

The Multiple Recruitment Systems of the African Weaver Ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae)

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Summary. 1. African weaver ants (*Oecophylla longinoda*) utilize no less than five recruitment systems to draw nestmates from the leaf nests to the remainder of the nest tree and to the foraging areas beyond: (a) recruitment to new food sources, mediated by odor trails produced from the rectal gland, a newly discovered exocrine organ, together with tactile stimuli presented during mouth-opening, antennation, and head-wagging; (b) recruitment to new terrain, entailing odor trails released from the rectal gland and tactile stimulation through antennation; (c) emigration to new sites; (d) short-range recruitment to territorial intruders, during which the terminal abdominal sternite is maximally exposed and dragged for short distances over the ground to release an attractant from the sternal gland, a second newly discovered structure; and (e) long-range recruitment to intruders, mediated by odor trails from the rectal gland and by antennation and intense body jerking.

These systems exist in addition to the elaborate pheromone-mediated alarm communication previously described by Bradshaw et al. (1975). In aggregate, the alarm and recruitment systems of *O. longinoda* constitute the most complex of such repertoires thus far discovered in ants.

2. Weaver ants recognize new terrain by means of both visual and olfactory cues, with the latter being the more effective. When major workers cannot cross gaps to the terrain by walking, they attempt to make the traverse by building bridges with their bodies. Individuals are attracted to the bridge site visually, but when the bridge is complete, they recruit nestmates to the new terrain with rectal-gland odor trails.

3. Workers mark newly acquired home range with randomly placed drops of fluid extruded from the rectal vesicle. They distinguish their own domain from that of alien conspecific colonies in part by means of the odor of the anal spots. When a section of terrain is found unmarked, the rate of anal-drop deposition is accelerated, even when adjacent areas are already heavily marked.

4. The anal substance is a true territorial pheromone: workers respond to alien spots initially with hostility and aversion, then by recruiting nestmates

to the vicinity. In laboratory experiments, workers entering an arena simultaneously with workers from alien colonies always gained the initial advantage in the ensuing conflict if they had previously been allowed to mark the arena. When the arena was placed in a spatial position familiar to one colony but possessed a floor previously marked by the second colony, the second colony still won. To our knowledge these results represent the first demonstration of a true territorial pheromone in the social insects.

5. During foraging the *Oecophylla* workers move independently of one another and are distributed at random (Poisson distributed) or with slight temporary clumping of no more than two or three workers. Short-range recruitment of intruders causes the ants to shift to a more distinctly clumped pattern, involving as many as ten or more workers, at the same time that long-range recruitment brings more defenders into the vicinity. Together the two forms of response result in a more efficient capture of intruders that are too large to be immobilized by only one or two workers.

6. The complex recruitment and territorial behavior displayed by *O. longinoda* is considered to be part of the adaptation of these relatively large ants to a strongly arboreal existence. The similarity of four of the recruitment systems to each other (1a, b, c, and e above) is interpreted as an example of signal economy in the evolution of social insect communication systems. The parallel evolution has been enhanced by the lack of any strong functional distinction between territorial defense and predation (see Discussion).

7. Signal ritualization appears to have occurred in at least two contexts: the modification of body thrusting during territorial battles into the jerking signal used in long-range recruitment of nestmates to enemies; and the adoption of anal excrement in the chemical marking of territories.

Introduction

The study of recruitment systems in ants has begun to diversify during the past five years. In the 1950's and 1960's the straightforward identification of the glandular source of the trail pheromones was emphasized, with some attention being paid to the details of the trail-laying behavior and the nature of the accessory stimuli necessary to evoke the trail-following response in some species (Wilson, 1971; Maschwitz, 1975; Hölldobler, 1977). Now a new emphasis has begun to form: the analysis of the ecological significance of recruitment. The possession of one kind of recruitment system as opposed to another is seen to constitute adaptations by individual species to particular conditions in their environment. Indeed, the recruitment strategy appears to make little sense except with reference to the ecology of the species, while, conversely, the ecology of many species cannot be fully understood without a detailed knowledge of their recruitment procedures (Hölldobler, 1976a).

Ecologically dominant species are especially dependent on recruitment systems to control their environment. This is true, for example, of the African red weaver ant *Oecophylla longinoda*, the colonies of which spread their large territories over the canopies of forest trees and onto the surrounding ground.

From these domains the ants glean a wide variety of food items while warding off the intrusions of rival colonies. We report here the results of a laboratory study of this remarkable species which reveal what we believe is the most complex such system hitherto reported in ants. The *Oecophylla* employ various forms of recruitment to alarm nestmates, to defend the foraging area, to collect food, and to explore and dominate new terrain.

Materials and Methods

1. General Biology. *Oecophylla* is an exclusively Old World genus with a long geological history. Two species are known from the Oligocene Baltic amber of northern Europe, where the ant fauna consists of a mixture of elements allied both to the modern temperate Eurasian fauna and the fauna of tropical Asia. A third species, *O. leakeyi*, has been described from the Miocene of Kenya; the fossils constitute a portion of a single colony, the allometry and size-frequency distributions of which match the unique patterns of the living members of the genus (Wilson and Taylor, 1964). This circumstance, combined with the fact that the colony lived in a tropical forest environment and possessed naked pupae (a condition almost limited within the Formicinae to arboricolous species), suggests that *Oecophylla* has not changed its basic way of life since Miocene times, at least ten million years ago.

Two species of the genus are alive today. *O. smaragdina* ranges from India across almost all of tropical forested Asia to the Solomon Islands and Queensland, Australia. *O. longinoda* is widespread in the forested portions of tropical Africa (Wheeler, 1922). Over most of their ranges both species tend to be common, and in many localities they are among the several most abundant elements of the arboreal ant fauna. At least some of the success of the *Oecophylla* must be due to the ability of these large ants to construct nests directly from leaves still attached to the nest plant. As their popular name of weaver ants suggests, they bind the leaves together with silken threads spun by the larvae, which they hold between their mandibles and move back and forth like shuttles.

The most detailed general account of the natural history of *O. longinoda* has been provided by Way (1954). Other aspects of the life cycle, ecology, and behavior have been added by Ledoux (1950), Leston (1969, 1970, 1973), Room (1971), Gotwald (1972), Hemmingsen (1973), and Bradshaw et al. (1975). The ants nest exclusively in the canopies of living trees. In general only one colony occupies a given tree, while large colonies often extend their domain to more than one tree. Multiple silken nests are constructed in widely scattered sites through the canopy, with the workers running back and forth between them. Way (1954) recorded an exceptionally large colony on Zanzibar Island that occupied 151 nests spread over twelve trees and contained at least 480,000 workers and 280,000 immature forms. This colony, like all *O. longinoda* colonies that have been carefully dissected, was found to contain only one mother queen. New colonies are founded in the conventional claustral method by recently fecundated queens who shed their wings, seclude themselves on an unoccupied host plant, and rear a first brood of workers from the reserves carried in fatty and muscle tissue within their own bodies. There are two distinct castes: major workers, which do virtually all of the foraging, defend the colony, care for the queen, and assist in the care of the brood, and much smaller minor workers, most of which remain inside the leaf nests and function as nurses of the brood.

Oecophylla longinoda major workers are strongly predaceous, using their considerable strength and cooperative ability to capture a wide range of insect prey that venture onto their territories, including honeybees (*Apis*) and driver ants (*Dorylus*). The ants also assiduously attend homopterans for their 'honeydew' secretion. Although the foragers remain mostly on the trees and surrounding low vegetation, they also venture extensively onto the ground. The laboratory colonies studied at Harvard were exclusively diurnal in their foraging activity, with the population of foragers reaching a peak in the late morning. This matches the diel pattern observed in the field by Leston (1973).

The *Oecophylla* are highly aggressive toward intruders, including nearly all kinds of other ant species. As a consequence, these and other dominant ants show a mosaic distribution with

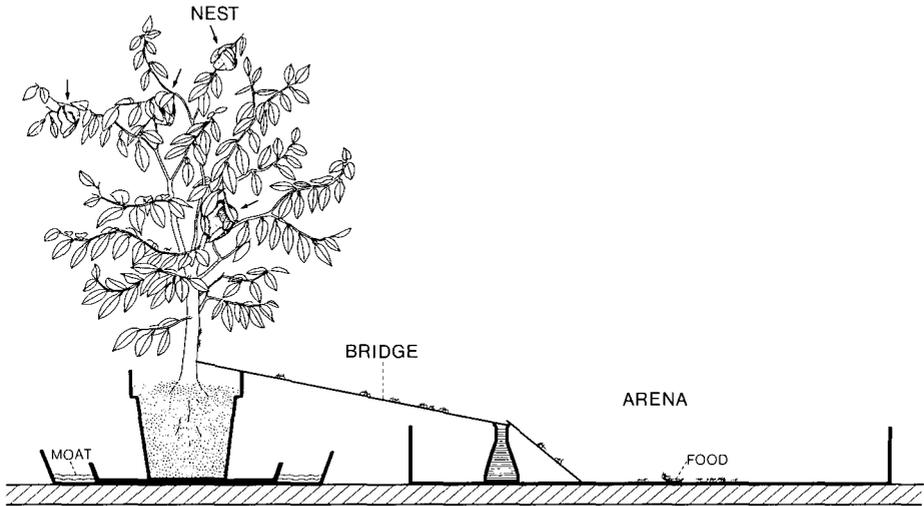


Fig. 1. Arrangement of nest tree and foraging arena used in the laboratory experiments on recruitment in *Oecophylla longinoda*

reference to their nest trees and surrounding foraging area. According to Leston (1970, 1973) and Room (1971), only a few species of *Pheidole* and a single species of *Crematogaster* (*?castaneus*) have been observed to be common associates of *O. longinoda* on the same trees in Africa.

2. Culturing Method and Experimental Arrangement. Our research has been based on small queen-right colonies collected at several localities near Mombasa, Kenya (Rabai and Mtwapa in Kilifi District and Matuga in Kwale District) and transferred to our laboratory at Harvard University. When allowed access to potted grapefruit trees (*Citrus paradisi*) and fig trees (*Ficus* sp.), the colonies occupied them within a few hours, constructing nests by folding leaves and binding them together with larval silk. Thereafter the ants thrived on a diet of freshly killed insects (mostly *Nauphoeta cinerea* cockroaches) and honey water. Water was supplied in test tubes, trapped at the bottom of the tubes by plugs of cotton. The tubes were laid at the base of the nest trees, where they were visited frequently by the *Oecophylla* and even used as bivouacs by the ants. The trees were also treated daily with a fine water spray.

The colonies were allowed access to rectangular foraging arenas 71 × 142 cm in floor area, surrounded by a 14-cm-high wall. Access was provided by a bridge of round sticks supported by Erlenmeyer flasks (Figs. 1 and 2). The ants were discouraged from climbing the walls of the arena by lining the walls with scotch tape and coating it with mineral oil. One colony was induced to live entirely in an artificial 'tree' consisting of test tubes held in clamps in a branching pattern around a metal holder. This colony, which flourished as well as those housed in natural trees, was useful for studies of behavior within the nest chambers. Where not mentioned otherwise, the statistical evaluation was based on Student's *t*-test and χ^2 -test.

Results

In the present study no less than five distinct recruitment systems were discovered, each with different combinations of behavioral components and each with a unique function. These systems are furthermore separate from the alarm communication mediated by mandibular gland pheromones (Bradshaw et al.,

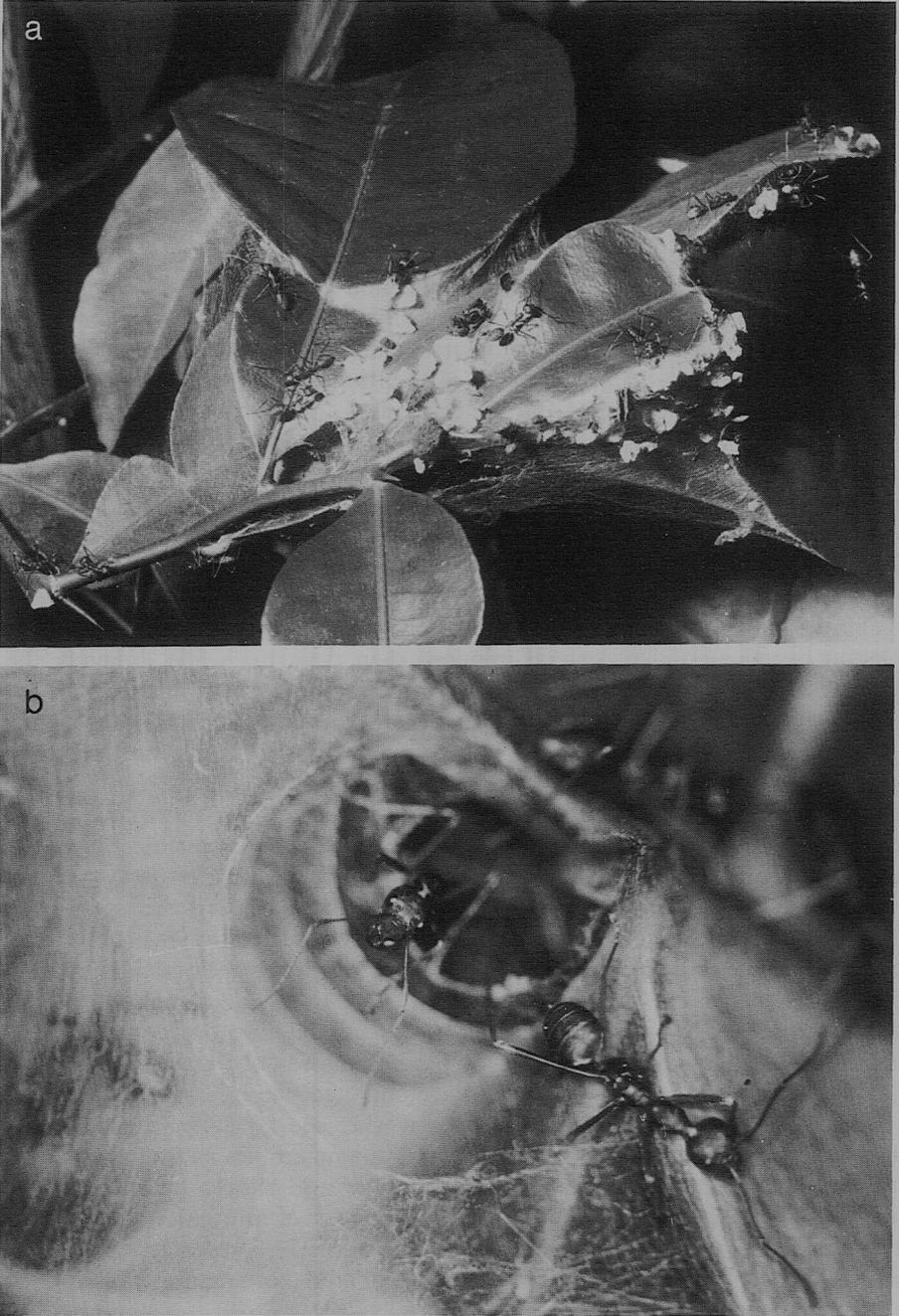


Fig. 2. **a** Leaf nest of *O. longinoda* constructed in a grapefruit tree within the laboratory. **b** Close view of nest entrance constructed of larval silk

1975). In the following sections we will first describe each system as it appears in a relatively unmodified laboratory environment, then characterize it further with the results of experiments.

