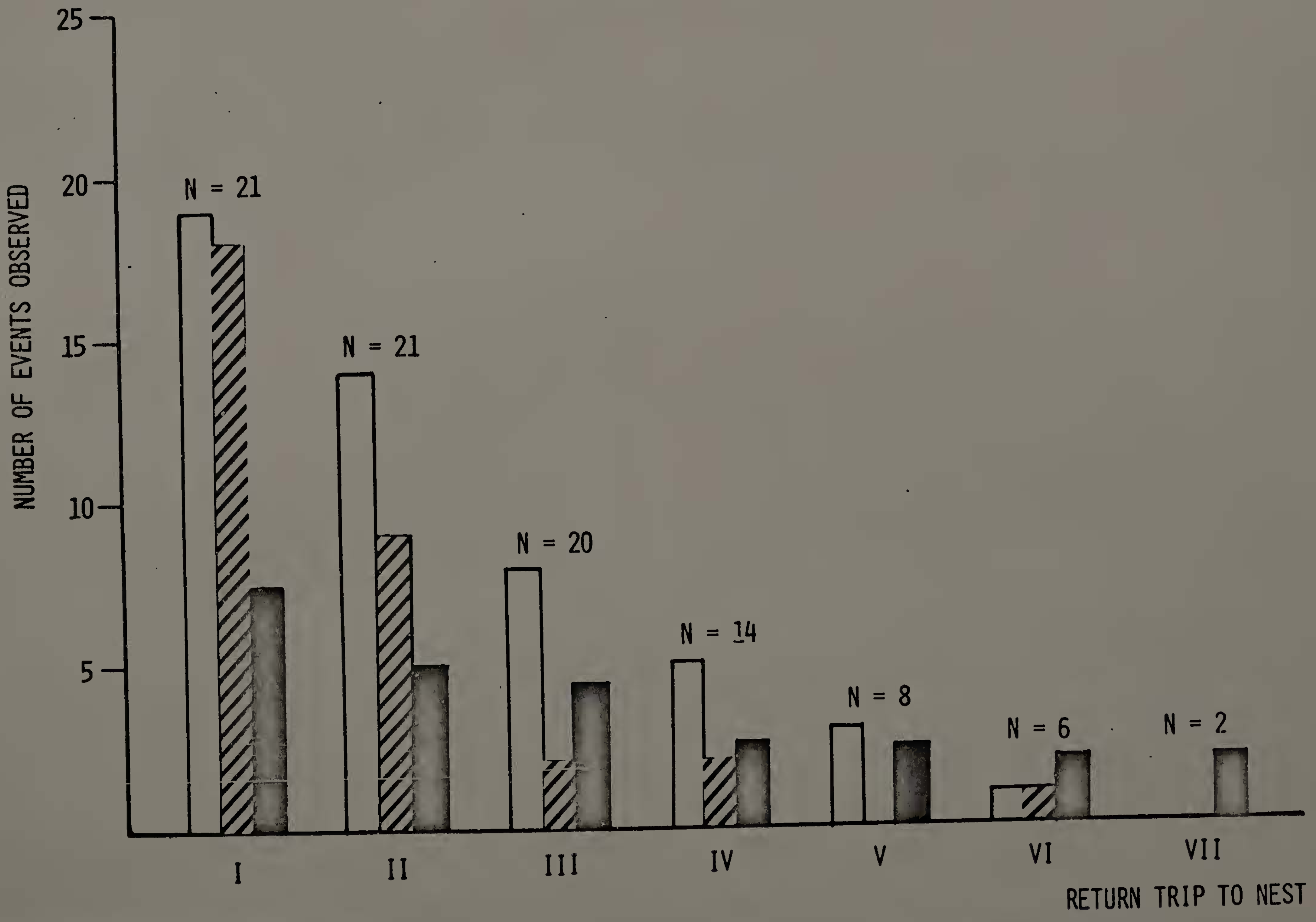
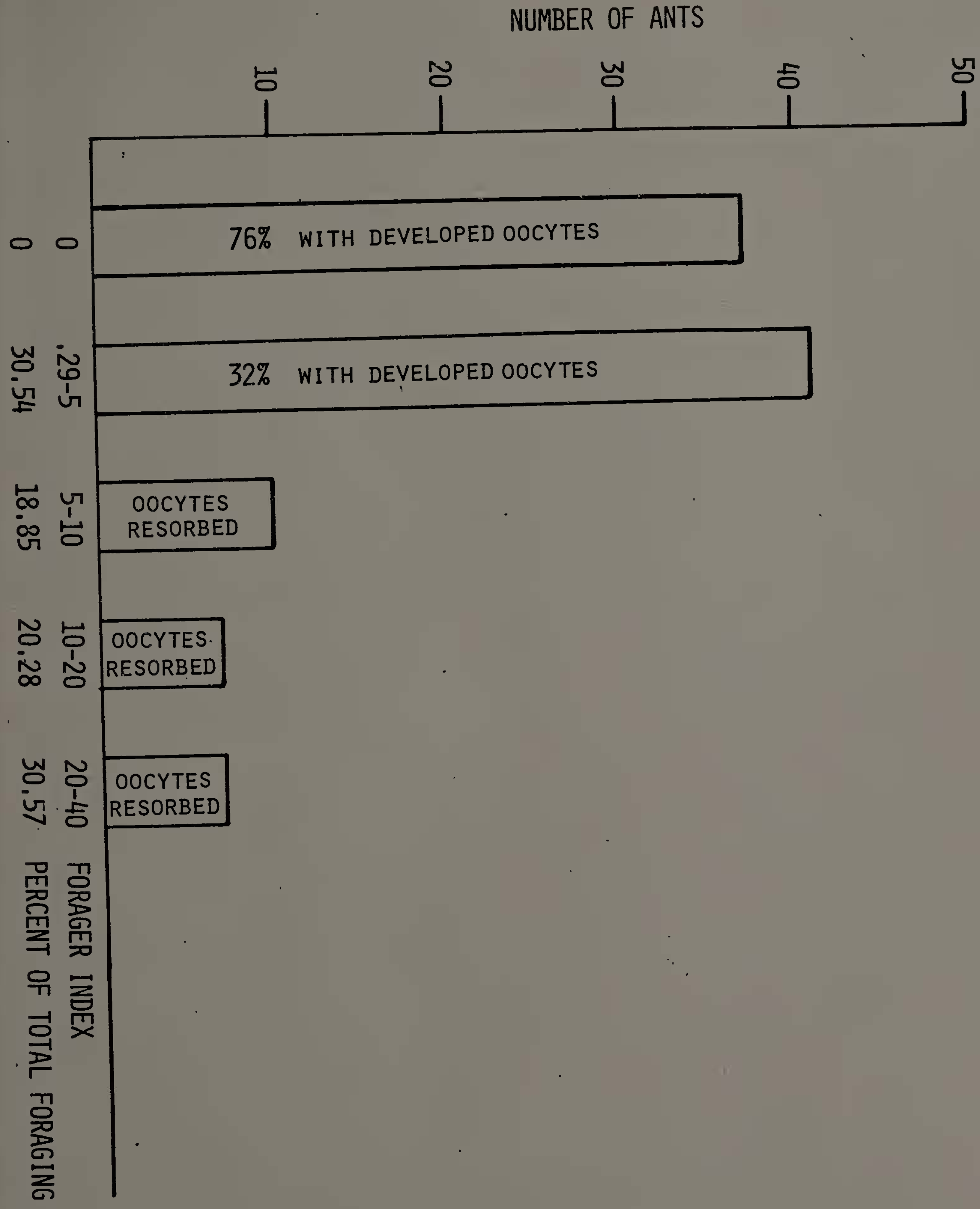

NUMBER OF EVENTS OBSERVED
25
20
15
10
5
N = 21
N = 21
N = 20
N = 14
N = 8
N = 6
N = 2
I
II
III
IV
V
VI
VII
RETURN TRIP TO NEST

Figure 9. Histogram showing the division of labor during foraging. Each individual in a colony of 102 workers was individually color coded and their foraging activities recorded during eight recruitment trials. The relative foraging index (RFI) of each group of workers is given with the percent of total foraging performed by that group and the state of the ovaries of workers. For further explaination see text.


NUMBER OF ANTS
10
20
30
40
50
76% WITH DEVELOPED OOCYTES
32% WITH DEVELOPED OOCYTES
OOCYTES RESORBED
OOCYTES RESORBED
OOCYTES RESORBED
0
.29-5
5-10
10-20
20-40
FORAGER INDEX
0
30.54
18.85
20.28
30.57
PERCENT OF TOTAL FORAGING