
Ethological Aspects of Chemical Communication in Ants

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I. INTRODUCTION

The complex organization of an ant society depends on the efficiency of many different forms of communication, involving a diversity of mechanical and chemical cues. The functional division into reproductive and sterile castes, the cooperation in rearing the young, in gathering food, defending the nest, exploring new foraging grounds, and establishing territorial borders are regulated by the precise transmission of these signals in time and space. Probably the best studied communication behavior in ants is chemical communication. Chemical releasers, or *pheromones* as they are commonly called, are produced in a variety of exocrine glands. When these communicative secretions are discharged to the outside, they usually release a specific behavioral response in members of the same species. In recent years considerable progress has been made in chemically identifying many of these pheromones. In this report, however, I will not emphasize the natural product chemistry of ant pheromones (for review see Wilson 1971; Law and Regnier 1971; Blum 1974), so much as concentrate on the ethological aspects of chemical communication in ants.

II. COMMUNICATION BETWEEN SEXUAL STAGES

Males and females of social insects, no less than those of solitary insects, must communicate in order to find each other. Although female sex attractants have been demonstrated in many insect orders, the experimental evidence for sexual communication in ants is still scarce. The reason for this might be that most ant species have a short nuptial flight period, which occurs only once a year. Consequently, in only a few species can the reproductive behavior be studied in the laboratory. Nevertheless, more recent data demonstrate that in ants sexual behavior is regulated by chemical signals at least in part.

In the carpenter ant (*Camponotus herculeanus*) it has been demonstrated that the mass takeoff during the nuptial flight of both sexes is synchronized by a strongly smelling secretion released from the mandibular glands of the males. The males release this synchronizing pheromone during the peak of the swarming activity, at which time the females are stimulated to take off also (Hölldobler and Maschwitz, 1965). Although several compounds from the male mandibular glands are now chemically identified (Brand *et al.*, 1973; Falke, 1968), the effective component seems still to remain unknown. The mechanisms by which the females are attracted to one another after they have left the nest, as well as those controlling copulatory behavior, were only recently uncovered in a few species.

In the ponerine species *Rhytidoponera metallica* alate females are either absent or rare and apparently do not play a role in colony reproduction. Instead a portion of workers, externally morphologically indistinguishable from their fellows, possess functional spermatheca, are inseminated by males, and serve as reproductives in the colony (Whelden, 1960; Haskins and Whelden 1965). Since none of these worker reproductives or "ergatoids" has wings by which they can conduct nuptial flights, they have to employ other means to advertise their "readiness" for mating and attract flying males. We have now succeeded in analyzing the female sexual calling behavior in *Rhytidoponera metallica* (Hölldobler and Haskins, 1977). Ergatoid *R. metallica* emerge from the nest and group quietly near their nest entrance, with the head and thorax lowered to the ground, the gaster raised and arched, and the intersegmental membrane between the last two segments dorsally extended (Fig. 1). Males flying out from other nests are attracted by these "calling" females. On drawing close to a female the male first touches her with his antennae, then grasps the female's thorax with the mandibles. While riding on her back, he extends his copulatory apparatus in search of the female's genitalia. If she is ready to mate, she turns her abdomen slightly to the side, so that the male is able to couple. Then the male releases his mandibular grip on the female's thorax. With the pair in this position the copulation can last from a few seconds to several minutes (Fig. 1). During calling the female exposes a large, hitherto unrecognized gland, which opens dorsally between the last two abdomi-

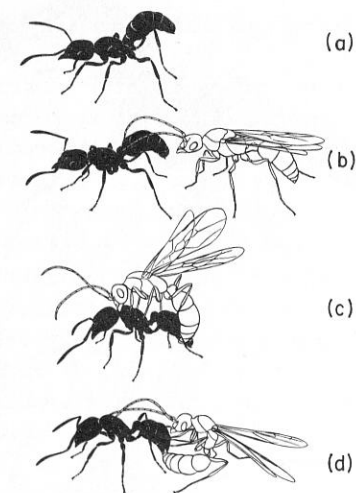


FIG. 1. Mating in *Rhytidoponera metallica*. From above: (a) Ergatoid female (black) in calling posture, during which the dorsal intersegmental membrane between the last two segments is extended. (b) A male (white) approaches a calling female, touching her with his antennae. (c) The male grasps the female at the thorax and mounts her. Simultaneously he extends his copulatory organ in a search for the female's genitals. (d) Copulation: the male has released his mandibular grip on the female's thorax. The drawings are based on photographs and observations. (From Hölldobler and Haskins, 1977.)

nal tergites (Fig. 2). We called this organ the *tergal gland* and were able to demonstrate that its secretions release agitated locomotion and attraction in *R. metallica* males. When several males were exposed to tergal gland secretions, some of them attempted to mount one another. When a worker was made available, some males tried to mate with it, even though it was not "calling." These results strongly suggest that some *Rhytidoponera metallica* workers discharge a sex attractant from the tergal gland during sexual calling. A similar calling behavior has been described in the myrmicine ant *Harpagoxenus sublaevis*, the calling females of which release a sex pheromone from the poison gland (Buschinger, 1968, 1972). Similarly we could demonstrate that another myrmicine species, *Xenomyrmex floridanus*, produces a sex pheromone in the poison gland, while a third, pharaoh's ant (*Monomorium pharaonis*), manufactures it in the Dufour's gland (Hölldobler, 1971a; Hölldobler and Wüst, 1973).

This leads us to another very little investigated aspect of reproductive behavior in ants, namely, the behavioral mechanisms of reproductive isolation in closely related sympatrically living species. In some areas of the southwestern United States several species of the harvester ant (*Pogonomyrmex*) do coexist in the same habitat. Our recent investigations demonstrated that the sympatric species

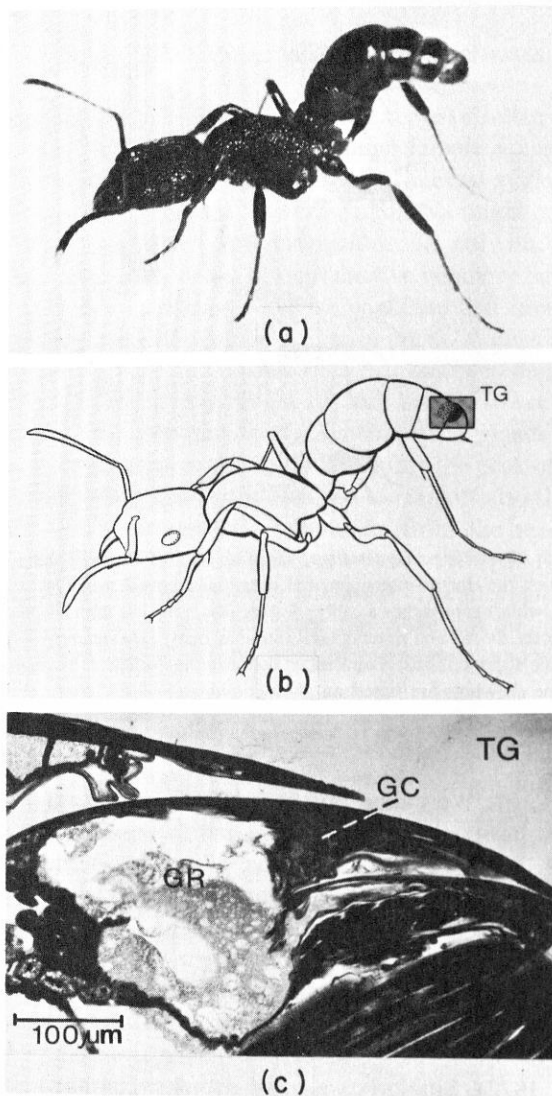


FIG. 2. *Rhytidoponera metallica* female in calling posture (a). Note the expanded intersegmental membrane between the last two tergites, the location where the tergal gland (TG) opens to the outside (b). (c) Longitudinal section through the gaster of a *R. metallica* female, showing the tergal gland (TG) with its glandular cells (GC) and reservoir (GR). (From Hölldobler and Haskins, 1977.)

Pogonomyrmex maricopa, *P. desertorum*, *P. barbatus*, and *P. rugosus* are reproductively isolated in part by their distinct daily nuptial flight rhythms (Hölldobler, 1977a). *Pogonomyrmex maricopa* swarms in the morning between the hours of 10:00 and 11:30, followed by *P. desertorum* (11:00–13:00), while the

remaining two species conduct their nuptial flights in the afternoon (*P. barbatus* 15:30–17:00; *P. rugosus* 16:30–18:00). In addition, however, these species are also separated by the use of communal mating sites. For example, an intensive search for the mating aggregations of *P. rugosus* over an area of about 360,000 square meters revealed a single place on the ground to which winged reproductive forms from a wide area converged, primarily by flying upwind. This arena was approximately 60 × 80 m. The first individuals to arrive were males, which alighted and ran about in a frenzied manner. Soon afterward females also began to arrive. As soon as each female alighted, she was surrounded by 3–10 males (Fig. 3). At the height of the activity thousands of such mating clusters literally covered the ground, with as many as 50 mating clusters concentrated in 1 m².