1. Recruitment to Food

a) Description of Behavior. When workers discovered a food mass too large to move, they recruited workers to the site of the discovery by what appeared to be a combination of a trail pheromone and tactile signals. Recruitment to food was distinguished from other recruitment systems by the combined following three characteristics: (1) before returning homeward, some of the discoverers laid 'signposts' in the vicinity of the food by depositing short looping trails in several directions out from the food mass; (2) a more elaborate tactile display was frequently employed, during which the trail-laying ant antennated the nestmate encountered, opened its mandibles as though offering food, and waved its head slowly over that of the nestmate; and (3) food exchange often occurred. When the colony was hungry, the frequency and intensity of trail-laying increased markedly. A more detailed account of food-recruitment will now be given.

The first ants to encounter pools of honey water fed to repletion or near repletion over a period of several minutes, then departed while dragging the tips of their abdomens over the substratum. Some of these trail-layers headed directly back toward the nest. Others made one to several looping movements in various directions for ten centimeters or less in the vicinity of the food discovery, in what appeared to be 'signpost' marking. Still others, forming less than ten percent of the whole, deposited steady trails 90° or more away from the direction of the nest in what appeared to be a disoriented state. The odor trails laid by these first scouts did not seem to be adequate either to trigger or to orient following by nestmates; other foragers crossing the trails even within seconds of their deposit were not visibly affected by their presence. Nevertheless, we were confident that pheromone trails were being laid. Workers recruited from the nest vicinity (evidently in part by tactile signals, to be described below) followed the initial trails with a moderate degree of fidelity, while in later stages of the recruitment process masses of ants traveled along what was clearly a central trunk trail of accumulated pheromones.

When a trail-layer encountered a sister worker she typically turned toward her, antennating her head rapidly and opening the mandibles as though offering to regurgitate food. The head was commonly waved slowly back and forth over that of the nestmate. The greater the hunger of the colony, the more intense and prolonged were these signals. In a minority of cases, actual regurgitation of food occurred, but the donor never surrendered more than a small fraction of its crop contents.

Following each encounter the trail-layer had a strong tendency to turn 180° and to run back for variable distances in the direction of the food, still dragging the tip of its abdomen over the ground. Consequently only a very few of the initial trail-layers, generally less than 10 percent, ran all of the 260-cm

stretch from the food source to the leaf nests without reversing direction. This tendency to wheel back and forth caused the recruitment of new workers to proceed nestward only gradually: foragers in the arena were initially contacted at a higher rate than those on the tree trunk, which were contacted faster in turn than those in the leaf nests. The process was reinforced by the remarkable fact, which we do not believe to have been reported in any other species, for contacted workers to lay odor trails back and forth on their own. It was further reinforced by the strong response of workers that had not been fed, causing the recruiters to be delayed by peripheral workers. After these workers had received food, or proceeded on to the food site themselves, or both, the recruiters were delayed less frequently and were able to proceed all the way to the leaf nests more rapidly. The final result was the establishment of a chain of multiple odor trails running all the way from the food find to the leaf nests.

The recruitment process itself was most clearly marked at the leaf nests. Within half a minute after a trail-laying, food-laden forager entered a leaf nest, a group of workers typically left the nest excitedly and ran down the tree trunk in the direction of the food find. In 12 observations made of this phenomenon, the number of workers departing in the first 30 s ranged from 6 to 28 ($\bar{x}=14.5$, $SD=6.4$); prior to this activity, only one or two ants at most emerged during each 30-s interval. The trail-layer became more agitated in its contacts with nestmates as it entered the leaf nest and it often accompanied them back out, continuing to drag the tip of its abdomen as it proceeded down the trunk of the tree. That recruitment was occurring was also demonstrated by the buildup of the number of workers in the foraging arena to levels high above those occurring in the absence of food. The 'reinforcer' workers previously described—those laying trails without having yet visited the food site—did not appear to be effective in recruiting nestmates. When such individuals entered the leaf nests, groups of workers did not come out as was the case after the entry of food-laden recruiters. Typical case histories are illustrated in Figures 3 and 4.

In order to observe the recruitment process more closely, we conducted food recruitment experiments with the colony housed in the artificial tree constructed of glass test tubes. Food-laden workers were seen to make short, fast runs at resting nestmates. They typically approached individuals head-on, antennating them and waving their heads sidewise through several complete movements delivered at 2–3 times per second. Often the mandibles were also opened in what appeared to be brief food-offering movements. Usually about five workers were addressed in this manner before food exchange actually occurred. After liquid had been transferred, the recruiters continued to run in seemingly random looping patterns through the tube chambers, an action that created strong excitement among their nestmates. Many of the ants thus aroused then left the nest and ran out along the odor trail, in some cases departing even before the recruiters themselves. Some of them reinforced the odor trail while traveling outward, even before they had visited the food source. In a sample of eight such recruitment episodes watched from start to finish, the recruiters remained within the tube nests for 75–360 s ($\bar{x}=179.9 \pm 85.1$ s),

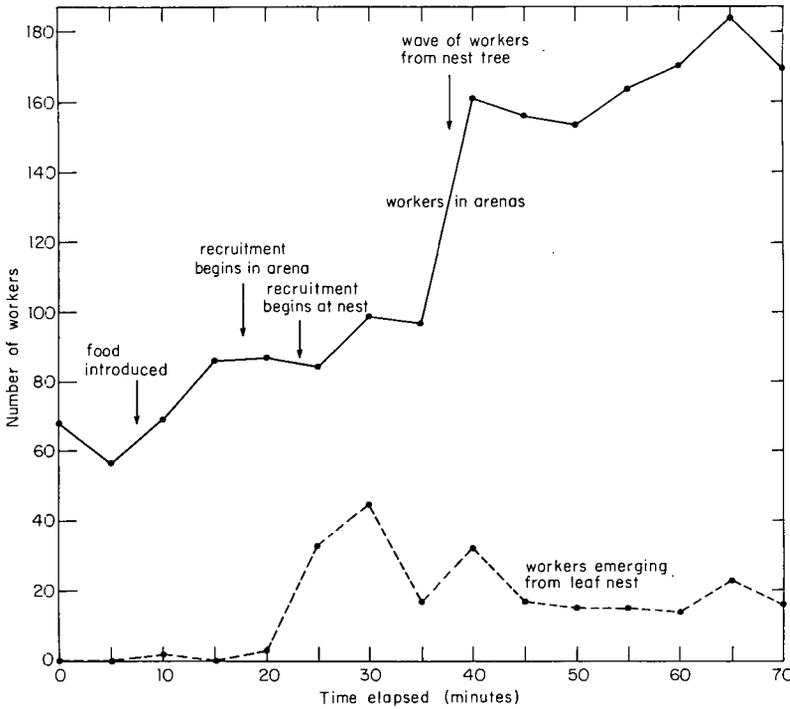


Fig. 3. Levels of activities of foraging workers during recruitment to honey water. In this experiment, two foraging arenas were placed end to end and connected by simple stick bridges; the food was placed at the far end of the far arena, at a distance of 260 cm from the base of the nest tree. At 5-min intervals the number of workers present in the arenas at one moment was taken (upper solid curve); at the same time the workers emerging from the leaf nests during the previous 5 min were counted (dashed line)

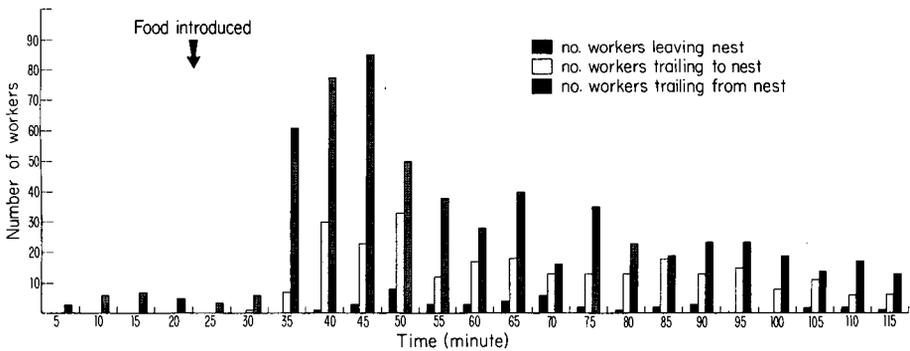


Fig. 4. A second case history of recruitment to food (sugar water) among *Oecophylla* workers. In this case the details of activity in the immediate vicinity of a web nest are given

during which time they encountered an average of 16.9 ± 9.5 nestmates and engaged in food exchange 5.5 ± 2.4 times.

Toward the end of the recruitment process, the incoming recruiter workers experienced increasing difficulty in getting rid of their food, due to the fact that a large percentage of the nest workers already had filled or partially filled crops. By this stage the rate of trail-laying and the outward flow of workers decreased markedly (Fig. 4).

Although recruitment to food masses was accomplished mostly by major workers (which further conducted all of the foraging), a small number of minor workers also emerged from the leaf nests when excitement in the colony was highest. The largest number we saw outside at any moment was seven; at the same moment 187 major workers were in the foraging area. The minor workers did not venture far beyond the leaf nests. Only rarely did one come all the way off the tree and onto the flat surface of the arenas.

After traffic to a large sugar source had run for a while, the ants accumulated one to several persistent trunk trails that led in a relatively straight line from the food to the nest. The workers were able to travel accurately along the trails, increasing the rate of transport in the average volume of liquid carried per ant.

b) Glandular Source of Trail Pheromone. Because many species of formicine ants lay trails with hindgut contents, we tried to trace the hindgut material

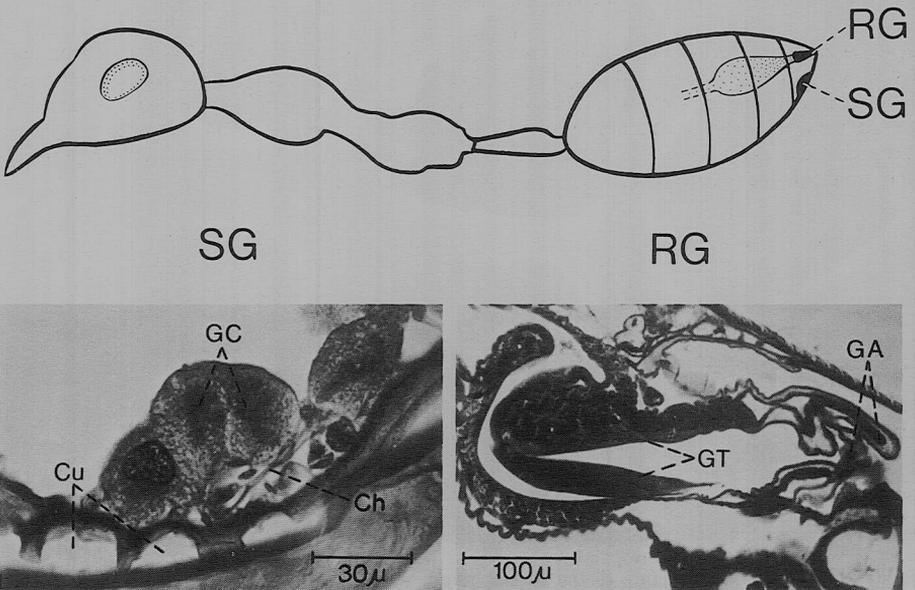


Fig. 5. The two newly discovered exocrine glands of *O. longinoda* are depicted in this diagram of a major worker. The lower photographs show longitudinal sections of the glands. The sternal gland (SG) consists of cells (GC) lining the inner wall of the terminal abdominal sternite; they are connected by intracellular channels (Ch) to outer cups (Cu) in which the pheromone accumulates. The rectal gland (RG) is an infolding of the rectal wall that includes glandular tissue (GT) and an eversible gland applicator (GA)