Females often copulated with as many as four males in succession. After mating, the females freed themselves from the surrounding males, climbed on grass leaves, and took off again from the mating arena. Some of them flew long distances (more than 100 m), others only short distances before landing a second time. Then each shed her wings and started to excavate a shallow nest chamber in the soil. General activity in the mating arena lasted about 2 hr, ceasing altogether around 19:00 hr. By this time almost all females had left, and the males were beginning to withdraw into shelters around the aggregation area such as crevices beneath grass clumps or little holes in the soil. There the males remained clustered overnight and through the following day until 15:00–16:00, when they become active again. Then, as on the preceding day, new males arrived in the

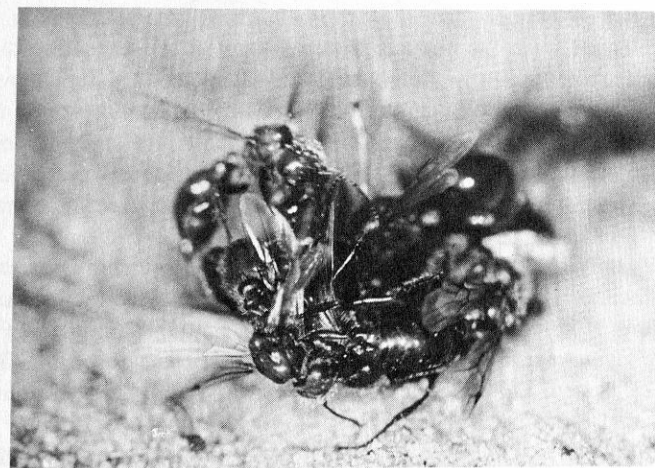


FIG. 3. Mating cluster of *Pogonomyrmex rugosus*. A female is surrounded by approximately 10 males. (From Hölldobler, 1976b.)

mating arena, and shortly afterwards new females flew in. These cycles continued for three additional consecutive days.

In the following two years we found mating aggregations of *P. rugosus* in the same arena. Two additional *P. rugosus* arenas were found, one about 1000 m and the other about 900 m distant from the first site. These also appeared again in the same two areas the following year.

Similar observations were made with *P. barbatus*. Of a total of eight mating sites, five were utilized again in the following year. Their areas varied from approximately 10×20 m to 40×50 m. As in *P. rugosus*, males formed sleeping aggregations and stayed at the places up to seven consecutive days. Somewhat different behavior was displayed by the two remaining species of *Pogonomyrmex*. Unlike *P. barbatus* and *P. rugosus*, which aggregated on the ground, *P. maricopa* and *P. desertorum* selected trees or bushes (approximately 2–4 m high) to gather for mating activities. Although there seems to be greater flexibility in choosing specific trees, we found four particular trees that served repeatedly as mating sites in two consecutive years.

No topographic cues have yet been found that characterize the specific traditional communal mating arenas. In all four species, however, the males discharge a mandibular gland secretion upon landing at the site. The sweet odor of the secretion, which apparently stems from one of its two major components, 4-methyl-3-heptanone or the respective alcohol (McGurk *et al.*, 1966), can sometimes be smelled by observers 10–15 m downwind. Since the males as well as the females approach the site by flying upwind, it seemed likely that they are attracted by this specific pheromone. We plan to test this hypothesis in the near future.

How do the males recognize their reproductive partners, and how is sexual behavior released once the sexuals have assembled at the mating sites? Our experimental results clearly demonstrated that poison gland secretions of *Pogonomyrmex* females stimulate sexual behavior in *Pogonomyrmex* males. In addition, circumstantial evidence strongly indicates that a species-specific surface pheromone is also involved, and that this substance is perceived by the males only when they approach closely enough to make direct antennal contact (Hölldobler, 1977a).

In insects only honeybee drones have been known to assemble every year at the same locations (Zwarlicki and Morse, 1963; Ruttner and Ruttner, 1965, 1972; Strang 1970). Our investigations of the mating strategies of the four sympatric *Pogonomyrmex* species revealed what appears to be the first vertebrate-like lek system known in ants. Usually in a vertebrate lek, males occupy small personal territories in which they engage in special displays. Females, which are attracted to the leks, presumably by the communal display, choose one of the males, in some cases after comparing the individual male displays. Although *Pogonomyrmex* males do not occupy personal territories, male competi-

tion is extremely high and, as in other leks, females seem to be able to select for especially persistent male partners. Presumably females are more strongly attracted to areas where many males are assembled and where they have a choice, in comparison to single males. In fact it is expected that the female's choice strategy forces male aggregations. On the other hand, as Alexander (1975, p. 71) has pointed out, "once mating is largely or entirely restricted to male aggregations... every male profits from cooperation." It is obvious that large groups of *Pogonomyrmex* males that discharge a lek pheromone collectively attract a larger number of females. It thus appears to us that the courting assemblies of harvester ants resemble in many ways the lek behavior of vertebrates.

III. ALARM COMMUNICATION

Like many solitary insects, social insects use chemicals to repel predators. In social insects, however, defensive responses are closely connected with alarm communication. In many cases the discharge of alarm pheromones and defensive substances is accompanied by characteristic body movements and postures (Fig. 4). The species of *Formica* spray mixtures of formic acid and Dufour's gland

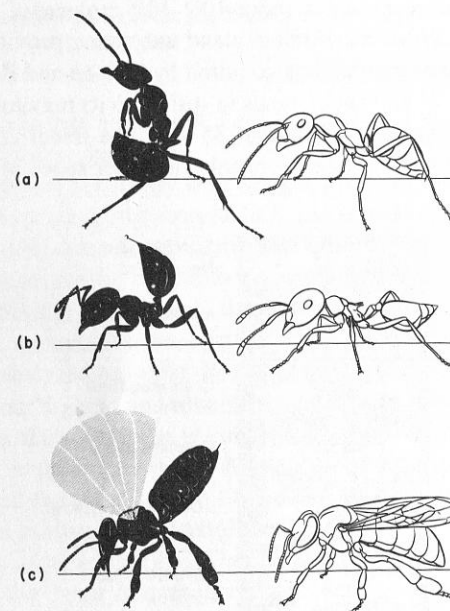


FIG. 4. The alarm-defense behavior (black) is contrasted with the normal posture (white). (a) *Formica polycetena*; (b) *Crematogaster ashmeadi*; (c) *Apis mellifera*. (From Hölldobler, 1970b.)

secretions, both serving simultaneously as defensive substances and alarm pheromones (Maschwitz, 1964). During the emission the ants bend their gasters forward beneath their legs. Species of the myrmicine genus *Crematogaster* lift their abdomen to a characteristic vertical position or even forward over the head while releasing the defensive secretion through the sting and alarm pheromones from the mandibular glands (Blum *et al.*, 1969). The same defensive behavior has been observed in Dolichoderinae, in *Oecophylla*, in *Solenopsis fugax*, *Monomorium pharaonis*, and in many other myrmicine species. Wilson (1958), and Butenandt *et al.* (1959) carried out the first experimental investigations on alarm pheromones in ants. Butenandt and co-workers worked with the leaf cutter ant *Atta sexdens*, while Wilson studied the harvester ant *Pogonomyrmex badius*. In both species workers discharge a strongly smelling substance out of the mandibular glands (the morphological location of various pheromone glands is illustrated in Fig. 5) if they perceive some kind of threatening stimulus. McGurk *et al.* (1966) identified this alarm pheromone of *Pogonomyrmex* as 4-methyl-3-heptanone. Wilson and Bossert (1963) were able to study precisely the behavioral and physiological parameters of chemical alarm communication. By directly measuring the effects of the pheromone from whole crushed glands they found that workers respond to the threshold concentration averaging 10^{10} molecules per cubic centimeter by moving toward the odor source. The total capacity of the gland reservoir is about 10^{15} – 10^{16} molecules. As a consequence the entire content of the mandibular gland substance provides a brief signal. According to the experimental data acquired by Wilson and Bossert, the amount of alarm pheromone of one ant expands in still air to its maximum radius of about 6 cm in 13 sec and fades out in about 35 sec. The lower concentration at the periphery releases attraction behavior; only the inner space of higher concentra-

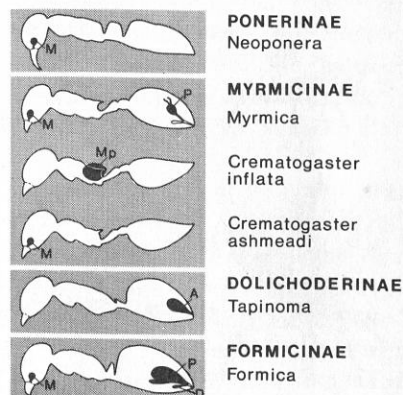


FIG. 5. Alarm pheromone glands in ants: A = anal gland, D = Dufour's gland, M = mandibular gland, Mp = metapleural gland, P = poison gland. (From Hölldobler, 1977b.)

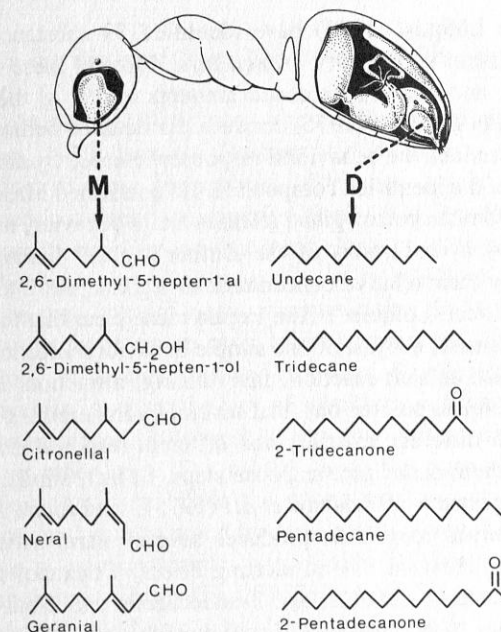


FIG. 6. Substances found in the mandibular gland and Dufour's gland of the ant *Acanthomyops claviger*. Undecane and the mandibular gland substances function both as defensive substances and as alarm substances. D = Dufour's gland, M = mandibular gland. (After Regnier and Wilson, 1968.)

tion, which expands to a radius of 3 cm and fades out in about 8 sec, induces real alarm and aggressive behavior.

These parameters seem very well designed for an economical alarm system. If the danger is local and only short lasting, the signal fades out quickly and only a small group of workers in the immediate vicinity are alerted. If, however, the danger is more persistent, the number of workers discharging the signal increases rapidly, and the signal "travels" through the colony.

The alarm communication system of *Acanthomyops claviger* (Fig. 6) is another well-analyzed example. Regnier and Wilson (1968) found that undecane from the Dufour's gland and a number of terpenes produced in the mandibular glands release alarm response at concentrations of 10^9 – 10^{12} molecules per cubic centimeter. The quantity of these substances combined in one ant totals about 8 μ g. Behavioral experiments have shown that the chemical alarm signal generated by all volatile substances of a single worker releases a response in nestmates up to a distance of about 10 cm. This defensive strategy is well adjusted to the structure of the large *Acanthomyops* colonies, which live widely dispersed through subterranean nests. As in *Pogonomyrmex badius*, the *Acanthomyops* signal fades out rather quickly unless reinforced by other alarming ants.

Bergström and Löfquist (1973) have identified 39 substances from the secretions of the Dufour's gland of *Formica rufa*. Most of these substances were present in traces, and only 11 exceeded amounts of 1% of the total glandular secretions. Recently Löfquist (1976) conducted a detailed behavioral study during which he determined the behavioral responses released by single components and by mixtures of the identified compounds. He confirmed Maschwitz's finding that formic acid from the poison gland releases alarm behavior, and he also found that the combined hydrocarbons of the Dufour's gland function as an alarm signal. Apparently their relative concentrations regulate the intensity and duration of the alarm effect. Löfquist's study again made clear that the alarm defense behavior in ants consists not just of one simple behavioral reaction but of several response steps, such as alert reaction, fast running, attraction, and attack. It is conceivable, as Löfquist pointed out, that several hydrocarbons of a homologous series, due to their different volatility and different response threshold concentrations, regulate these behavioral response steps. In fact, similar considerations were recently suggested by Bradshaw *et al.* (1975), who found that the African weaver ant *Oecophylla longinoda* produces several alarm substances in their mandibular glands. Hexanal has an alerting effect, 1-hexanol functions as an attractant and orientating stimulus, and 3-undecanone and 2-butyl-2-octenal release attack behavior. It is interesting to note that hexenal is the most volatile and 2-butyl-2-octenal the least volatile compound. The first substance alerts nestmates several centimeters away; when the alerted ants have rushed to the source of disturbance, attack and biting behavior is released by the latter substance.

Although alarm signals are not very species specific, the efficiency of an alarm pheromone nevertheless seems to depend on certain structural characteristics. Blum *et al.* (1966) tested a series of 49 ketones on *Iridomyrmex pruinosus* to find out the relationship between chemical structure and alarm-inducing power. The natural alarm pheromone is 2-heptanone. By increasing the number of carbon atoms from 3 to 13 a very low activity was elicited by the first (C_3 - C_4) and the last (C_{11} - C_{13}) of the 2-alkanone series. An optimal reaction occurred between C_6 and C_9 . Other structural variations, such as a displacement of the carbonyl group, the introduction of a second ketone group or the presence of side-chain methyl groups, usually lowered the response-eliciting efficiency of the substance. Similar results were obtained by Regnier and Wilson (1968) for *Acanthomyops claviger*. They found that alkanes falling between C_{10} and C_{13} usually elicited good response from the workers and showed excellent properties as alarm substances. The main component of the natural alarm substances is undecane, a C_{11} alkane. Riley *et al.* (1974a, b) recently found that workers of *Atta texana* and *A. cephalotes* produce only the (+) isomer of the alarm pheromone 4-methyl-3-heptanone. In behavioral tests it was apparently demonstrated that

workers of *A. texana* distinguish the (+) isomer of this ketone from the (-) isomer.

Many alarm pheromones have been chemically identified (see reviews by Gabba and Pavan, 1970; Law and Regnier, 1971; Wilson, 1971; Pain, 1973; Blum 1974). Most of them are ketones, aldehydes, acids, or hydrocarbons. They are produced in a variety of exocrine glands (see Fig. 5). In summarizing the behavioral results one can say that most alarm pheromones in ants are not very specific. This is not surprising because there is little if any selective pressure to develop species specificity of alarm communication. In fact, in many cases it seems even advantageous to be able to understand the alarm signals of a neighboring colony of another species. However, Regnier and Wilson (1971) demonstrated one case in which the lack of specificity can turn to a disadvantage under some circumstances. It is well known that certain ant species conduct "slave raids" on other ants. The raiders bring the pupae of the raided ant colonies into their own nest. When the young workers eclose to adults, they function in the raiders' nest as brood tenders, nest builders, foragers. The raider workers continue to conduct mainly "slave raids." Often the raiders are obviously superior in fighting ability (Fig. 7). *Polyergus*, for example, has specially adapted saber-shaped mandibles. The slave-raiding species *Formica pergandei* and *F. subintegra*, do not carry such armament but instead possess remarkably enlarged Dufour's glands. Regnier and Wilson identified as principal components of the glandular substances decyl acetate, dodecyl acetate, and tetradecyl acetate. One worker of *F. subintegra* contains the relatively enormous amount of 700 μ g of these substances. During the slave raids the raider ants discharge these substances upon encountering prey workers and apparently stimulate nestmates to join them in the fighting. In addition, they spray large amounts of the acetates on defending slave ants. It is interesting that these substances not only alarm and stimulate the raider species but they also highly excite the slave ant species. The high concentration of the discharged acetate mixture, however, completely "confuses" the slave ants. They become disoriented, making it easy for the raiders to penetrate the slave ants' nest and to remove the pupae.

The response behavior to an alarm signal varies in time and space, and it varies in different groups and castes of the society. For example, if the signal is discharged close to the nest, it releases aggressive behavior, but at a greater distance from the nest it elicits escape behavior (Maschwitz, 1964). Furthermore, young workers usually retreat into the nest when they smell the alarm signal, while older workers, especially those belonging to the soldier castes, move out and display aggressive behavior (Cammaerts-Tricot, 1975; Wilson 1975).

Cammaerts-Tricot (1974) and Wilson (1975, 1976) have demonstrated that some ant species organize a colony defense by recruiting nestmates with the aid of chemical trails laid down from the vicinity of the intruders back to the nest.

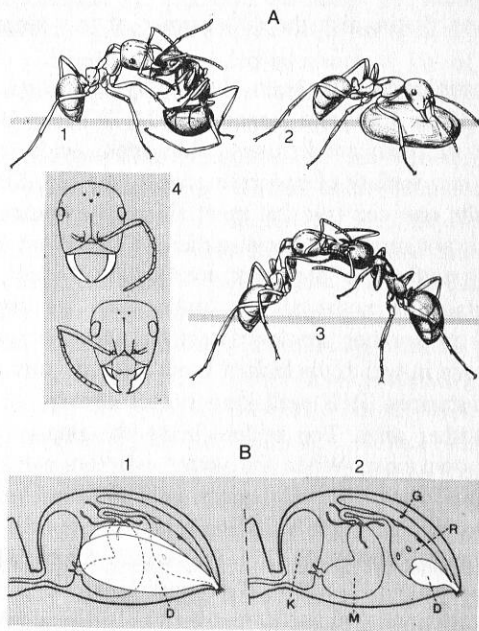


FIG. 7. (A) (1) A worker of the slave raider ant *Polyergus rufescens* (left) attacks a slave ant *Formica fusca* (right); (2) the slave raider carries a pupa of *F. fusca* homeward; (3) a *Polyergus* worker is fed by a *F. fusca* slave ant, which has eclosed from a captured pupa; (4) the saber-shaped mandibles of *Polyergus* are contrasted with the "normal" mandibles of the slave ant species, *Formica fusca*. (B) (1) Gaster of the slave raider ant *Formica subintegra*, showing the enormously developed Dufour's gland (D); (2) gaster of the slave ant *Formica subsericea* with normal Dufour's gland. G = poison gland, R = hindgut, K = crop, M = midgut. (From Hölldobler, 1973a.)

For instance, Wilson discovered that only a few workers of the fire ant *Solenopsis invicta*, introduced into the foraging arena of a *Pheidole dentata* nest invariably release a typical defensive response. Some of the foraging *Pheidole* minor workers

... grapple with the intruders, while others flee momentarily and run in irregular circles through the surrounding area. Within several minutes, some of the minor workers run back to the nest, dragging the tips of their abdomens over the ground. The trail thus deposited attracts both minor and major workers from the nest in the direction of the invaders. The trail pheromone comes from the poison gland and is emitted through the sting. ... Upon arriving at the battle scene the major workers become highly excited, snapping at the fire ants with their powerful mandibles and soon chopping them to pieces (Wilson, 1975, p. 798).