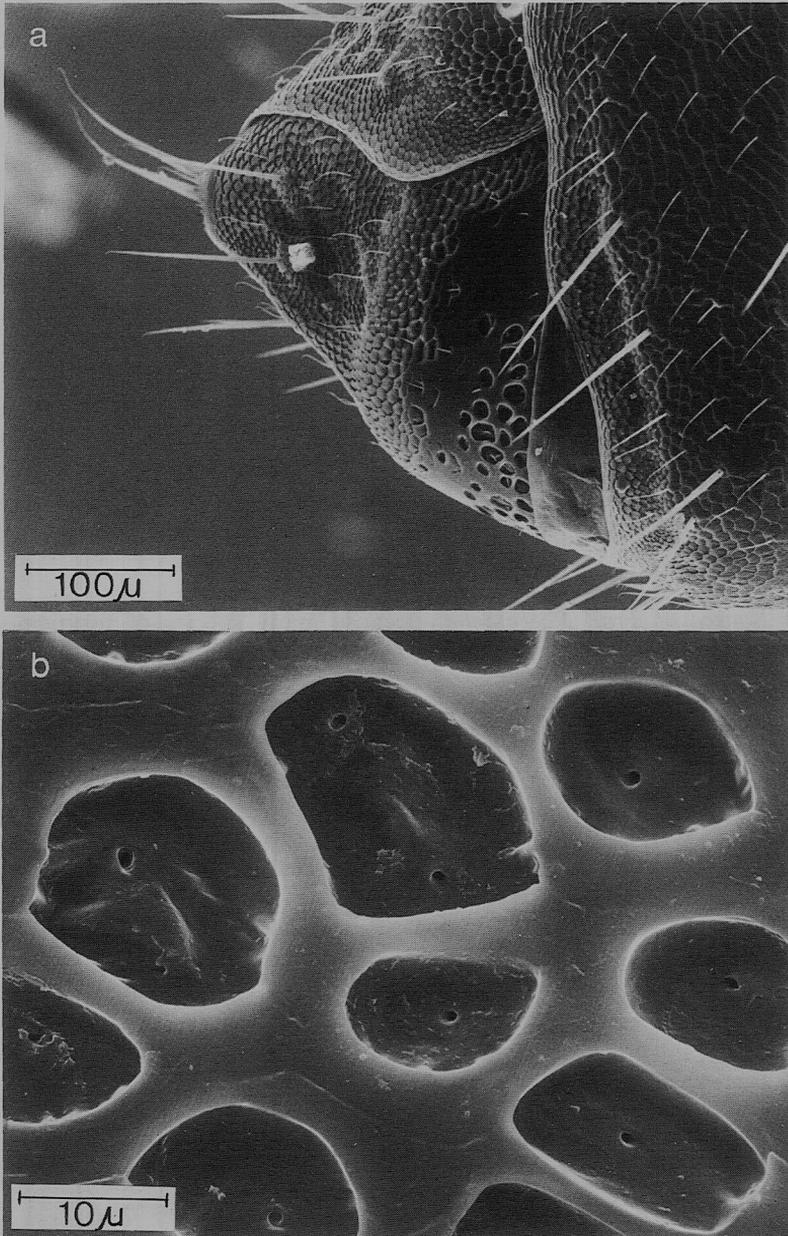


Fig. 6a and b. External structure of the sternal gland, revealed by scanning electron micrographs. **a** The terminal abdominal segment of a major worker has been rotated upward to expose its anterior lower surface, bearing the cups in which sternal-gland pheromone is accumulated. **b** Closer view of the cups, showing the minute openings to the underlying glandular cells

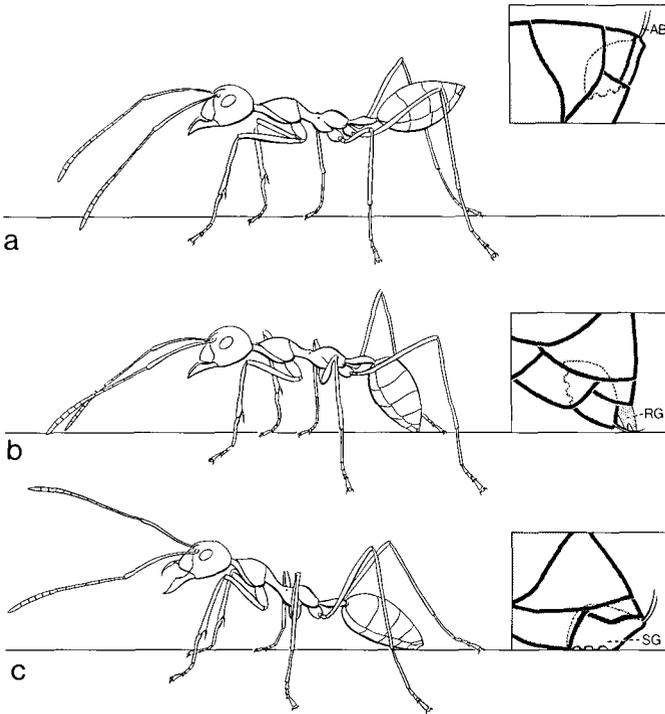


Fig. 7a-c. The modes of application of pheromones from the rectal gland and sternal gland by major workers of *O. longinoda*. **a** Ordinary running posture of a worker; as shown in the inset to the right, the terminal abdominal segment is held so that the sternal gland surface is covered by the penultimate abdominal sternite, and the rectal gland remains retracted within the wall of the rectal vesicle. **b** Worker laying odor trail from the extruded rectal gland, which 'rides' on the bristles of the acidopore, located just beneath the anus; the sternal gland surface remains covered. **c** Worker depositing sternal gland substance onto the substratum; the terminal abdominal segment has been rotated upward to expose the gland openings, while the rectal gland remains retracted

by feeding the ants with honey water dyed red with Azorubin S (Chroma-Gesellschaft, Schmid and Co., 7 Stuttgart-Untertürkheim, Federal Republic of Germany). After several days the hindgut contents were colored intensely red, but we could not detect any trace of the dye in the recruitment trails laid by the ants. We tentatively concluded that no rectal bladder contents are discharged during trail laying. Furthermore, histological investigation revealed two previously unrecognized glandular structures that might be involved in recruitment communication (Hölldobler and Wilson, 1976). One we called the rectal gland, an invagination of the lower rear surface of the rectal sac with a strongly developed glandular epithelium. The other structure was called the sternal gland, because of its location on the last abdominal sternite (Fig. 5). This structure consists of an array of single glandular cells that send short channels into cuticular cups on the outer surface of the sternite (Fig. 6).

Our observations of trail laying ants during food recruitment, together with the analysis of close-up slow-motion pictures of trail laying ants (70 f/s), clearly

revealed that the trail laying ant lowers her abdomen, rotates the terminal segment downward and extends her rectal gland. Thus exposed, the gland can just be seen with the naked eye as a white speck on the tip of the abdomen. It is dragged lightly over the substratum, apparently resting on a 'sled' composed of two pairs of long bristles that lead back from the upper edge of the acidopore (Fig. 7). However, this observation alone does not prove that the pheromone comes from the rectal gland. In an attempt to establish beyond a reasonable doubt the anatomical origin of the trail substance, we dissected and prepared extracts of the following body parts, considered to be the most likely repositories of pheromones: rectal gland, sternal gland, Dufour's gland, poison gland, and rectal bladder (which empties directly out of the anus). For the following experiments these organs were freshly dissected from single workers and smeared with the tips of hardwood applicator sticks over the papered floor of arenas to create artificial trails 30 cm in length. The number of workers that followed each trail during the first 5 min was then recorded. From the beginning it was evident that the responses of workers recently motivated by the recruitment efforts of a nestmate were different from those presented with artificial trails without prior stimulation. Accordingly, we conducted experiments in which the workers were first allowed to be antennated by nestmates and then to run along natural trails to honey baits in the arena. Next the baits were removed and artificial trails laid on fresh paper beyond the ends of the natural trails. In order to run parallel experiments in the absence of such motivation, the artificial trails were laid over the same paths on the paper without the intervention of feeding or trail-laying by recruiters.

The results, presented in Table 1, lead to two striking conclusions. First, the rectal gland—and no other part of the hindgut—is the source of the trail substance. It is true that moderate, short-lived following was also elicited by the preparations of sternal, Dufour's, and poison glands. But because the behavior had aggressive components, including raising of the abdomen, opening of the mandibles, and rapid directed movement, we interpreted the activity to be mostly or entirely a response to alarm pheromones in the two glands. This view is consistent with a previous finding that in other formicine genera Dufour's

Table 1. The number of workers following a 30-cm artificial trail made from various single-gland preparations. The responses of motivated workers, i.e., those approaching the artificial trails just after encountering a trail-laying nestmate, are compared with the responses of workers not so motivated. Data given are the number of replications (*n*), average number of workers following during the first 5-min period (\bar{x}), and the standard deviation of the number of followers (SD)

	Unmotivated			Motivated		
	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD
Rectal gland	10	0.2	—	5	12.6	5.4
Sternal gland	10	8.2	4.2	5	6.4	4.6
Dufour's gland	10	3.4	2.1	5	2.6	2.2
Poison gland	10	1.5	1.9	5	1.0	2.2
Rectal bladder	10	0.4	1.3	5	1.8	2.2

and poison gland secretions serve as alarm substances (Hölldobler, 1977). It also accords with other results, to be reported later in this article, that implicate the sternal gland substances in the specialized behavior of short-range recruitment. In contrast, trails composed of rectal gland extract induced prolonged following by much larger numbers of ants, which oriented in a calm manner indistinguishable from that displayed by workers traveling along natural odor trails. Preparations made from the remainder of the abdomen caused no perceptible reaction. The differences in response to the various organs were consistent during five replications employing two colonies. We conclude that the pheromone used in long-range recruitment originates in the rectal gland and is dispensed when the ant everts the gland and drags it over the substratum.

The second notable result is that the ants respond to the rectal-gland trail only if they have been previously excited. This effect helps to explain the observations, made on numerous other occasions, that ants crossing natural trails without meeting a recruiter did not follow the trails. By elimination, it appears likely that the essential accessory stimulus is the tactile contact experience during antennation from the recruiting ant.

We were able to confirm the role of the hindgut (incorporating the rectal gland) as the source of the trail substance in the course of a second set of experiments conducted under very different circumstances. *Oecophylla* colonies organize emigrations from one nest site to another by recruitment that employs antennation (sometimes accompanied by body jerking) and odor trails. Both trail-laying and following were closely similar to that observed during food recruitment (other details of the emigration process will be given later). We compared the activity of the rectal and sternal glands by presenting artificial trails made from both. Fifteen hindguts were placed in 0.5 ml ether; in a second preparation 15 sternal glands were also placed in 0.5 ml ether. Artificial trails 30 cm in length were then drawn with the two extracts at 45° angles away from the natural emigration trail and on opposite sides, so that they diverged at an angle of 90° from each other. The number of workers leaving the natural trail and following each artificial trail during the first 5 min was then recorded.

The results of this second experiment, given in Table 2, confirm that hindgut substances (and presumably those originating in the rectal gland) are more potent than substances in the sternal gland. However, the stimulus is truly effective only when visual cues are removed. When the ants followed the natural

Table 2. The following of artificial trails by workers attracted away from a natural emigration trail. Data are provided for ants orienting when the room was lighted, during which visual stimuli competed with the trails, as well as when the room was darkened. The data given are the number of replications (n), the mean number of workers responding (\bar{x}), and the standard deviation (SD)

Glandular source	Light on			Light off		
	n	\bar{x}	SD	n	\bar{x}	SD
Hindgut	3	4.7	1.5	9	19.9	9.5
Sternal gland	3	2.0	2.0	9	2.0	2.5

trail in a strong artificial light to which they had been accustomed, very few were diverted by the artificial trail. But when the light was turned off, so that the only illumination came from a night sky outside a nearby window, many more ants were diverted, although the majority of ants still followed the natural trail. We interpreted the difference to be due to the fact that the emigrating ants learn visual cues in a well-lighted room and rely at least in part on them when presented with a choice between the original, natural trail and deviating artificial trails.

c) Recruitment to Different Kinds of Food. Regardless of the degree of hunger of individual colonies, workers were recruited much more strongly to honey and sugar water than to insect prey (cockroaches of the genus *Nauphoeta cinerae*), even when the prey were large in size and had been fixed in position with pins. We offer the following hypothesis to explain the difference. Under natural conditions sugar is normally obtained from the honeydew excretions of fixed populations of homopterous insects (Leston, 1969, 1973). Cooperative retrieval of this kind of food therefore depends on long-range recruitment. In contrast, insect prey are captured and carried to the nests by workers operating singly or in small groups (Way, 1954; Gotwald, 1972). It appears to be of adaptive value for colonies to recruit more strongly to sugar sources than to insect prey.

2. Exploration of New Terrain

a) Description of Behavior. When foraging workers of *Oecophylla longinoda* were permitted to enter a new area close to the nest but not previously visited by the colony, they explored it excitedly and without hesitation. During this time the ants were alert and aggressive. When objects were moved within their field of vision they often shifted into a distinctive hostile posture: facing the source of the stimulus, the ants raised their bodies slightly, pointed the abdomen straight up, and opened the mandibles (Fig. 8). Following variable intervals, some of the workers returned directly to the nest tree while dragging the tips of their abdomens along the ground. This part of the behavior appeared identical to that observed in *Oecophylla* workers engaged in the deposit of odor trails during food recruitment. The rectal gland was extruded and dragged over the ground in the same manner. We have interpreted the full procedure as recruitment of nestmates to the new terrain.

As the returning worker encountered sister workers on her homeward journey, she usually halted and antennated them vigorously. Also, she frequently displayed a jerking motion, which was answered by the recipient with one to two jerks. She then often turned back and dragged her abdomen for at least a brief journey back into the new terrain before turning around again in a homeward direction.