Furthermore Wilson demonstrated that *Pheidole dentata* is able to identify specifically its major enemy ant genus *Solenopsis*. Only one *Solenopsis* worker is

enough to release the effective alarm recruitment behavior in *Pheidole dentata*. Indeed, several *Solenopsis* species seem to be specialized to raid and prey on other ant species, and, as a recent study suggests, some of them may employ powerful chemical strategies to invade nests of their prey species (Hölldobler, 1973b). For example, the European thief ant, *Solenopsis (Diplorhoptrum) fugax*, usually lives within the close vicinity of other ant colonies and preys on the brood of its neighbors. Scout workers of *Solenopsis* build an elaborate subterranean tunnel system leading into the neighboring species' brood chambers. As soon as the construction of these tunnels is completed, the scouts lay chemical trails back to their own nest and recruit masses of nestmates in order to invade and to raid the neighboring ant's brood nest. The recruitment pheromones by which the raids are organized originate from the Dufour's gland. While invading the brood chambers and preying on the brood, *Solenopsis* workers also discharge a highly effective and long lasting repellent substance from the poison gland. This secretion prevents the brood tending ants from defending their own larvae and enables *Solenopsis* to rob brood virtually without interference. Laboratory experiments have shown that the secretion of the poison gland releases an intense repellent reaction in workers of 18 different ant species. When a small entrance leading to the brood chamber of a *Lasius flavus* nest was contaminated with the secretion of a single *Solenopsis* poison gland, the entrance was not used by *Lasius* workers for almost 1 hr. These and other experiments have clearly demonstrated that *Solenopsis fugax* workers produce a powerful ant repellent in their poison gland, which enables them to invade the nests of other ant species and to prey on the foreign brood (Hölldobler, 1973b).

IV. RECRUITMENT COMMUNICATION

In order to efficiently exploit newly discovered food sources and nesting sites ant societies require both special communication and orientation signals. The study of recruitment systems in ants has begun to diversify during the past five years. In the 1950s and 1960s 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 (see reviews in Wilson, 1971; Blum, 1974; Maschwitz, 1975; Hölldobler, 1973a, 1977b). Now a new emphasis has begun to emerge: the analysis of the organizational levels and the ecological significance of recruitment. The possession of one kind of recruitment system as opposed to another seems 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.

The recruitment techniques employed by different groups of ant species vary considerably. The best studied recruitment behavior is the chemical trail communication. Carthy (1950, 1951) was one of the first to conduct an experimental study on trail laying in *Lasius fuliginosus*. He found strong circumstantial evidence that in this species the trail pheromone originates from the hindgut. This suggestion was later confirmed by Hangartner and Bernstein (1964). Wilson (1959a) working with the fire ant *Solenopsis invicta* (= *S. saevissima*), provided the first bioassay methods to test trail-following behavior even in the absence of a trail-laying ant. He laid artificial trails of different glandular extracts away from the nest entrance and from worker aggregations. By comparing the trail-following response of worker ants, he was able to identify the Dufour's gland as the source of the trail pheromone of the fire ants. This technique was subsequently used by many investigators, leading to the discovery of a number of trail pheromone glands in different taxonomic groups of ants (Fig. 8).

Wilson's (1962) analyses also revealed for the first time the organization of chemical mass communication in fire ants. It was found that the number of workers leaving the nest along the trail is controlled by the amount of trail substance discharged by workers already on the trail. Using the purified trail pheromone it was demonstrated that the number of ants drawn outside the nest is a linear function of the amount of the substance presented to the colony. This means that under natural conditions the number of workers being recruited can be

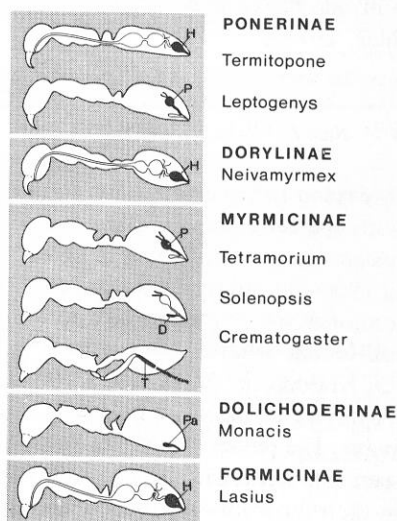


FIG. 8. Trail pheromone glands (black) in several species of five subfamilies of ants. H = hindgut, P = poison gland, D = Dufour's gland, T = tibial gland, Pa = Pavan's gland. (From Hölldobler, 1977b.)

accurately adjusted to the actual needs of recruits at the food source. In other words, the better the food source, the more workers lay an odor trail when they return to the nest. This increases the amount of trail substance discharged and in turn draws more ants to the food source. As the food slowly diminishes, fewer workers lay a trail, with the result that the concentration of the trail substance, which has a relatively high evaporation rate, decreases, and, in turn, a smaller number of workers is stimulated to leave the nest. The phenomenon is called *mass communication* because it entails the transmission of information that is meaningful only with reference to larger groups and cannot be exchanged between mere pairs of individuals. Subsequently, Hangartner (1969b) demonstrated that even individual ants can contribute to the flexibility of this mass communication system. Individual workers of *Solenopsis* are apparently able to adjust the amounts of their own pheromone emissions to the specific food needs of their colony and to the quality of the food source. By inducing the homing foragers to lay their trail on a soot-coated glass plate Hangartner found that the continuity of the sting trail increases with increasing starvation time of the colony, increasing quality of the food source, and decreasing distance between the food and the nest.

This mass communication system is certainly a highly advanced recruitment method. In an attempt to find out from which more primitive forms of recruitment communication this system may have evolved, it is necessary to analyze and compare less sophisticated modes of recruitment communication. The so-called "tandem running behavior" is generally considered to be one of the most primitive recruitment methods. Only one nestmate is recruited at a time, and the follower has to keep close antennal contact with the leader ant. This behavior has been described in a phylogenetically scattered array of species including *Camponotus sericeus* (Hingston, 1929), *Ponera eduardi* (LeMasne, 1952), *Cardiocondyla venestula* and *C. emeryi* (Wilson, 1959b), *Leptothorax acervorum* (Dobrzanski, 1966), and *Bothroponera tessierinoda* (Maschwitz *et al.*, 1974; Hölldobler *et al.*, 1973). Until recently, however, nothing had been learned about the precise nature of the signals involved.

The analyses of the signals by which tandem running is organized in the myrmecine ant *Leptothorax acervorum* have now led to the discovery of a new kind of signal in ant communication, for which we proposed the term "tandem calling" (Möglich *et al.*, 1974b). When a successful scouting forager of *Leptothorax acervorum* returns to the colony, it first regurgitates food to several nestmates. Then it turns around and raises its gaster upward into a slanting position. Simultaneously the sting is exposed and a droplet of a light liquid extruded (Fig. 9). Nestmates are attracted by this calling behavior. When the first ant arrives at the calling ant, it touches it on the hindlegs or gaster with its antennae, and tandem running starts. The recruiting ant leads the nestmate to the newly discovered food source. During tandem running the leader ant lowers the

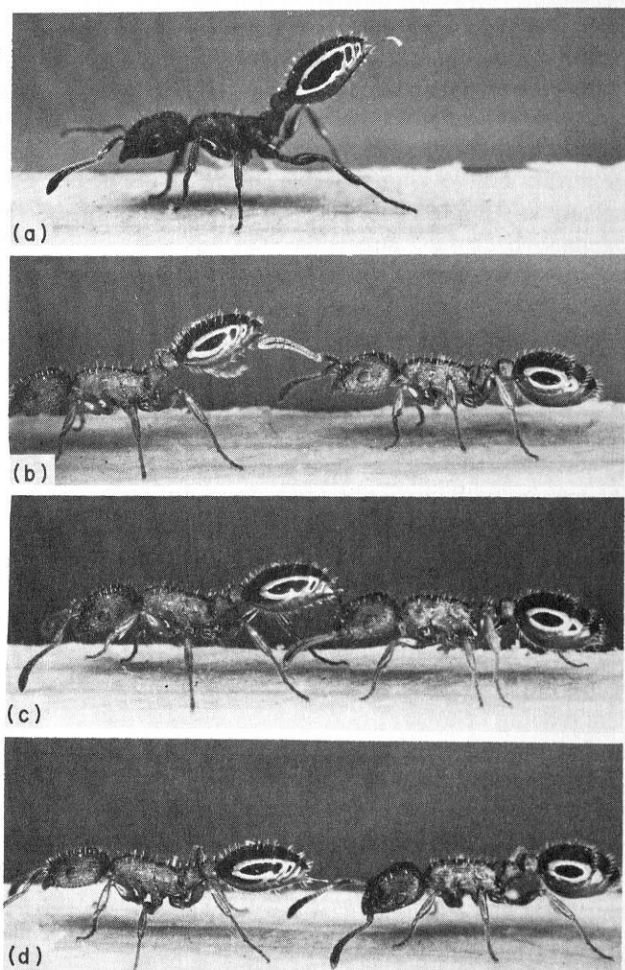


FIG. 9. Behavioral exchange of signals leading to tandem running in *Leptothorax acervorum*: (a) A recruiting worker assumes the calling position; (b and c) a nestmate arrives and touches the gaster (b) and hindlegs (c) of the calling ant with its antennae; (d) the calling ant lowers its gaster and tandem running starts. The sting of the recruiting ant remains extruded, but is not dragged over the surface. (From Möglich *et al.*, 1974b.)

gaster, but the sting remains extruded. It, however, is not dragged over the surface, as it is in the case of those ant species that lay chemical trails from their stings. The follower keeps close antennal contact with the leader, continuously touching its hindlegs and gaster. Whenever this contact is interrupted, for example, when the follower accidentally loses its leader or is removed experimentally, the leader immediately stops and resumes its calling posture. It may remain in this

posture for several minutes, continuously discharging the calling pheromone. Under normal circumstances the lost follower rather quickly orients back to the calling leader ant and tandem running continues. We have found similar tandem calling behavior in *Leptothorax muscorum* and *L. nylanderii*.

The analyses of this interesting recruitment behavior has revealed two signal modalities by which tandem running is organized:

1. If a tandem pair has been separated the leader immediately stops and assumes the calling posture. However, when the ant is carefully touched with a hair at the hindlegs or gaster with a frequency of at least two contacts per second, the leader continues running to the target area. This experiment shows that the absence of the tactile signals normally provided by the follower ant is sufficient to release "tandem calling" by a leader ant.

2. The calling pheromone originates from the poison gland. In our studies workers were strongly attracted to dummies that had been contaminated with poison gland secretions but not to secretions of the Dufour's gland. Further experiments revealed that the poison gland substance not only functions as a calling pheromone but plays an important role during tandem running itself by binding the follower ant to the leader. It was found that the leader could easily be replaced by a dummy contaminated with poison gland secretions. Gasters of freshly killed ants from which the sting with its glands had been removed could not replace a leader ant. However, when they were contaminated with secretions of the poison gland, they functioned effectively as leader dummies.

The discovery of a chemical "tandem calling" in *Leptothorax* throws considerable light on the evolution of chemical recruitment techniques in myrmicine ants. It now seems very plausible that the highly sophisticated chemical mass recruitment performed by *Solenopsis* and certain other myrmicine ants was derived from a more primitive chemical tandem calling behavior of the *Leptothorax* mode. With the exception of *Crematogaster*, which produces a trail pheromone in the tibial glands of the hindlegs (Leuthold, 1968b; Fletcher and Brand, 1968), all other myrmicine species generate the trail pheromone from one of the sting glands (see Fig. 8). It is conceivable that a chemical calling behavior, during which an alerting and attracting pheromone is discharged through the sting into the air, was one of the first steps that led to chemical trail laying and mass communication in myrmicine ants.

In addition the tandem calling behavior is also relevant to the evolution of sex pheromones in myrmicine ants. As mentioned above it has been demonstrated that in several myrmicine species the pheromones originate from the sting glands (Hölldobler, 1971a; Buschinger, 1972; Hölldobler and Wüst, 1973). It is interesting to note that in species in which wingless ergatoids attract males for mating, as for example *Harpagoxenus sublaevis* (Buschinger, 1968), the females display sexual calling behavior apparently identical to the tandem calling be-

havior of *Leptothorax*. This discovery supports the hypothesis that in at least some myrmicine ants sex attractants and recruitment pheromones had the same evolutionary origin. In fact, in some cases the same substances may function in specific situations as sex pheromones and in others as recruitment signals.

In formicine ants the trail pheromones originate from the hindgut (Blum and Wilson, 1964; Hangartner and Bernstein, 1964; Hangartner, 1969a; Hölldobler, 1971c; Hölldobler *et al.*, 1974; Barlin *et al.*, 1976). The analyses of the tandem running technique in the formicine species *Camponotus sericeus* has similarly revealed some of the basic behavioral patterns out of which the more sophisticated methods of "group recruitment" and "mass recruitment" employed by other formicine species may have been evolved (Hölldobler *et al.*, 1974; Möglich *et al.*, 1974a).

In *Camponotus sericeus* the first scouting ant to discover the food source typically fills its crop and returns to the nest. As the worker heads home, it touches its abdominal tip to the ground for short intervals. Tracer experiments have shown that the ant is depositing chemical signposts with material from her hindgut. Inside the nest she performs short-lasting fast runs, which are interrupted by food exchange and grooming behavior. After several regurgitations, the recruiter ant now performs brief food offerings while facing nestmates head on. During one recruitment performance such "rituals" were observed to be repeated 3–16 times. Apparently this behavior functions to keep nestmates in close contact with the successful scout ant. When the scout finally leaves the nest to return to the food source, those ants encountered by the recruiting ant usually try to follow the leader. However, ordinarily only one ant, the one that keeps closest antennal contact with the leader, succeeds in following it. Most of the recruited ants, after feeding at the food source, turn straight back to the nest where many of them start to recruit nestmates on their own. Experiments have shown that the hindgut trail, laid down by homing foragers, has no recruitment effect at all. Only experienced ants follow the trail and use it as an orientation cue. Similarly, during tandem running the presence or absence of the trail pheromone is insignificant. The leader ant and the follower are bound together by a continuous exchange of tactile signals and by a very persistent surface pheromone.

We discovered that *Camponotus sericeus* also employs the tandem running technique for recruitment of nestmates to new nesting sites. Since in this case a whole colony has to be recruited, the behavioral patterns initiating tandem running can be expected to be different from those used during recruitment to food sources. As depicted in Fig. 10, this is indeed the case. When facing the nestmate head on, the recruiter grasps it on the mandibles and pulls it heavily forward. Shortly afterwards it loosens the grip, turns completely around and presents its gaster to the nestmate. If the nestmate responds by touching the recruiting ant's gaster or hindlegs, tandem running starts. This behavioral sequence is very

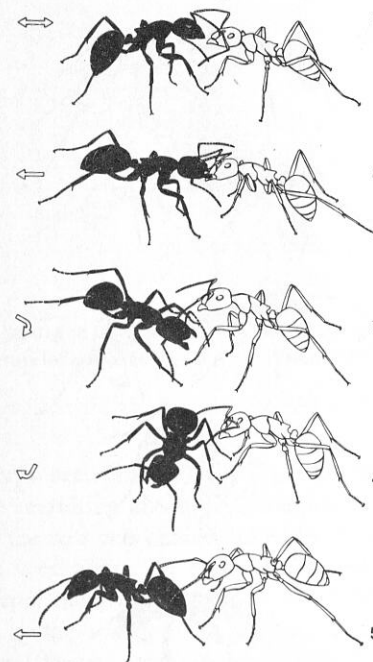


FIG. 10. Invitation behavior to tandem running in *Camponotus sericeus*. (1) the recruiter (black) approaches a nestmate (white) and displays for about 2–3 sec a jerking behavior. (2) The recruiting ant grasps the nestmate at the mandibles and pulls it a distance of about 2–20 cm. (3) The recruiter loosens its grip and (4) turns around 180 degrees. (5) The recruiter presents its gaster to the nestmate. The nestmate contacts the gaster and hindlegs of the leader ant, then tandem running starts. The arrows indicate the direction of the movements. (From Hölldobler *et al.*, 1974.)

stereotyped and is regularly employed when nestmates are invited to follow the signaller to a new nest. We therefore have called this behavior *invitation behavior*.

It is interesting to note that some of the ants that fail to respond to the "invitation signals" are carried to the target area. The first behavioral sequences that initiate carrying behavior are almost identical with that of the "invitation behavior." The main difference is, however, that the recruiting ant keeps the firm grip when turning around. The nestmate is thereby slightly lifted, a movement that apparently causes it to fold its legs tightly to the body and roll its gaster underneath. It is carried to the target area in this posture (Fig. 11). For more details about social carrying behavior and the division of labor during nest movings in ants see Möglich and Hölldobler (1974).

The analyses of the signals by which the tandem running recruitment technique of *Camponotus sericeus* is organized have revealed that mechanical signals and

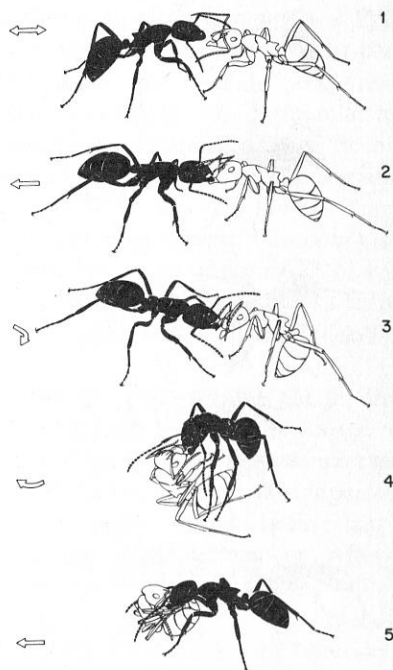


FIG. 11. Behavioral sequences that initiate carrying behavior. (1) The recruiter ant (black) approaches a nestmate (white) and displays a jerking behavior for 2–3 sec. (2) The recruiter grasps the nestmate at the mandibles and pulls it a distance of about 2–20 cm. (3) When the recruiter turns, it holds the nestmate with a firm grip; the nestmate is slightly lifted thereby. (4) The nestmate folds the legs and antennae tightly to the body and rolls the gaster inward. (5) In this posture it is carried to the target area. The arrows indicate the direction of the movements. (From Hölldobler *et al.*, 1974.)

motor patterns play an important role. Although chemical trails with hindgut contents are laid, they function only as orientation cues and do not release any recruitment effect. This brings us to the next higher organization level of recruitment communication in formicine ants, the so-called “group recruitment.”