Upon arriving at the web nests, the trail-laying ants entered without hesitation. Within seconds a strong new activity was detected: groups of workers emerged and proceeded down the nest tree and out in the direction of the unexplored terrain, without laying trails of their own. The number of workers

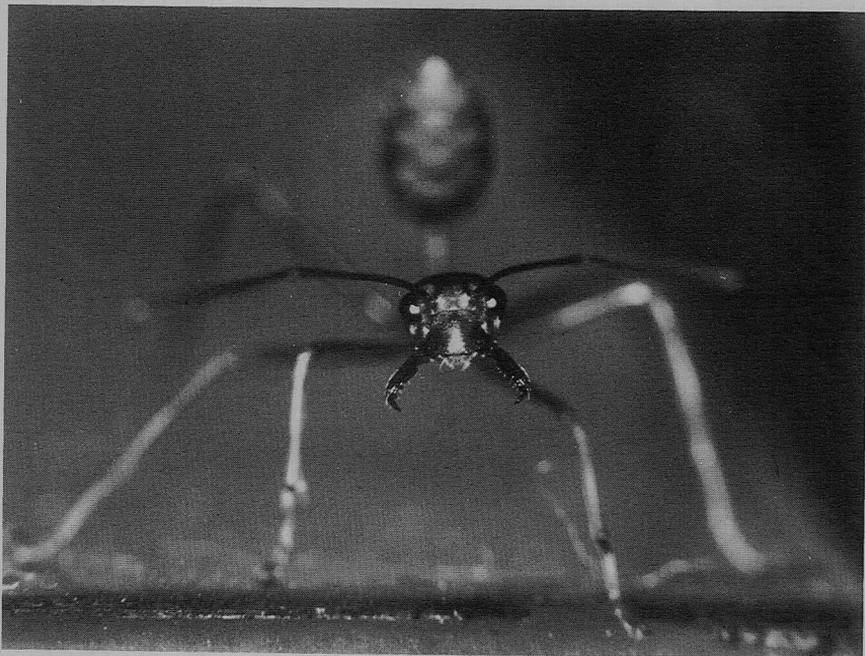


Fig. 8. Aggressive posture of a major worker of *O. longinoda*

laying odor trails rose sharply over a period of about half an hour, then declined toward zero during the next 1–2 h. The number of workers present in the arena rose to a higher peak somewhat later and thereafter declined at a much slower rate. The response was typical of recruited ants generally, and did not appear to differ from that of *Oecophylla* workers recruited to new food discoveries. A typical case history is provided in Figure 9.

Essentially the same response was obtained when 'new space' could be defined in one or the other several different ways: (1) a simple extension of surface added onto the existing arena and in the same direction from the nest tree as the arena; (2) new surface adjacent to the nest tree but projected outward in a new direction; and (3) new surface added vertically within a previously occupied space, such as a glass platform elevated on glass bottles within the boundaries of the colony's arena.

b) Bridge Building. When an object such as a new arena or potted tree was placed close to the *Oecophylla* nest tree but not close enough for individual workers to step over to it, a remarkable sequence of behaviors ensued. Workers first crowded together on the end of the leaf or twig closest to the new object. They were apparently attracted visually to this position; when the object was moved part way around the nest tree workers abandoned the old site and moved separately to whatever new position was closest to the object. No trail laying occurred during the movements. Upon arriving at the closest site the

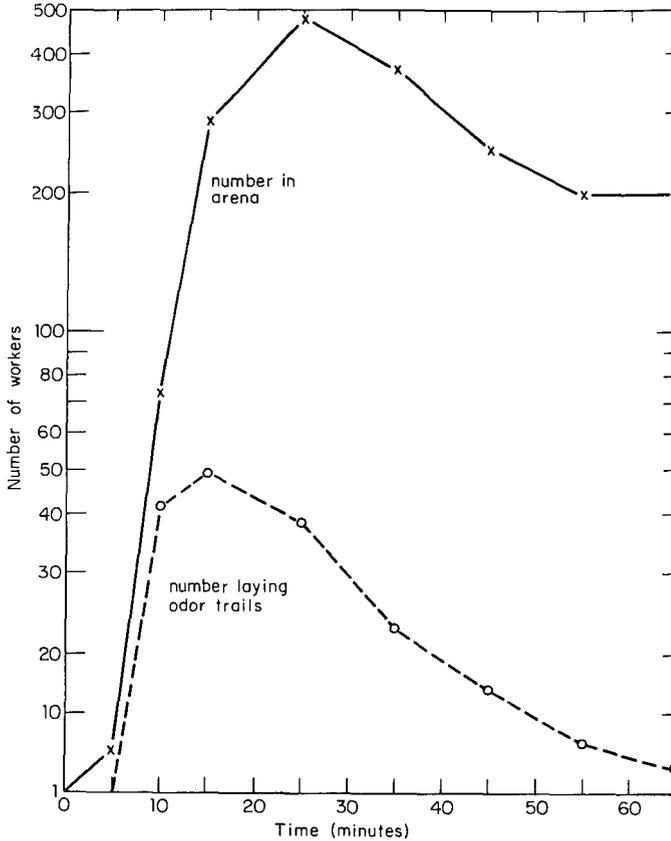


Fig. 9. Changes in trail laying and numbers of invading ants following the access of a colony to a new foraging arena

workers stretched their bodies outward toward the object, often holding this posture rigidly for periods of minutes. Other workers then clambered out over the bodies of their nestmates, and a living bridge began to take shape. When the bridge was completed and some of the ants were able to run over on to the object, the successful explorers then returned to the nest tree while laying odor trails from their rectal glands. The only time that such chemical recruitment occurred was after workers had crossed the bridge and examined the object on the other side. Odor trails were then laid heavily over the surface of the object and even onto the bodies of the nestmates forming the living bridge, a remarkable behavior illustrated in Figure 10. A rapid buildup of ants on the new object then ensued (Fig. 11).

3. Odor Cues in Home Range Recognition

How do foraging workers recognize new terrain as opposed to previously occupied home range? Odor cues appear to play at least a partial role. We

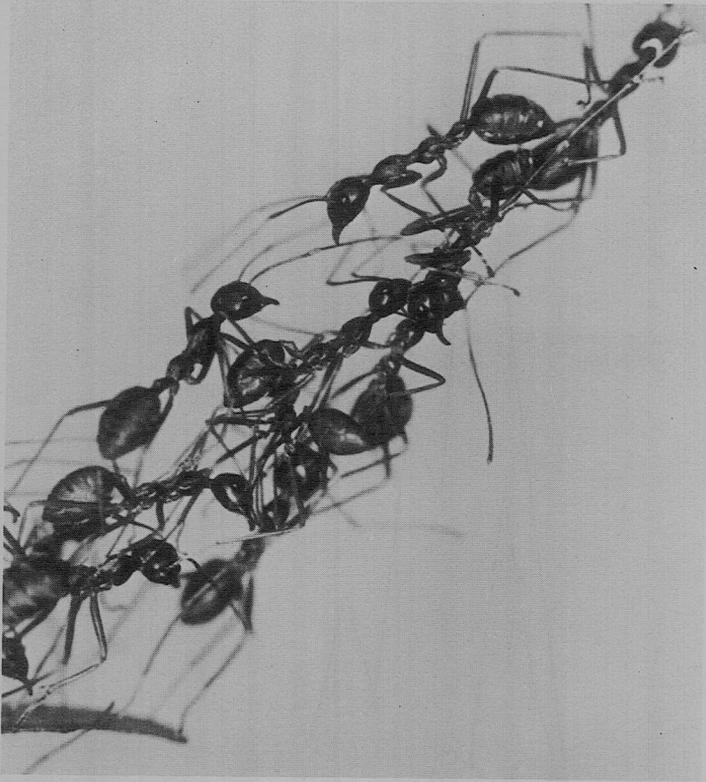


Fig. 10. Workers of *O. longinoda* form living bridges by linking their bodies into chains when exploring new terrain. The worker seen running over the upper portion of this bridge is laying an odor trail from her everted rectal gland directly onto the bodies of her nestmates. The trail will guide other members of the colony to a newly available foraging space

first reached this conclusion from the casual observation that when ants first enter a new space they periodically touched the tips of their abdomens to the substratum and extruded large drops of brown fluid from the anus. This material soon soaked into the surface or else hardened into shiny, shellac-like, shallow convex solids (Fig. 12). Several days after the ants had been fed the red dye, Azorubin S, the material began to appear in substantial quantities in newly laid anal spots, suggesting that the material originates at least in part from the rectal bladder.

When a colony was allowed access to a new arena the rate of spot deposition (spots/workers/h) increased. If the colony had been confined to the nest tree for a period of a few days previously, the deposition rate was extremely high. One colony containing several thousand workers deposited approximately 500 drops onto a fresh 71×142 cm arena surface during just the first hour. Thereafter the marking rate remained approximately constant.

The anal spots were not concentrated in a 'kitchen midden' or in any remote corner of the arena, the pattern used by workers of most other ant species

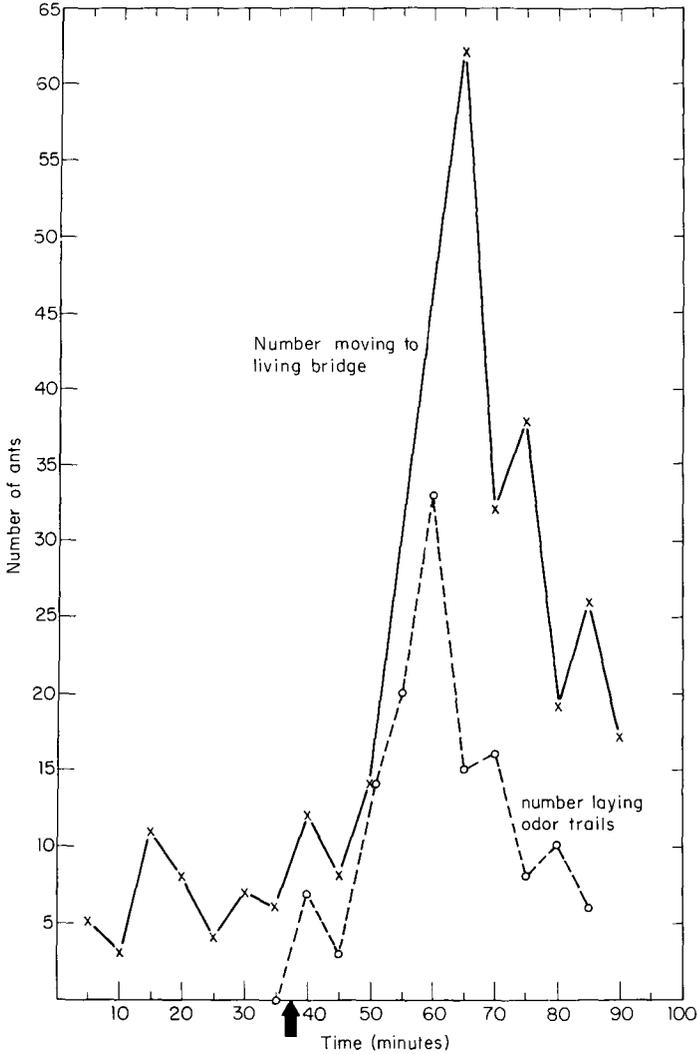


Fig. 11. When the living bridge (see Fig. 10) is completed, in this example at the time indicated by the vertical arrow, workers crossing over the bridge to the new terrain begin to lay odor trails and to recruit nestmates, resulting in a rapid increase in the number of ants approaching the bridge

when defecating. Although a slight gradient of decreasing density ran from the bridge exit to the far end of the arena, the spots were distributed essentially at random; over large portions of the arena, their locations proved to be Poisson distributed.

When bare areas were created within the home range, the workers increased the rate of deposition in these locations until the concentration of fecal material once again approached that in the immediately surrounding area. In a series

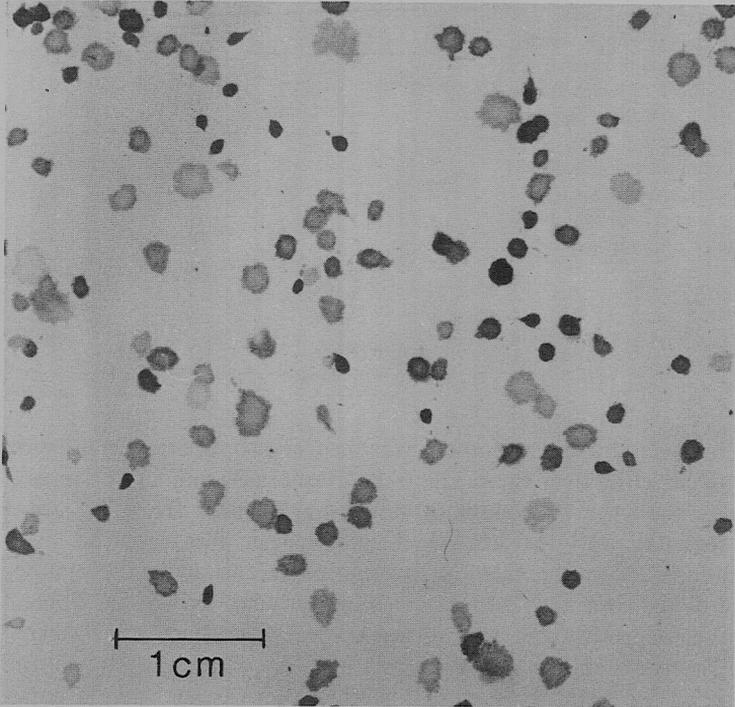


Fig. 12. Anal spots deposited by *O. longinoda* workers on a paper surface of the foraging arena. Experiments have shown that the spots contain a true territorial pheromone

of experiments, we partly covered the floor of a foraging arena with 8×13 cm index cards, allowing the ants to deposit drops on them for periods of 4–7 days. Then one card was replaced with a fresh card and left in position with the other, previously anal-spotted cards for 48 h. The rate of deposition of this and three adjacent cards was noted during the 48-h period. In six replications, with the new card being placed in different positions each time, the rate of anal-drop deposition on the new card always increased more than it did on the adjacent cards, usually by 20 percent and sometimes in excess of 100 percent. The probability that the result can be obtained by chance alone is less than 0.001. Thus the ants appeared to be spreading the fecal material more or less uniformly over their home range.