In this case one ant recruits about 5–30 nestmates at a time, and the recruited ants follow closely behind the leader ant to the target area. This behavior has been observed in *Camponotus compressus* (Hingston, 1929), *C. beebei* (Wilson, 1965), and *C. socius* (Hölldobler, 1971c). Working with *Camponotus socius* I found that scouts set chemical “sign posts” around newly discovered food sources and lay a trail with hindgut contents from the food source to the nest. The trail pheromone alone, however, does not release a significant recruitment effect. Inside the nest the recruiting ant performs a “waggle” display when facing nestmates head on (Fig. 12). The vibrations with head and thorax last 0.5–1.5 sec

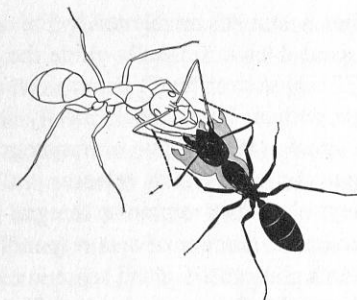


FIG. 12. Schematic illustration of the “waggle” movements of a recruiting ant (black) which encounters a nestmate. Arrow indicates the to and fro direction of the movement. (From Hölldobler, 1971c.)

with 6–12 strokes in 1 sec. Nestmates are alerted by this behavior and subsequently follow the recruiting ant to the food source. The significance of the motor display inside the nest was demonstrated by closing the gland openings of recruiting ants with wax plugs. In this way it was possible to separate the “waggle” display from the chemical signals, and thus it could be shown that only ants stimulated by the waggle display performed by a recruiting ant would follow an artificial trail drawn with hindgut contents. For a complete recruitment performance, however, the presence of a leader ant was still essential. Freshly recruited ants without a leader would follow a hindgut trail through a distance of only about 100 cm. Essentially similar behavioral patterns are involved during recruitment to new nest sites. The main differences are that the motor display is frequently more a “jerking” movement and in contrast to recruitment to food sources, males respond to the signals and hence are recruited. In *Camponotus socius*, as in *C. sericeus*, the “jerking movement” appears to have been derived from an intention movement which precedes carrying behavior. Indeed, when nestmates do not respond to this signal the jerking display initiates carrying behavior (Hölldobler, 1971c).

The next organizational level within the formicine ants is represented by those species in which the trail pheromone alone also does not elicit a recruitment effect, but in which stimulated ants follow the trail to the food source even in the absence of the recruiting ant. We found this to be the case in *Formica fusca* (Möglich and Hölldobler, 1975). In this species successful scouts lay a hindgut trail from the food source to the nest. The trail pheromone has no primary stimulating effect. However, after the scout has performed a vigorous waggle display inside the nest, frequently interrupted by food exchanges, nestmates rush out and follow the trail to the food source without being guided by the recruiting ant. *Camponotus pennsylvanicus* scouts returning from newly discovered food sources also lay odor trails. These individuals further stimulate nestmates by a

waggle motor display. When nestmates are alerted by the display, they follow the previously laid trail; the scout does not usually guide the recruited group to the target area (Traniello, 1977). However, in *C. pennsylvanicus* workers follow an artificial hindgut trail even without being mechanically stimulated by the scout ant. Furthermore, Barlin *et al.* (1976) have chromatographically identified a single peak of the hindgut contents which releases trail following behavior. Nevertheless, motor displays obviously remain an integral part of the recruitment process of *C. pennsylvanicus*; the number of ants responding to an artificial trail consisting of hindgut contents plus poison gland secretion is higher if a scout was allowed to stimulate nestmates by the motor display. These results suggest that recruitment behavior in *C. pennsylvanicus* is of higher organizational level than that of *Formica fusca*. From here it is only a small step to the chemical mass communication, where the trail pheromone alone functions as the recruitment signal and the outflow of foragers is controlled by the amount of pheromone discharged.

The cumulative studies have made clear that motor displays and mechanical signals play an important role during recruitment communication in many ant species (see also Sudd, 1957; Szlep and Jacobi, 1967; Leuthold, 1968a; Szlep-Fessel, 1970). It appears, however, that during the evolutionary process of "designing" more efficient recruitment techniques, these signals became less important with the increasing sophistication of the chemical recruitment system.

There is another important clue from these studies concerning the means by which hindgut material became involved in the recruitment process in formicine ants. Hindgut contents are necessarily frequently discharged by ants. A comparative study has revealed that in many species ants do not defecate randomly but preferably visit specific locations. Besides certain sites inside the nest, other preferred locations include the peripheral nest borders, garbage dumps, and trunk trails leading to permanent food sources or connecting two nest entrances. Thus, these disposal areas seem to be ideally suited to serve as chemical cues in home range orientation, and indeed, this has been documented in a number of species (Hölldobler, 1971c; Hölldobler *et al.*, 1974). These results suggest that in formicine species the trail recruitment communication behavior might have evolved by a gradual ritualization of the defecation process. We can speculate that in the first step hindgut material became an important cue in home range orientation and then was transformed into a more specific orienting and stimulating signal used during recruitment behavior.

The specificity of trail pheromones varies considerably among ant species. Most of our knowledge is based on behavioral investigations, since almost nothing is known about the chemical nature of the trail pheromones. It was only recently that Tumlinson *et al.* (1971, 1972) chemically identified the first such pheromone. The trail substance of leaf-cutting ants (*Atta texana*) is evidently

methyl-4-methylpyrrole-2-carboxylate; this substance has been isolated from the poison gland secretions and found to release a strong trail-following behavior in many attine species. Blum *et al.* (1964), working with poison gland extracts had already shown that the trail pheromone of *Atta* releases trail following in many leaf cutting species. A much higher trail pheromone specificity was discovered by Hangartner (1967) in *Lasius fuliginosus*. Although *L. fuliginosus* workers were able to "read" the trail pheromone of many formicine species (with exception of that from *L. flavus*), its own trail could be understood by none of the other species tested. Huwyler *et al.* (1973, 1975) identified as major components in the hindgut contents of *L. fuliginosus* hexanoic acid, heptanoic acid, octanoic acid, nonanoic acid, and decanoic acid. All these acids released trail following behavior in *L. fuliginosus* workers.

Wilson (1962) compared the specificity of trail pheromones in fire ants (*Solenopsis*), which lay trails with secretions from the Dufour's gland. Artificial trails laid with the pheromone of *S. xyloni* released trail-following behavior in *S. invicta* (= *S. saevissima*) and *S. geminata*, but *S. geminata* trails had no effect on the other species. On the other hand, the secretions of *S. invicta* produced no response in *S. xyloni*. Yet, surprisingly, the Dufour's gland secretion of the dacetine ant *Daceton armigerum* invoked strong following in *S. invicta*.

A similar partial specificity of trail pheromones has been reported from other genera, such as *Eciton* (Torgerson and Akre, 1970), *Camponotus* (Barlin *et al.*, 1976), and *Monomorium* (Blum, 1966). According to Blum's investigations the recruitment pheromone of the genus *Monomorium* originates from the poison gland. His specificity tests were therefore carried out with poison gland extracts. However, our own experiments demonstrated that *Monomorium pharaonis* discharges its recruitment pheromone from the Dufour's gland (Hölldobler, 1973b; Möglich, unpublished observations), whereas poison gland secretions release only a very weak trail-following response. These contradictory findings cannot be easily explained.

Recently we analyzed the stimulus modalities responsible for an effective recruitment and group retrieving system which together enable *Novomessor* to transport large prey in a highly coordinated fashion. When a scout ant of *Novomessor* discovers a prey too large to be carried by one ant, it first releases poison gland secretions. *Novomessor* foragers are attracted from as far away as 100 cm by running upwind toward the prey. In case not enough ants can be recruited in this way, one of the foragers runs back to the nest laying a short-lived chemical trail with poison gland secretion. Five to ten additional workers rush out of the nest and, by following the trail, quickly arrive at the prey. In addition, stridulatory signals produced by individual foragers at the prey and transmitted by substrate vibrations to other nestmates modulate the chemical recruitment signals and coordinate the group retrieving of the large prey objects (Hölldobler,

Stanton, and Markl, in prep.). It is interesting to note that *N. albisetosus* also follows artificial trails laid with the poison gland secretion of *N. cockerelli*, but *N. cockerelli* does not follow the poison gland secretion of *N. albisetosus*.

Among different ant species the persistence of chemical trails varies considerably. In those species that use less permanent food sources (insect prey), the recruitment trails are usually short lived, while in other species utilizing long-lasting food sources (especially plants bearing aphids and other honeydew-producing homopteran insects) the trail pheromones are more persistent. Hangartner (1967) studied the physical nature of the relatively high persistence of the chemical trails in *Lasius fuliginosus* and found that in this species the persistence of a trail depends on the volume of substance discharged and on the porosity of the surface. In addition an inactivated trail can be reactivated after days by moistening it with water. Similar results were obtained for the neotropical army ants (*Eciton*), the trails of which can persist for about one week when deposited during the dry season. During the rainy season the same trails are much less persistent (Torgerson and Akre, 1970). In some species, such as *Atta texana*, the trail pheromone contains a short-lived and long-lived component (Moser and Silverstein, 1967).