Since we had previously noted that *Oecophylla* responds rapidly to a newly available terrain by increased trail laying and recruitment of nestmates onto the new area, the next experimental series was designed to test whether a change of the anal spotting can alter the behavior. The following experimental procedure was used. For several weeks a colony was permitted access to an arena, the paper floor of which was heavily marked with anal spots (mean = 165.2 spots/25 cm²). For the control test the arena was disconnected from the nest tree and all ants were removed from the arena and returned to the tree. After

Table 3. Number of workers laying odor trails over bridges to arenas in which visual and chemical cues were left unchanged (control) as opposed to those in which fresh paper was placed on the arena floor changing the chemical cues (experimental).

A, original paper had remained in place until heavily spotted, then was replaced with fresh paper; B, original paper had remained in place a shorter time resulting in much lighter prior spotting

A		B	
Control	Experimental	Control	Experimental
11	103	14	27
72	138	15	23
1	94	2	6
13	77	14	78
18	59	11	18
17	108	9	10
9	38	5	12
$p < 0.001$		$p > 0.1$	

30 min the bridge between the tree and arena was returned to its original position and all trailing ants traveling over the bridge were counted during eight consecutive 5-min periods. Then the procedure of returning the ants from the arena to the tree was repeated and the heavily marked paper was replaced by a fresh one. After 30 min the bridge was put back in place and again the number of trailing ants moving over the bridge was counted. As shown in Table 3 (part A), the number of trail laying ants increased significantly ($p < 0.01$) when the marked paper floor was replaced by an unmarked one, although the position of the arena remained the same. However, this effect was weaker when a paper less intensively marked by anal spots was replaced by a fresh paper. For example, when the colony had been allowed to mark a paper during a two-day period prior to the experiment, the paper had an average spot density of 18.9 ± 4.7 spots/25 cm² ($n=7$ experiments). After this marked paper had been replaced by an unmarked one, the number of trail-laying ants did not significantly increase (Table 3, part B). This last effect indicates that when pheromones are weaker, the ants use cues in other sensory modalities, for example, landmarks, to identify their home range.

4. Visual Cues in Home Range Recognition

It had been apparent from the earliest casual observations that *Oecophylla* foragers remember the direction of the established foraging areas. When the wooden bridges to the arenas were removed at night, the foragers could be found the next morning crowded on the side of the nest from which the bridges had led, even when the nest tree had been rotated in order to exclude chemical orientation. A series of experiments revealed the role of learned visual orientation in the recognition of occupied as opposed to unexplored terrain. Our procedures firstly addressed the question: can a change of the positional orientation of the arena alone release increased trail laying and recruitment in *Oecophylla* foragers? For several weeks a colony was connected with an arena in which the paper floor had been initially heavily marked with anal spots (165.2 spots/25 cm²). For the control test the arena was disconnected from the nest tree

Table 4. Number of workers laying odor trails over bridges to arenas in which visual and chemical cues had been left unchanged (control) or shifted 90° in alignment, changing visual cues without replacing the paper covering the arena floor (experimental). Compare with Table 3, pertaining to arenas in which the chemical cues but not the visual cues had been changed

Control	Experimental
33	81
44	77
36	103
12	26
4	35
1	40
3	81
$p < 0.01$	

and all ants were returned from the arena to the tree. After 30 min the arena and nest tree were reconnected and all trailing ants moving over the bridge were counted during eight consecutive 5-min periods. The experimental test was conducted in the same way, except that the arena was rotated through 90° with reference to the nest tree and the numerous other visual landmarks present in the laboratory room. Now the ants had the same strong odor environment as before, but in traveling to the arena they were moving out at an angle of 90° from the original line of departure. As Table 4 shows, the number of trailing ants increased significantly ($p < 0.01$) after the arena's alignment had been changed.

In a second series of experiments two arenas were arranged next to the nest tree so that their long axes diverged 90°. For several days *Oecophylla* were allowed access to one of the arenas (arena A) and were allowed to see but not to visit the second arena (arena B). In a control experiment, the ants were removed from arena A the evening before and the arena floor was freshly papered, removing most or all of the odor cues. Then on the following morning the ants were allowed back into arena A, and the number laying odor trails on the arena floor, as well as the total number present there, were recorded during the first 30 min. The *Oecophylla* were still denied access to arena B. On alternate days the visual environment was changed in the following way: the procedures of the control experiment were repeated, except that now arenas A and B were switched in position, and the bridge was joined to arena A in its new position (arena B, now in the position occupied previously by arena A, was still left unconnected to the nest tree). Now the ants had the same odor environment as before (in case some odor cues were left after freshly papering the arena), but in traveling to arena A they were moving out at an angle of 90° from the original line of departure.

The data show that the *Oecophylla* workers lay odor trails at a higher rate when presented with this simple alteration in visual stimuli. The rates of trail-laying in four control experiments were 0, 0.23, 0.23 and 0.42, respectively, where the numbers given are the trail-laying episodes/ant/30 min. The rates of trail-laying in two rotation experiments were 0.76 and 1.80, respectively. The differences in rates between the control and rotation experiments are significant at the 95% confidence level. The number of workers accumulating in the rotated arenas was also much higher.

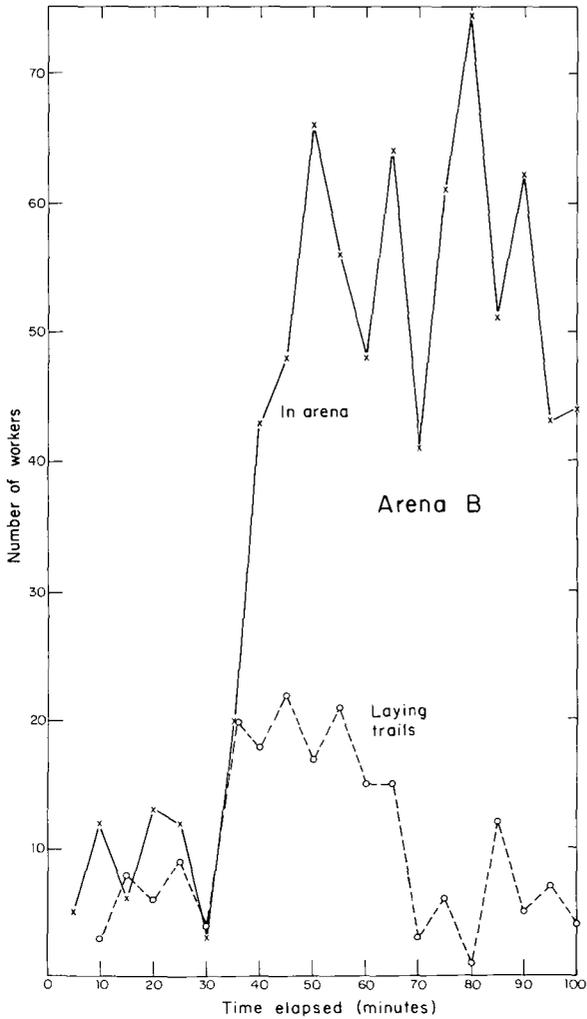
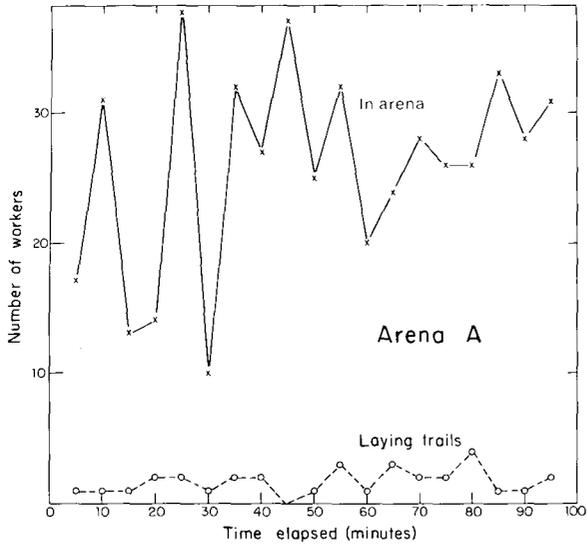


Fig. 13. A comparison of responses by workers to an arena (*A*) having the same alignment as the original arena, in opposition to an arena (*B*) rotated 90° from the original. The arenas were presented simultaneously and both had fresh paper floors, equalizing odor cues

Similar results were obtained when a nest tree was connected simultaneously with two new arenas, of which one replaced the colony's home arena and the other diverged from its long axis by 90°. In five replications a significantly larger number of ants laid recruitment trails into the latter arena (new position) which in turn caused a stronger invasion by nestmates into this space. A representative example is provided in Figure 13.

Finally, we devised a test to learn whether a mere extension of the available terrain, unaccompanied by a rotation in the direction of the accessible space, would also induce an increase in trail laying. This was achieved by simply adding arena A onto the end of arena B, with both leading away from the nest tree in the direction familiar to the ants. The two arenas were connected by a broad bridge. The rates of trail laying in the far arena (arena A) in the two experiments performed were 2.9 and 5.0, respectively, where the numbers represent number of trail-laying episodes/worker/30 min. The rates observed in the extension experiments were furthermore higher than in the rotation experiments. The difference appeared to be due to the attraction of the ants for the elevated paper bridge connecting the two arenas. The foragers accumulated there to a large degree, were apparently excited by the area, and conducted intense trail-laying in the vicinity. We have noted that *Oecophylla* workers in general are more attracted to elevated structures than to flat surfaces while exploring, and they most of all prefer to move along ridges.

In still more tests we measured the rate at which the exploring workers deposited anal drops during the first 7 h. When colonies were presented with a fresh paper surface only, and no change was made in the position of the arena, the rate of deposition (in drops/ant/7 h) was 0.63, 0.24, and 0.77 in three colonies, respectively. When the same colonies were presented with fresh paper in arenas that had been rotated 90°, the rate of deposition was 1.16, 1.01, and 1.24, respectively. The difference is significant at the 95% level. Thus the workers approximately doubled the rate of anal spotting when given a novel spatial stimulus. Later, in section 7g, we will show that the anal marks contain a colony-specific identification pheromone.

5. Emigration

When colonies brought from Kenya were given the opportunity to move from their original, now dried-out leaf nests to potted trees in the laboratory, they responded promptly and decisively. A well-organized emigration began within minutes in most instances and was all but completed within several hours. We followed four such episodes in close detail. In each case the ants treated the fresh tree essentially as new terrain: exploring workers investigated it quickly and returned to recruit nestmates with rectal-gland odor trails. Masses of major workers accumulated on certain leaves and branch tips of the trees, and the ants then proceeded to fold the leaves and to pull them together in a complex sequence of movements (for a description of this behavior, see Wilson, 1971; Hemmingsen, 1973). Very soon major workers began to carry larvae in the middle-size class able to spin silk, and used them to bind the leaves together at the new nest sites.

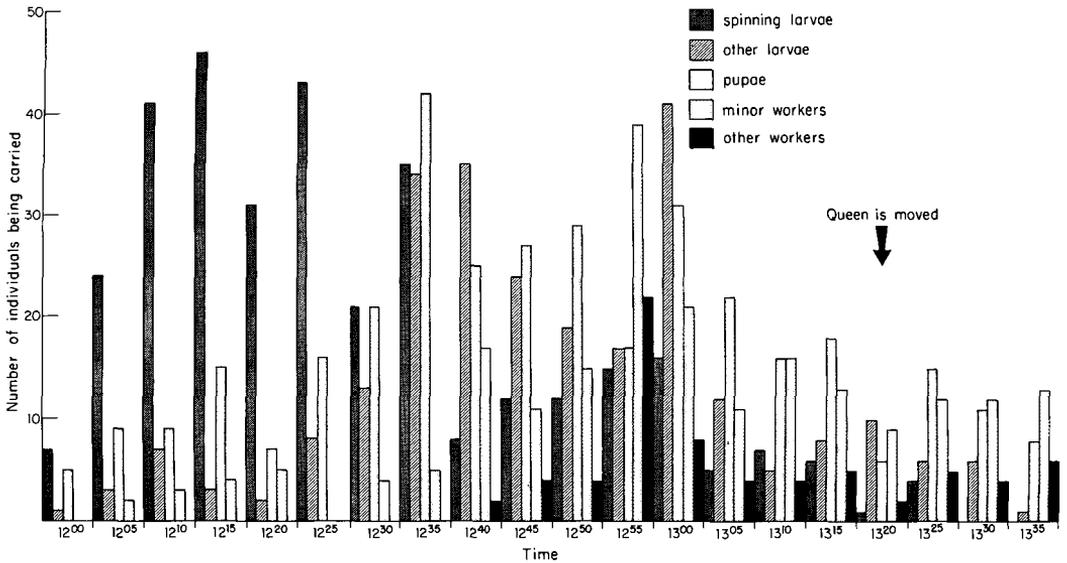


Fig. 14. The emigration of an *Oecophylla longinoda* colony to a new nest tree in the laboratory. The data given are the numbers of individuals of various classes carried by major workers onto the nest tree

From this beginning the colony traveled across in a fixed marching order (Fig. 14). After the major workers made the new leaf nests secure with the aid of larvae, they carried an increasing number of older larvae and pupae, succeeded by a rising proportion of minor workers and finally by other major workers. At its height the parade closely followed a trunk trail. Additional recruitment through antennation and trail laying continued throughout the remainder of the emigration but at a lower overall intensity. Thus emigration was achieved through a combination of recruitment and physical transport.