This leads us to another important function of chemical trails in ants. As already discussed above, some of the formicine trails composed of hindgut material contain relatively long lasting trail substances that serve mainly as chemical cues in home range orientation. These orientation trails, or trunk trails as they are commonly called, can play a major role in regulating territorial behavior and in partitioning of foraging grounds. This has recently been demonstrated for species of the myrmicine harvesting ant genus *Pogonomyrmex*.

V. COMMUNICATION AND TERRITORIAL STRATEGIES

Workers of *Pogonomyrmex* lay chemical trails with poison gland secretions to recruit nestmates to new rich seed falls (Hölldobler and Wilson, 1970; Hölldobler, 1976b). These recruitment pheromones are relatively short lived. However, laboratory and field experiments have revealed that in addition more enduring chemical signposts are concurrently deposited along the recruitment trails. The latter substances function as orientation cues, so that long after the recruitment signal has vanished, motivated foragers can still follow the same track (Hölldobler, 1971d). Circumstantial evidence indicates that these cues originate at least in part from the Dufour's gland. We have evidence of species specificity in the mixture of compounds of the Dufour's glands of *Pogonomyrmex* (Regnier *et al.*, 1973; Hölldobler and Regnier, unpublished observations). In addition, Hangartner *et al.* (1970) showed that *Pogonomyrmex badius* workers are able to distinguish the odor of their own nest material from that of other nests. In our

most recent laboratory experiments we found that even trunk trails contain colony-specific chemical cues that enable the ants to choose the trails leading to their own nest as opposed to those leading to a neighboring colony. Furthermore, it was possible to demonstrate (Hölldobler, 1976b) that the use of chemically and visually marked trunk trails, which originate from recruitment trails, guarantees an efficient partitioning of foraging grounds. Trunk trails used by *Pogonomyrmex barbatus* and *P. rugosus* during foraging and homing have the effect of permitting the avoidance of aggressive confrontations between neighboring colonies of the same species. The trails channel the mass of foragers of hostile neighboring nests into diverging directions, before each ant pursues its individual foraging exploration. This system subtly partitions the foraging ground. Although foraging areas of conspecific colonies can overlap, aggressive interactions are usually less intense than at the core areas (trunk trails plus nest yards), which normally do not overlap and are vigorously defended.

African weaver ants (*Oecophylla longinoda*) employ a different technique for establishing and maintaining territories (Hölldobler and Wilson, 1977). Weaver ants are exceptionally abundant, aggressive, and territorial, a circumstance that makes them of significance in tropical forest ecology (Leston, 1970). We found that workers of *Oecophylla longinoda* recruit nestmates to previously unoccupied space by means of odor trails laid from the rectal gland, a hitherto unrecognized muscled organ located at the rear of the rectal sac. When colonies of *O. longinoda* are transferred from the field and confined to a potted citrus tree in the laboratory, the major workers patrol the available surrounding space restlessly. If a second tree is placed near the nest tree, groups of workers, orienting visually, mass on the nearest twig or branch in an attempt to reach the other tree by forming living bridges with their bodies. The longest living bridge we observed measured 17 cm. If they succeed, those crossing over begin to lay trails back and forth across the new space. Many return all the way to the nest, and while so doing lay trails directly across the bodies of nestmates making the living bridge (Fig. 13). A combination of chemical and tactile signals (but not the chemical trail alone) excites workers and induces them to move outward along the trail. This mode of communication, which we have termed *long-range recruitment*, results in an outpouring of additional workers onto the fresh space.

The discovery of recruitment to new space has led us to investigate by which cues the weaver ants differentiate between new and old areas. We found that a combination of chemical and visual cues are involved. For example we can release the recruitment process to new space simply by changing the visual surrounding, but also, although to a lesser degree, by changing the chemical make up of the environment. Furthermore we have found that the ants deposit their own chemical signposts, which, at least in part, originate from the rectal sac. These substances are different from those secreted from the rectal gland, and they serve as true territorial pheromones. We established that weaver ant colonies

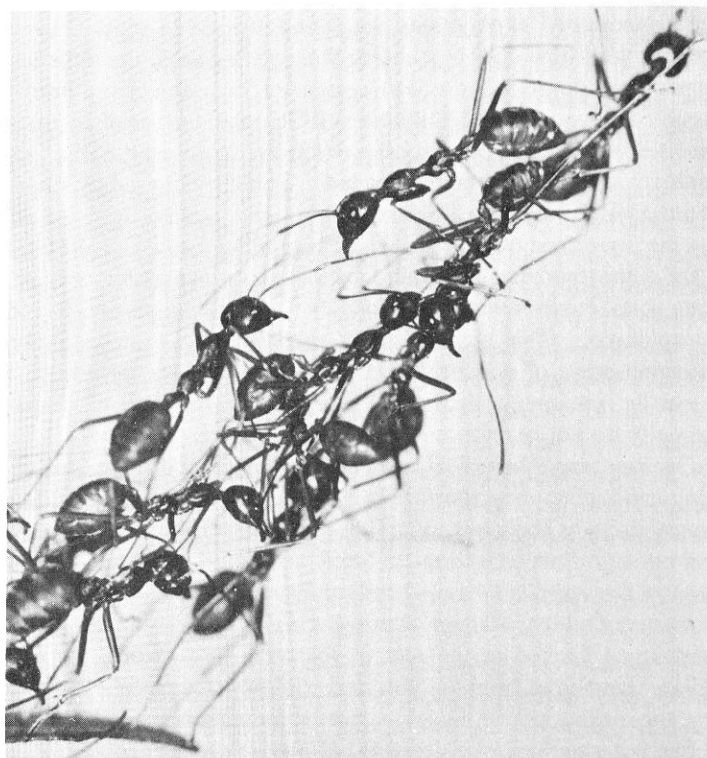


FIG. 13. Workers of the weaver ant *Oecophylla longinoda* form living bridges by linking their bodies into chains. The worker seen running over the upper portion of this bridge is laying an odor trail from her everted rectal gland directly onto the bodies of her nestmates. The trail will guide other members of the colony to a newly available foraging space. (From Hölldobler and Wilson, 1977.)

discriminate between the territorial signposts of their own colony and that of other colonies. A second form of communication in *Oecophylla longinoda* is referred to loosely as short-range recruitment (Hölldobler and Wilson, 1977). When workers encounter alien *Oecophylla* workers or other kinds of insects too large for them to seize, they chase the intruders through distances of 15 cm or more while dragging the end of the abdomen (but not the anus or acidopore) over the ground. In this way, the worker dispenses an attractant-arrestant pheromone from the sternal gland, located on the last abdominal sternite. Nestmates are attracted over distances of up to 10 cm to the area where the display occurred and tend to settle there in loose clusters. The result is a change in the overall spatial pattern of *Oecophylla* workers in those portions of the territory through which the intruders move, from random or weakly clumped distributions to moderately or strongly clumped distributions. During laboratory trials clusters of workers were

able to restrain and subdue invaders in much shorter periods of time than were single defenders. Under prolonged stress from invaders, additional forces are recruited to the combat area with the aid of a conspicuous jerking motor display signal and the rectal-gland trail substance.

In the honey ant (*Myrmecocystus mimicus*) I discovered a still different territorial strategy (Hölldobler, 1976a). *Myrmecocystus mimicus* is abundant in the mesquite-acacia community in the southwestern United States, and like other members of its genus, it has a special honeypot caste, which functions as living storage containers. When their crops are filled to capacity, their gasters are expanded to almost the size of a cherry. Neighboring colonies of *M. mimicus* conduct territorial tournaments, in which hundreds of ants perform highly stereotyped display fights. These tournaments can last for several days, being interrupted only at night when the species is normally inactive. During the contest the ants walk high on legs held in a stilt position while raising the gaster and head. When two hostile workers meet, they turn to confront each other head on (Fig. 14a). Subsequently they engage in a more prolonged lateral display (Fig. 14b, c) during which each raises its gaster even higher and bends it toward its opponent. Simultaneously, the opponents drum their antennae intensively on each other's abdomen and kick each other with their forelegs. These exchanges are almost the only physical contact, although each ant seems to push sideways as if to dislodge the other one. After 10–30 sec one of the ants usually yields, and the encounter ends. The ants continue to move on stilt legs, quickly meet other opponents, and the whole ceremony is then repeated.