Many of the minor workers walked to the new nest sites. Some showed a curious hesitation in transit, traveling back and forth on the trunk trail over extended periods of time without making forward progress. On one occasion, we observed 27 minors simultaneously pacing up and down a 90 cm stretch of the trail; most of these miniature individuals covered stretches of 40 cm or longer before turning back to repeat the process. On several occasions individuals appeared to be laying odor trails. We cannot be sure that a pheromone was being deposited, but the overall behavior of the minors was distinctive enough to suggest that they were reinforcing the odor trail. It is possible that their hesitancy represents an adaptive response as part of the division of labor within the colony. Although the minors cannot carry larger brood and nestmates nearly as efficiently as their major nestmates, they can contribute to the reinforcement of the trunk trail.

Finally, the queen always left the old nest only after a large part of the remainder of the colony had emigrated. She traveled under her own power but was covered throughout by a dense retinue of major workers. Other observations

in the all-glass observation nest have shown that the queen also moves around in the brood chambers on her own, while being heavily attended by major workers.

6. The Deployment of Foragers

Once the *Oecophylla* workers occupied a new space, they dispersed throughout it each day during their foraging excursions. The ants moved in such a way that at each given moment a weak gradient of declining concentration extended from the tree nest outward, while in local areas the foragers approached a seemingly random distribution. The randomness of distribution can be defined more precisely as a Poisson distribution. To test this notion with reference to the *Oecophylla* foragers, we divided the floor of the foraging arena next to the nest tree into 93 marked quadrats 10×10 cm in extent and took counts of the ants in each quadrat at different times of the day and on different days. Our results (see, e.g., Table 5) show that at all times the ants were distributed either in a manner not distinguishable from a Poisson distribution or else very slightly clumped (the actual data were compared with the calculated

Table 5. Spatial distribution of *Oecophylla longinoda* workers in a foraging arena divided into 93 10×10 cm quadrats. Data were taken from the same population of foragers 1 h apart and represent the two extremes in a set of five such samples. (See also the set of similar data in Table 6)

First replicate			Second replicate		
Number of ants in quadrat	Number of quadrats with given number of ants	Number of quadrats expected from Poisson distribution	Number of ants in quadrat	Number of quadrats with given number of ants	Number of quadrats expected from Poisson distribution
0	71	63	0	69	67
1	13	24	1	18	21
2	5	5	2	6	3.4
3	3	0.7	3	0	0.4
4	1	0	4	0	0
5	0	0	5	0	0
6	0	0	6	0	0
7	0	0	7	0	0
8	0	0	8	0	0
$\frac{\text{variance}}{\text{mean}} = 1.724$			$\frac{\text{variance}}{\text{mean}} = 1.076$		
Probability that distribution deviates from the calculated Poisson distribution by chance and hence is not clumped is less than 0.001. Hence distribution is probably clumped			Probability that distribution deviates from the calculated Poisson distribution by chance alone exceeds 0.30. Hence distribution may be Poisson		

values of a perfect Poisson distribution and the significance of the differences in the two distributions estimated by the Chi-square test).

The clumping was caused by the brief attraction of workers to each other during casual encounters. The attraction rarely persisted for more than a few seconds and seldom resulted in more than four workers occupying the same 10×10 cm quadrat.

The density of foragers depended greatly on the state of hunger of the colony. During a period of several weeks, when food recruitment was being studied in one particular colony, the number of foragers in the arena at the morning activity peak varied over a factor of more than ten times in correspondence to the feeding schedule. When the colony was fed a moderate amount, once every two or three days, the number of workers in the arena usually ranged between 30 and 50. When the colony had been starved for a week, the number rose to 60–80. After saturation feeding with honey water over a period of several days, the number fell to below ten.

Regardless of the state of colony nutrition and the density of foraging workers, the foragers deployed randomly or in slightly clumped patterns as just described. However, when food masses or enemy ants were discovered in the arenas the behavior of the foragers changed dramatically. The ants then showed a strong tendency to clump, while new foragers were recruited to the vicinity.

7. Territorial and Predatory Behavior

a) Evidence of Territoriality. In favorable African habitats *Oecophylla longinoda* populations are more or less evenly distributed. Each colony occupies one to several trees, over which it maintains exclusive possession. Members of alien *Oecophylla* colonies, as well as those belonging to other larger, aggressive species, are attacked and cleared from an extensive area around the leaf nests. The interactions are so intense that 'no-ant's' zones clear of foraging workers sometimes separate adjacent territories in the field (Way, 1954; Leston, 1969). Leston found that when *Oecophylla* colonies were extirpated by mechanical or chemical means from selected plots in Ghana, new colonies saturated the area to about the same density within one year.

This clearcut evidence of territorial behavior is easily duplicated in the laboratory. Workers of our captive colonies restlessly patrolled their nest trees and adjacent arenas. They attacked and killed members of alien *Oecophylla* colonies as well as those belonging to other ant species and carried them to the leaf nests, where the victims were apparently eaten. When members of two colonies were given access to the same arena they fought viciously, inflicting heavy mortality on each other until we separated them. Because of the unusual sharpness and rapidity of the action, we decided to undertake a systematic study of territoriality and predation under laboratory conditions.

b) Reaction to Intruders. When a human observer walked around the foraging arenas, or a hand or other large object was waved within a meter or two of the foraging workers, the ants typically halted, and many assumed the alert

posture illustrated in Figure 8. If an object was thrust at the workers they sometimes rushed at it and occasionally even attempted to seize it before breaking away and retreating; often the workers simply ran away without offering any resistance. Continued harassment of this kind resulted in a decrease in the number of workers in the arena, as some of the foragers returned to the nest tree. When we tapped sharply on the arena floor, most or all of the workers ran directly homeward.

When workers of a small ant species, *Pheidole dentata*, were introduced to the arena, the *Oecophylla* invariably charged them and attempted to seize the intruders with their mandibles. In about a third of the cases the *Oecophylla* were successful at the first attempt; otherwise they chased the more agile *Pheidole* for one or two centimeters before giving up. In time all of the *Pheidole* were caught and killed, usually by one or two *Oecophylla*. Workers of the fire ant *Solenopsis invicta*, equally small in size relative to the *Oecophylla*, were also charged directly by the weaver ants. But the *Oecophylla* quickly broke away and retreated, often cleaning themselves vigorously. They were evidently repulsed by the venom that the fire ants attempted to smear on them.

c) *Short-Range Recruitment.* When larger ants, including alien *Oecophylla* and workers of the Florida harvester ant *Pogonomyrmex badius* and African tree ant *Polyrhachis militaris*, were introduced, the *Oecophylla* major workers displayed a wholly new set of behavior patterns. They charged the intruders and attempted to seize them. In many instances they failed, as before. However, in most such cases *the workers failing to hold on to the intruders chased them for distances of 15 cm or more while dragging the last abdominal sternite over the ground* (Fig. 7, lower). The behavior was entirely different from ordinary trail-laying employed during recruitment to new terrain and to food discoveries. The ants touched the ground with a portion of the sternite located anterior to the abdominal tip, rather than the tip itself (the tip bears the acidopore and anus). Their movements were excited and jerky, of the kind associated with the attack on enemies, in contrast to the relatively leisurely, more even movements employed during trail-laying from new terrain and food. Nestmates in the vicinity (for distances up to 10 cm) were attracted by nestmates behaving in this fashion. They tended to move toward the displayers and then, together with the recruiting ant, to slow down and settle in clumps where the display had occurred. Even when the displayers moved to a new location, the area where the display occurred remained attractive to her nestmates. The interaction resulted in the accumulation of small groups of workers in the places where intruders had been encountered. For this reason we refer to it as 'short-range recruitment to enemies'. An example of the alteration in spatial pattern due to the recruitment is given in Table 6.

The important result of short-term recruitment, confirmed in repeated laboratory trials, was that clumps of workers were able to retain and subdue invaders in much shorter periods of time than were single individuals.

d) *Source of the Short-Range Recruitment Pheromone.* Because short-range recruitment involves touching the substratum with a portion of the abdomen

Table 6. Clumping of *Oecophylla* workers following the introduction of five African tree ants (*Polyrhachis militaris*) into an arena patrolled by *Oecophylla longinoda* workers. The numbers reflect the changing pattern of spatial distribution of the *Oecophylla* over an array of 93 10 × 10 cm quadrats

Time (min)	Total no. of ants	Mean no. per quadrat	Variance	$\frac{\text{Variance}}{\text{Mean}}$	Clumping in spatial pattern
0	86	0.925	1.575	1.703	Weak
5	90	0.968	1.558	1.610	Weak
10	77	0.828	1.411	1.704	Weak
20	74	0.796	1.152	1.447	Weak
<i>Polyrhachis</i> introduced at 25 min					
30	87	0.935	4.039	4.320	Moderate
35	96	1.032	3.429	3.323	Moderate
40	108	1.161	4.673	4.025	Moderate
45	103	1.108	3.085	2.784	Moderate
50	123	1.322	3.960	2.995	Moderate
55	88	0.946	3.771	3.986	Moderate

anterior to the anus and acidopore, with no sign of an extrusion of the rectal gland, we considered the newly discovered sternal gland (Figs. 5–7) to be a likely source of the pheromone.

In fact, when approximately one-gland equivalents were placed in *Oecophylla*-sized dummies of folded filter paper and presented to *Oecophylla* major workers on their territories, the ants responded in a manner indistinguishable from that comprising natural short-range recruitment. The details of the experimental procedure are as follows. The preparations of a given body part usually consisted of the accumulated parts from 10 to 30 major workers placed in 0.5 ml ether and chilled for an hour or longer. The fraction of extract then injected into a dummy was calibrated so as to contain the equivalent of approximately one body part. Another method was simply to crush a single body part directly into the paper dummy. Following either technique the dummy containing the material was then tested in competition with a control dummy (containing either an injection of pure ether or nothing at all, depending on whether the experimental dummy received an ether extract or an unextracted gland) or with an experimental dummy containing the equivalent of another kind of body part. We recorded the number of ants approaching within 5 cm of the two dummies during a sequence of 16 30-s periods. The results are summarized in Table 7. The sternal gland preparations proved much more attractive than simple controls, and the response of the ants to them was seemingly identical to their response during natural short-term recruitment. Poison glands and Dufour's glands were also attractive, although to a somewhat lesser degree. This is not surprising, since these glands have been shown to contain alarm pheromones in other species of formicine ants (Hölldobler, 1977). And in fact

Table 7. Attraction to preparations of various body parts by *O. longinoda* workers on their territories. In each replication of the five series (I–V) the equivalent of one body part was presented in competition with a dummy treated with ether alone (series I), left entirely untreated (II), or containing a different body part (III–V). The number given for each replication is the average number of ants attracted during a sequence of 16 30-s periods

Series	Replication number						<i>p</i>
	1	2	3	4	5	6	
I Untreated control	2.3	2.7	4.2	3.8	3.5	1.8	<0.001
Sternal gland extract	9.9	5.6	13.5	9.2	9.4	6.9	
II Untreated control	0.3	1.7	1.0	—	—	—	<0.01
Fresh sternal gland	3.7	4.6	5.5	—	—	—	
III Hindgut extract	1.2	1.3	1.6	2.5	2.3	—	<0.001
Sternal gland extract	8.2	4.5	6.9	8.1	6.9	—	
IV Poison gland extract	6.3	3.9	3.8	4.3	3.6	—	>0.1
Sternal gland extract	10.8	3.3	6.9	4.5	9.5	—	
V Dufour's gland extract	10.6	3.2	4.4	2.9	3.6	—	>0.1
Sternal gland extract	6.1	5.1	5.3	5.6	4.3	—	

they produced more aggressive responses, which were not followed by clustering in the manner induced by short-range recruitment.

Other lines of evidence support the conclusion that the sternal gland is the source of the pheromone used in short-range recruitment. When *Oecophylla* workers were picked off their territory with the fingers or a pair of forceps and held lightly, they rotated the terminal abdominal segment upward to expose the shining cuticular surface that covers the sternal gland. When released back onto the territory, they immediately performed the typical display of short-range recruitment. *Oecophylla* workers grappling during territorial fights lifted their abdomens and exposed the sternal glands by the same upward rotation of the terminal abdominal segment. When they broke apart they too performed the characteristic abdomen-dragging of short-term recruitment.

e) Long-Range Recruitment. When contacts with enemies became frequent, a few of the ants returned to the nest laying odor trails in the conventional manner. When such ants reached the nest tree, they stimulated nestmates to leave for the arena where the invasion had taken place. We refer to this interaction as 'long-range recruitment to enemies.' It differed from other forms of recruitment in at least four respects:

(1) The workers did not always begin to lay a trail as soon as the *Pogonomyrmex*, *Polyrhachis*, or alien *Oecophylla* were contacted. This behavior usually began only after a delay, often of a minute or more, and typically after engaging in short-range recruitment. Thus as the trail was deposited, the intruder was often not close to the trail's terminus.

(2) At low intensities the path of the trail-layer was typically very irregular in pattern and was interrupted frequently by periods of ordinary locomotion. The interruptions occurred most commonly after the recruiter had encountered

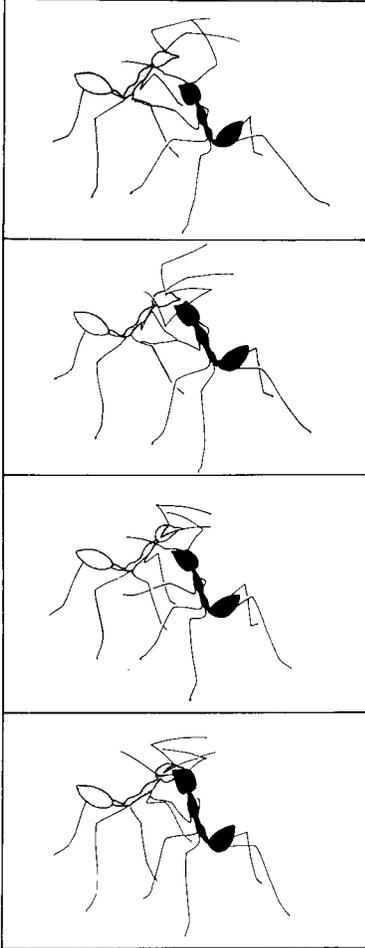


Fig. 15. Alarm-recruitment to enemies. Following an encounter with alien ants, especially invading members of other *Oecophylla* colonies, excited weaver ants greet nestmates with a rapid back-and-forth jerking movement. This figure was drawn from four successive frames in a motion picture taken at 25f/s; the recruiting ant is depicted in black

nestmates. At high intensities the path was much more direct, and trail-laying was continuous over long stretches.

(3) Like workers laying trails to new terrain, and unlike those laying trails to food, the workers engaged in long-range recruitment to enemies failed to put down 'signposts' with tight looping movements in the vicinity of the source of stimulation. The closest approach to this behavior was the very different 'short-range recruitment' just described.

(4) In most instances the trail layers at the very least briefly antennated the heads of nestmates they encountered. When highly excited, especially after encountering alien *Oecophylla* workers, the ants jerked their bodies rapidly in the direction of the nestmates (3–12 back-and-forth jerks/s) (Fig. 15). Most jerking encounters lasted less than a second (0.3–0.8 s). This behavior closely resembles the maneuvering of *Oecophylla* workers during territorial fighting (which will be discussed later), to the extent that it can be interpreted as a ritualized version of that more overtly aggressive response. Some of the nestmates



Fig. 16. A worker of the African tree ant *Polyrhachis militaris* has been spreadeagled and immobilized by *Oecophylla* workers in the laboratory foraging arena. The capture of this large ant requires the initial cooperation of at least three *Oecophylla* workers, and the effort is abetted by both long-range and short-range recruitment of defending nestmates to the vicinity

encountered by a jerking trail layer began laying odor trails of their own, and they also exhibited the jerking motor display when they encountered still other workers, even though they had not yet experienced the enemy stimulus themselves. This is a rare example of chain communication in a social insect.

f) Entrapping the Enemy. In most cases observed, long-range recruitment caused a slow and modest buildup of *Oecophylla* workers in the arena where the intruders had been contacted. Simultaneously, the workers were deployed increasingly into small groups by short-range recruitment. The result was a higher rate of capture and immobilization of the enemy. *Pogonomyrmex* workers could seldom be held down by less than two *Oecophylla* working together, while three or four *Oecophylla* were required to immobilize the still larger *Polyrhachis*. In the initial stages of the invasion (when 5–10 of the alien ants were introduced), the density of the *Oecophylla* was sufficiently low and their deployment so close to random that each intruder seldom encountered more than a single *Oecophylla* at a time, and it therefore usually escaped with ease. As the *Oecophylla* increased in numbers and formed more clumps, the intruders were seized by groups of workers at higher frequencies. Eventually all were halted, spreadeagled by packs of the *Oecophylla*, and killed (Fig. 16). The corpses were then carried to the nest tree by groups of *Oecophylla* and eaten.

g) *A Territorial Pheromone*. As documented previously, workers respond to fresh surfaces by increasing the rate of deposition of anal spots, and the material was laid over the territorial surface at an approximately uniform rate of density. Is it possible that the anal liquid contains pheromones by which the ants recognize their own territories and avoid—or at least respond differently to—the territories of other colonies? If such conditions occur, the identification substances qualify as territorial pheromones, the existence of which would be of exceptional interest in ecology.

The ability of *Oecophylla* major workers to recognize their own deposits was tested by the following method. A colony was allowed to mark the papered floor of an arena for a period of several days. Then the ants were removed overnight, and the arena was shifted slightly to one side to make room for a second, identical arena that had been marked by an alien colony of *Oecophylla*. The alignment of the two arenas was the same as that of the original arena in its undisplaced position. The colony was then given access to both arenas simultaneously by the emplacement of thin wooden bridges. Four replications were performed, employing two colonies and both possible arrangements of the arenas (that is, experimental arena either to the right or left of the control arena). The results strongly indicated the presence of a colony-specific territorial pheromone. The first major workers to enter the alien arena displayed greater caution and a significantly higher rate of aggressive posturing, which consisted of opening the mandibles and raising the abdomen above the remainder of the body (Fig. 8). This response was obtained even though no alien workers had been in the arena for over 12 h and none were then even in sight elsewhere. The exploring ants showed a special interest in the anal spots, often stopping to inspect individual ones with their antennae. After a few minutes some of the foragers then returned to their nest tree while laying odor trails, and a full-scale recruitment to the alien arena began. Some recruitment to the familiar arena occurred simultaneously but at a significantly lower level.

A similar series of experiments was conducted with a third colony. In this case, however, we allowed the *Oecophylla* foragers to enter three different arenas: the home arena; a new arena, with a freshly papered floor; and an arena from an alien colony. Three replications were performed, with the spatial arrangement of the arenas being changed each time in order to minimize visual cues. The results, which are exemplified in Figure 17, clearly confirmed the previous findings: workers entering the alien arena responded with stronger recruitment efforts and more aggressive displays than did workers entering the new arena or the home arena.

In order to be certain that the ants were recognizing their own deposits and not some other feature of the particular arena unknown to us, we conducted the following additional experiment. Pieces of fresh paper 15 × 15 cm in area were placed on the floors of arenas occupied by *Oecophylla* colonies, and the ants were allowed to mark them with anal spots over a period of two or more days. The marked pieces were removed briefly and then reinserted into the original arena or in the arena of another colony. Freshly cut, unmarked squares were also offered as general controls. The behavior of the major workers approaching the various squares was then recorded in detail during four or

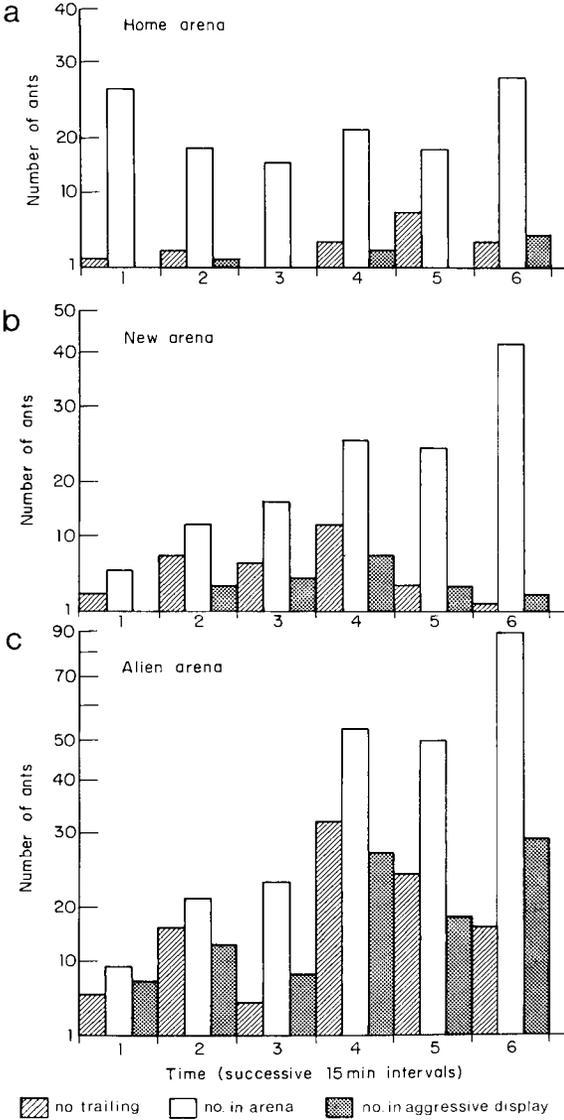


Fig. 17a-c. *Oecophylla* major workers entering an arena previously marked by an alien *Oecophylla* colony responded with frequent aggressive displays and stronger recruitment effort (c). Those entering an arena with a fresh paper floor (b) or an arena previously marked by their nestmates (a) were less aggressive and showed weaker recruitment efforts. The scale of the ordinate is logarithmic

five successive 2-min intervals. The provenance and significance of each category of squares were as follows:

Control 1. A fresh, unmarked 15 × 15 cm square of paper was introduced to colony A as a general control.

Table 8. The responses of foraging *Oecophylla longinoda* colonies to unmarked paper squares and similar squares marked by their own nestmates and members of an alien colony. The numbers are the average counts of responses over 4–5 successive 2-min intervals

Kind of square offered	Stepping onto square	Repelled by square	In aggressive display	Inspecting anal spots
Control 1: fresh paper	20.2	0.2	0.2	—
Control 2: A paper to A colony	20.3	0	0.3	0.8
Control 3: B paper to B colony	9.5	0	0.2	1.2
Experimental 1: B paper to A colony	12.0	2.7	7.7	8.7
Experimental 2: B paper to A colony	12.5	2.2	4.2	6.0

Control 2. A square previously marked by colony A was reintroduced to colony A in order to measure the response of colony A to its own pheromone.

Control 3. A square previously marked by colony B was reintroduced to colony B in order to measure the response of colony B to its own pheromone.

Experimental 1. A square previously marked by colony B was introduced to colony A to note the response of A to an alien colony's pheromone; the first of two identical tests.

Experimental 2. A repetition of experimental 1 above, differing only in that a second square marked by B was introduced to A; the second of two identical tests.

The data, summarized in Table 8, reveal in an unequivocal fashion that the *Oecophylla* workers were able to distinguish the deposits of alien colonies. They responded with a higher frequency of initial aversion and aggressive displays, and their attention was directed to the anal spots themselves in so consistent a manner as to support the hypothesis that at least some of the territorial pheromone is contained in these droplets.

Furthermore, the pheromone is persistent. The same intensity of response to an alien square in aversion and aggression display was obtained 12 days after the square had been removed from the arena of the alien colony.

Experiments were next designed in an attempt to localize the anatomical origin of the territorial substances. When the *Oecophylla* were fed honey water dyed red with Azorubin S (Chroma), the dye accumulated in the hindgut after several days and then began to appear in substantial quantities in the anal spots. Since the dye was at this time almost exclusively limited within the body to the hindgut, we concluded that at least some of the contents of the

Table 9. The responses of foraging *Oecophylla longinoda* workers to paper squares (5 × 5 cm) experimentally spotted with contents of 20 hindguts dissected out of their own nestmates (control) and members of an alien colony (experimental). The numbers are the average numbers of responses over 4–5 successive 2-min intervals (with standard deviation). Five replicated experiments (I–V) were conducted, each with its own set of test papers

Experiment	Control	Experimental	P
A. Mean number of workers stepping onto paper			
I	19.0 ± 11.9	22.4 ± 11.2	—
II	7.2 ± 6.8	13.7 ± 6.8	—
III	15.5 ± 6.9	14.0 ± 3.9	—
IV	12.7 ± 5.7	16.0 ± 4.1	—
V	16.1 ± 9.5	18.5 ± 8.1	—
B. Percentage of workers showing aggressive display			
I	30.2 ± 21.1	53.9 ± 12.1	0.05 < p < 0.1
II	18.4 ± 13.5	60.7 ± 11.9	< 0.01
III	24.1 ± 16.9	64.2 ± 9.5	< 0.01
IV	44.1 ± 11.4	48.4 ± 8.6	> 0.1
V	50.1 ± 17.7	54.8 ± 12.9	> 0.1
C. Percentage of workers inspecting spots			
I	30.6 ± 15.9	52.9 ± 4.3	< 0.02
II	18.9 ± 23.1	44.1 ± 32.7	> 0.1
III	13.9 ± 11.5	26.3 ± 16.0	> 0.1
IV	41.1 ± 19.7	41.5 ± 29.9	> 0.1
V	35.6 ± 5.0	43.6 ± 12.7	> 0.1

anal spots did indeed originate from the rectal vesicle. We then dissected 20 rectal bladders from workers of a foreign colony and squeezed their contents onto the surface of a 5 × 5 cm paper square in a pattern of randomly distributed spots. A second paper square was similarly spotted with the rectal sac contents of 20 workers from the home colony. One to two days later, the two squares were laid simultaneously on the floor of the arena of the home colony, 30 cm from each other, and the responses of nearby foraging workers were noted. The results of five replications are presented in Table 9. No significant difference was found in the initial attractiveness of the two kinds of squares (section A, Table 9). However, the alien marks induced a higher frequency of hostile posturing (B) as well as closer inspection (C). In all five replications the alien spots induced greater amounts of posturing; the difference was significant at the 99% confidence level in two of the replications and significant at the 90% confidence level in a third. Similarly, the alien spots were inspected by a higher percentage of workers in all five replications, with the difference being significant at the 98% confidence level in one.

The differences in responses to artificially applied spots were not as great as those observed in the earlier experiments conducted with natural spots (Ta-

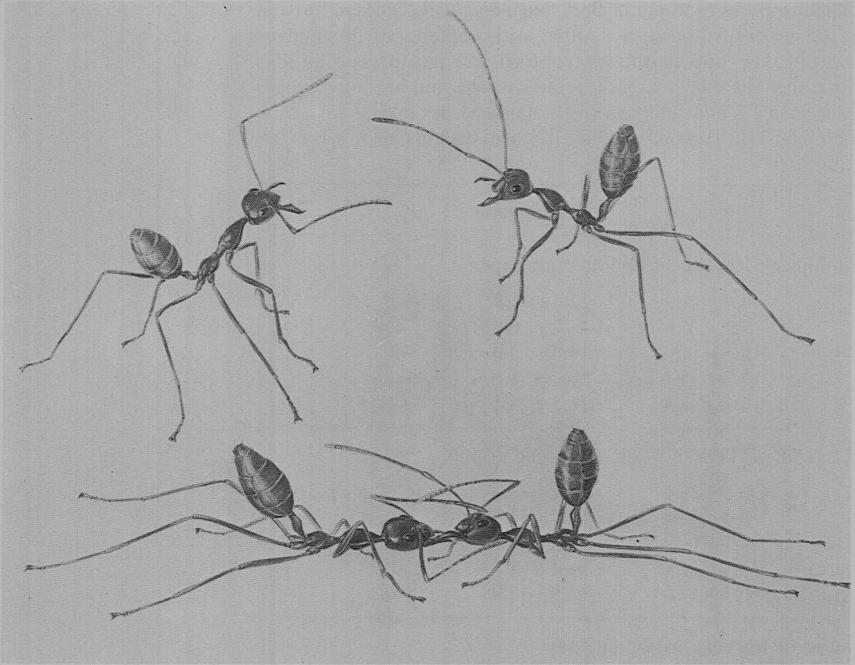


Fig. 18. Workers of different colonies conduct combat by rearing up on their legs and mandibles in a threat display (*above*), dodging around one another, and seizing one another with their mandibles (*lower*). Many such encounters end in injury or death. (Painting by Turid Hölldobler)

ble 8). This disparity probably resulted at least in part from tissue contaminants entering the rectal fluid when the sacs were removed and opened, even though the dissections were conducted very carefully. The presence of such contaminants was indicated by the fact that artificially created spots from nestmates caused a more hostile reaction than natural spots from nestmates. However, uncertainty over the amount of contamination makes it impossible to decide whether the territorial pheromone originates entirely from the rectal sac or is augmented in some way from materials originating elsewhere in the abdomen.

h) Warfare. When major workers from two *O. longinoda* colonies were permitted to enter an arena simultaneously, they quickly joined in a territorial battle. As individual pairs of opponents met, they reared up by straightening their legs and proceeded to dodge around each other like prancing, stiff-legged dancers (Fig. 18). This behavior was remarkably like that observed by Hölldobler (1976b) in the territorial wars of the honeypot ant *Myrmecocystus mimicus*. But whereas the *Myrmecocystus* relied principally on shoving and butting, the *Oecophylla* quickly added more deadly movements. Each thrust back and forth was an attempt to bite her opponent. When one succeeded in grasping a mandible, antenna, leg, or other part of the enemy's body thin enough to secure a good

grip, she bit down and pulled back on her legs. Sometimes the mandibles cut directly through, lopping off one of the appendages or slashing open the abdominal wall. Often the ant either let go and maneuvered for a better grip or else held on while trying to drag the opponent backward. At this point one or more of her nestmates might join the attack, taking advantage of the temporary immobilization of the enemy. The ant under attack then found herself spread-eagled by enemies pulling in different directions. In most instances she was dispatched over the next few minutes by further mandibular cuts.

Encounters with alien members of the same species were exceptionally exciting to the *Oecophylla* major workers. Those not detained in combat dashed in swift and irregular patterns over the arena floor, their mandibles open and abdomens frequently lifted to a vertical position. Some returned to the nest tree while laying odor trails in the characteristic manner of intense long-range recruitment. As the trail layers encountered nestmates they antennated them vigorously while jerking their bodies back and forth in swift, exaggerated movements (Fig. 15). The ants jerked at a frequency of 8–12 back-and-forth movements/s, and their displays usually lasted less than a second (0.3–0.8 s). We were impressed by the close similarity between this body signal and the motions displayed by the same ants when dodging around enemy *Oecophylla* workers. The signal can be plausibly interpreted as a ritualized version of overt fighting behavior.

During the experiments those colonies won that were able to assemble the heaviest battalions of major workers. To use the celebrated phrase of General Nathan Bedford Forrest during the American Civil War, the winners arrived at the battle scene 'fustest with the mostest.' The colony with the highest density of workers present was victorious in the largest percentage of duels, since small groups were able to gang up more frequently on single opponents. As the combat d'usure proceeded, and fatalities mounted, the more weakly represented colony was gradually eliminated from the arena. It finally was able to hold ground on the thin wooden bridges leading to its nest tree, where small masses of workers were sufficient to halt superior forces of enemy invaders. Occasionally, a colony forced back at first eventually turned the tide when earlier recruitment efforts resulted in a new surge of major workers entering the field.

It seemed to us that colonies engaging an enemy in their own arena had an initial advantage due to the greater readiness with which their foragers entered the familiar ground. In order to test this impression and to determine the cues being used by the ants themselves, we performed the following experiments. We allowed two vigorous, queenright colonies (A and B) to become thoroughly familiar with their own, separate arenas; the workers were also allowed to mark the papered floors with anal spots for a period of two or more days. The long axes of the two arenas were set at an angle of 90° to each other. We then removed the foragers overnight, and the following morning permitted workers from both colonies to come into one or the other two arenas simultaneously. Just before this step, however, the spatial arrangement of the colonies and the test arena was changed so as to give one colony or the other the advantage of prior familiarity with the visual cues, or odor cues, or both kinds of cues:

Table 10. The outcome of the first 30 min of territorial warfare between two colonies of *O. longinoda* (A and B), in which one colony or the other enjoyed the prior advantage of familiar odor cues (territorial pheromone), visual cues, or both

Replica- tion number	Visual cues		Odor cues		No. of workers laying trails (first 30 min)		Colony with familiar odor cue	Colony winning after 30 min
	A	B	A	B	A	B		
1		X		X	26	114	B	B
2		X	X		118	32	A	A
3		X		X	0	196	B	B
4		X	X		157	12	A	A
5	X		X		148	47	A	A
6		X	X		not recorded	not recorded	A	A
7	X			X	not recorded	not recorded	B	B
8	X		X		273	118	A	A
9	X			X	not recorded	not recorded	B	B

(a) Colony A and its arena were left in place and colony B was moved to the opposite end of A's arena; thus A had the advantage of prior familiarity with both visual and odor cues.

(b) Colony B was given the advantage of the above arrangement.

(c) Colony A was left in place, but the arena of B was substituted for its own arena, and colony B was shifted to the far end of the arena. Thus the visual advantage went to A, odor advantage to B.

(d) The reverse of (c) above, giving the visual advantage to B and odor advantage to A.

The responses of the two colonies were then recorded during the first 30 min. The data of nine replications are given in Table 10. In every case, the colony with the advantage of a familiar odor environment was ahead in the battle after the first 30 min, even when the colony was in an unfamiliar visual environment. The probability that such a sequence could occur by chance alone is only 1/256.

The result is perhaps not surprising, in view of the fact that foragers entering an arena previously marked by an alien colony showed greater aversion and hesitancy. As shown in Figure 17, they also laid odor trails and recruited nestmates at a higher initial rate. Sometimes the tide of battle was reversed as the retreating colony received a new surge of recruited workers. But the important consequence is the initial advantage gained by workers on ground marked by their nestmates. The effect is additional evidence of the existence of a true territorial pheromone.

Discussion

Five recruitment systems have now been identified in *Oecophylla longinoda*. They are directed respectively to food, new terrain, new nest sites and the organisation of emigration, enemies at short range, and enemies at long range. The characteristic traits of each are summarized in Table 11.

Table 11. Basic properties of the five recruitment systems of the African weaver ant *Oecophylla longinoda*

System	Chemical signals	Tactile signals	Pattern of movement	Apparent function
1. Recruitment to food	Odor trail from rectal gland; regurgitation of liquid crop contents	Antennation; head waving; mandible opening associated with food offering	Occasional signpost marking with looping trails laid around food source; main trail directly to nest	Recruitment of major workers to immobile food source, especially sugary materials
2. Recruitment to new terrain	Odor trail from rectal gland	Antennation, occasionally body jerking	Main trail directly to nest; broad looping movements resembling signpost marking; proceeds only after foragers physically contact terrain; increase in frequency of anal spotting	Recruitment of major workers to new terrain
3. Emigration	Odor trail from rectal gland	Antennation; physical transport of nestmates and tactile invitation of signals leading to transport	Main trail directly to nest site; no signpost marking; categories of nestmates carried follow predictable sequence	Emigration of colony to new nest site
4. Short-range recruitment to enemies	Short looping trails from sternal gland and exposure of gland surface with abdomen lifted in air	None	Trails short, looping, and limited to vicinity of contact with enemy	Attracts and arrests movement of nestmates; induces clumping and quicker capture of invaders and prey
5. Long-range recruitment to enemies	Odor trail from rectal gland	Antennation; at higher intensities, body jerking	Main trail leads directly to nest; no signposts laid	Attracts major workers to vicinity of invaders and prey; operates in conjunction with short-range recruitment; especially intense during territorial wars with conspecifics

In aggregate the five systems constitute the most complex and sophisticated such repertory yet discovered in any ant species. Given that this is a real distinction and not just the product of more careful research on *O. longinoda* in comparison with that previously devoted to other ant species, the question of interest is why the African weaver ant employs more complex communication. We suggest that it is a combination of the large worker size and strongly arboricolous life characteristic of the species, which two modifications have made it advantageous for *O. longinoda* colonies to maintain total and strict control over the areas surrounding their nests.

A smaller species than *O. longinoda* might be able to coexist with other ant species on the surface of trees by appropriating its own microhabitat and leaving other microhabitats to its competitors. Thus, like certain species of *Leptothorax* and *Melissotarsus*, such a form might specialize for life within and upon the bark, leaving hollow twigs and the upper surface of the tree to other small specialists. *O. longinoda* does not have this option. Its large size virtually dictates that it rely in part on larger, scarcer food items. Consequently a colony, unless it is to remain very small in population, must range widely over its nest tree—and beyond. The surface area of the tree is limited, and the biomass of potential prey in grams per unit area is less than on the ground, which is composed of complex layers of leaf litter, humus, soil, and large pieces of rotting wood. The weaver ant colony will find considerable advantage in excluding competitor colonies of all but the smallest or dietarily most different species. This exclusion *Oecophylla* accomplishes, as we have seen in the introductory section. The African weaver ant is exceptionally aggressive, and its territorial behavior is well organized and efficient. With this consideration in mind it is perhaps not surprising to learn that the *Oecophylla* workers utilize special communication systems both to speed the occupation of new terrain and to defend it once converted into territory.

These systems are distinctive, yet all except short-range recruitment to enemies still share many features with each other. It appears as if a basic, primitive system (food recruitment?) has been modified by slightly mutated replications of the behavior patterns. This case provides one more example, added to a number already elucidated (Wilson, 1971) of signal economy, that is, the utilization of the same or similar signals and behavior patterns, in differing combinations, to achieve different functions. Although *Oecophylla* may have occupied the same life style for over ten million years, it has differentiated four of its recruitment methods (to food, to territory, to new nest sites, and to enemies at long range) only slightly. On the other hand, it has invented one wholly new form of communication—short-range recruitment to enemies. Our interpretation of the significance of this novel method is that it serves to shift the foragers from an essentially random spatial pattern to one of moderate clumping, in which it is easier to subdue larger and more formidable opponents. The *Oecophylla* do not use short-range recruitment and do not clump in the presence of small intruders that can be handled by single defenders; they continue to move so as to maintain a random or at most slightly clumped pattern, which is more efficient for sweeping out small objects.

We have been impressed by the lack of a clear distinction between territorial defense and predation in the repertory of weaver ants. When intruders are killed, they are treated as prey and carried back to the nest to be eaten. To the extent that a dangerous enemy cannot be told apart from a benign intruder, the very distinction between territorial defense and simple predation is also blurred. And the close similarity between recruitment to intruders and recruitment to food makes more sense: they can be conceived as merely ends of a single continuum.

Yet the ants do make a distinction between principal kinds of food in their form of recruitment. In particular, they employ long-range recruitment much less frequently to large prey items than they do to honey. Watching the capture and retrieval of prey on numerous occasions, we have discerned what we believe to be the significance of this curious difference. Large, active prey elicit short-range recruitment and clustering of foragers already present in the general vicinity. These individuals are usually able to subdue such prey items and carry them back to the nest without help. Sugar sources, on the other hand, are commonly more extensive and longer-lasting, especially when in the field they consist of populations of homopterous insects. In such cases, long-range recruitment provides the more efficient means of harvesting.

Finally, the discovery of a territorial pheromone in *O. longinoda* deserves special emphasis. In our opinion, a true territorial pheromone should be defined as a substance used to mark the living or foraging space of an animal and that by itself induces aversive behavior in intruders of the same species. Many kinds of mammals, from rodents to ungulates, carnivores, and prosimians, mark their home ranges with scent. Authors commonly ascribe at least a partial territorial function to the pheromones, but the evidence is anecdotal and relatively weak in most cases (Shorey, 1976). On the other hand, strong experimental evidence has been adduced in the mouse *Mus musculus* and the European rabbit *Oryctolagus cuniculus* that scent deposited within territories induces increased alertness and a tendency to flee on the part of intruders (Mackintosh, 1973; Jones and Nowell, 1974; Mykytowycz, 1968). The odor alone inhibits trespassing of the territory by male mice (Mackintosh, 1973). Recently, Peters and Mech (1975) have summarized anecdotal evidence indicating that wolves employ urinary scent as a territorial pheromone.

To our knowledge no true territorial pheromone has previously been demonstrated in the social insects. It is possible that the existence of such a communication system in *O. longinoda* is an anomaly, representing one more aspect of the extreme development of territorial behavior in this ant. On the other hand, additional cases in ants may well be revealed when similar research is conducted on the more than ten thousand other species known to exist on earth.

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