How do these territorial tournaments originate? When foragers venture into an alien territory, they encounter the residents at frequent intervals, whereupon they invariably commence a display fight. Subsequently, some scouts return to their colony while dragging their abdominal tips over the ground and thus summoning forces of their nestmates to the challenged territorial border. When the opposing worker forces meet, massive display tournaments ensue. Real physical fights usually end fatally for both opponents but occur only rarely. When one colony is considerably stronger than the other, the tournaments end quickly through sheer weight of numbers, and the weaker colony is raided. Of 28 territorial invasions observed, 5 ended with the raiding of the weaker colony. During these raids the queens were killed or driven off. The larvae, pupae, callow workers, and honeypot workers were carried or dragged to the nest of the raiders. This process required several days and terminated only when the raided colony ceased to exist. Field observations and laboratory experiments demonstrated that the surviving workers as well as the honeypots and brood of the raided colony were incorporated to a large extent into the raiders' nest. Since all cases of slave making in ants hitherto recorded have involved two different species, this is the first evidence for intraspecific slavery in ants. Experiments have shown that the territorial raids of *M. mimicus* are organized by an alarm-recruitment system. The ants

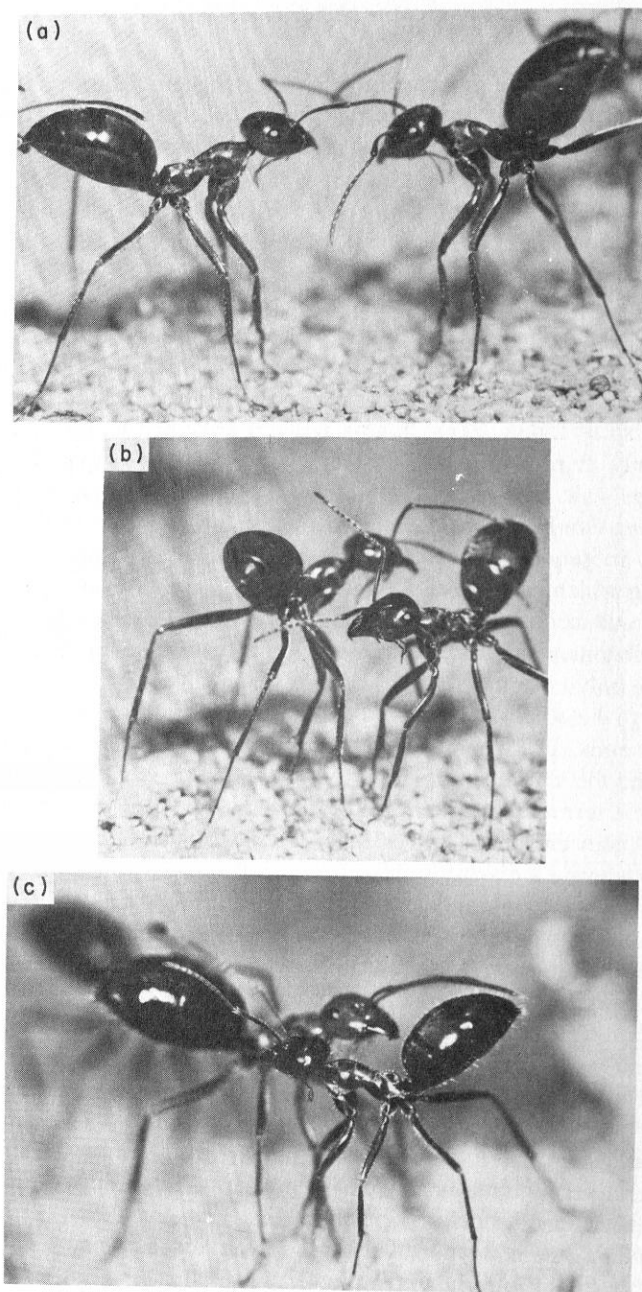


FIG. 14. The stereotyped display patterns of *Myrmecocystus mimicus*: (a) stilt walking and head-on confrontation; (b) beginning of lateral display; (c) full lateral display and antennal drumming. (From Hölldobler, 1976a.)

are alerted by a jerking motor display performed by the recruiting scouts, and they are subsequently guided to the combat area by a hindgut-pheromone trail laid by the scout ants.

VI. COMMUNICATION BETWEEN ANTS AND THEIR GUESTS

We have seen that the complex life within the insect society depends on the efficiency of many different forms of communication. It is therefore notable that a large number of solitary arthropods have acquired the capacity to provide the correct signals to these social insects. They have "broken the code" and are thereby able to take advantage of the benefits of the societies. Ant colonies contain an especially large number of these solitary arthropods. The guests, which are commonly known as myrmecophiles, include many members of the order Coleoptera (beetles) but also many mites, collembolans, flies, wasps, and members of other insect groups. In this section I will present several examples where it has been possible to analyze the mechanisms of interspecific communication between ants and their guests. Different species of myrmecophiles occupy different sites within an ant colony. Some species live along the trails of the ants, others at the garbage dumps outside the nest, others within the outermost nest chambers, while still others are found within the brood chambers (Hölldobler, 1971b, 1972, 1973a). In each case the requirements of interspecific communication are different.

Some of the most advanced myrmecophilic relationships are found in the staphylinid beetles *Lomechusa strumosa* and several species of the genus *Atemeles*. *Lomechusa strumosa* lives with the red slave-making ant *Formica sanguinea* in Europe. *Atemeles pubicollis*, also a European species, is normally found with the mound-making wood ant *Formica polyctena* during the summer. But in the winter it inhabits the nests of ants of the genus *Myrmica*. We know from the observations of Wasmann, made 60 years ago, that these beetles are both fed and reared by their host ants. The behavioral patterns of the larvae of these beetles are similar for the various species; in particular the larvae prey to a certain extent on their host ants' larvae. It is therefore astonishing that the brood-keeping ants not only tolerate these predators but also feed them as they do their own brood.

Both chemical and mechanical interspecific communication is involved in these unusual relationships. The beetle larvae show a characteristic begging behavior toward their host ants. As soon as they are touched by an ant, they rear upward and try to make contact with the ant's head. If they succeed, they tap the ant's labium with their own mouthparts (Fig. 15). This apparently releases regurgitation of food by the ant. The ant larvae beg for food in much the same way but less intensely.



FIG. 15. Larva of *Atemeles* is given a droplet of food by an ant attendant in the brood chamber of a nest of *Formica* ants. (From Hölldobler, 1971b.)

By feeding ants on honey mixed with radioactive sodium phosphate it is possible to measure the social exchange of food in a colony. These experiments show that when myrmecophilous beetle larvae are present in the brood chamber they obtain a proportionately greater share of the food than the host-ant larvae. The presence of ant larvae does not affect the food flow to the beetle larvae whereas ant larvae always receive less food when they compete with beetle larvae. This finding suggests that the releasing signals presented by the beetle larvae to the brood-keeping ants may be more effective than those presented by the ant larvae themselves.

The beetle larvae are also frequently and intensely groomed by the brood-keeping ants; thus, it seemed probable that chemical signals are also involved in this interspecific relationship. The transfer of substances from the larvae to the brood-keeping ants could, in fact, be demonstrated by experiments with radioactive tracers. These substances are probably secreted by glandular cells, which occur dorsolaterally in the integument of each segment. The biological significance of the secretions was elucidated by the following experiments. Beetle larvae were completely covered with shellac to prevent the liberation of the secretion. They were then placed outside the nest entrance, together with freshly killed but otherwise untreated control larvae. The ants quickly carried the control animals into the brood chamber. The shellac-covered larvae, on the other hand, were either ignored or carried to the garbage dump. It was found that for adoption to be successful at least one segment of the larva must be shellac free. Furthermore, it was possible to show that after extracting all the secretions with

acetone the larvae were no longer attractive. However, if the extracted larvae were contaminated with secretions from normal larvae, they once again became attractive. Even filter paper dummies soaked in such secretions were carried into the brood chambers.

In sum, the experiments show that the adoption of the beetle larvae and their care within the ant colony depend on chemical signals. It may be that the beetle larvae imitate a pheromone, which the ant larvae themselves use in releasing brood-keeping behavior in the adult ants. In obtaining food from the brood-keeping ants, however, the beetle larvae imitate and even exaggerate the food-begging behavior of the ant larvae (Hölldobler, 1967).

The question next arises of how the ant colony manages to survive the intense predation and food parasitism by the beetle larvae. Our observations have suggested a very simple answer. The beetle larvae are cannibalistic, and this factor alone is effective in limiting the number of beetle larvae in the brood chambers at any time. *Lomechusa* larvae normally occur singly throughout the brood chambers, in contrast to the ant larvae which are usually clustered together.

After a period of growth the beetle larvae pupate in the summer. At the beginning of autumn they eclose as adult beetles. The newly hatched *Lomechusa* beetles leave the ant nest and after a short period of migration seek adoption in another nest of the same host ant species. *Atemeles* beetles, on the other hand, migrate from the *Formica* nest, where they have been raised, to the nests of the ant genus *Myrmica*. They winter inside the *Myrmica* brood chambers and in the springtime return to a *Formica* nest to breed (Wasmann, 1910; Hölldobler, 1970a). The fact that the adult beetle is tolerated and is fed in the nests of ants belonging to two different subfamilies suggests that it is able to communicate efficiently in two different "languages."

The *Atemeles* face a major problem in finding their way from one host species to another. *Formica polystena* nests normally occur in woodland, while *Myrmica* nests are found in the grassland around the woods. Experiments have revealed that when *Atemeles* leave the *Formica* nest they show high locomotor and flight activity and orientate toward light. This may well explain how they manage to reach the relatively open *Myrmica* habitat. Once they reach the grassland, the beetles must distinguish the *Myrmica* ants from among the other species present and locate their nests. Laboratory experiments have revealed that they identify the *Myrmica* nests by specific odors. Windborne species-specific odors are equally important in the spring movement back to the *Formica* nests.

Having found the hosts, the beetles must secure their own adoption. The process involves the four sequential steps depicted in Fig. 16. First, the beetle taps the ant lightly with its antennae and raises the tip of the abdomen toward it. The latter structure contains what I have called the *appeasement glands*. The secretions of these glands, which are immediately licked up by the ant, seem to

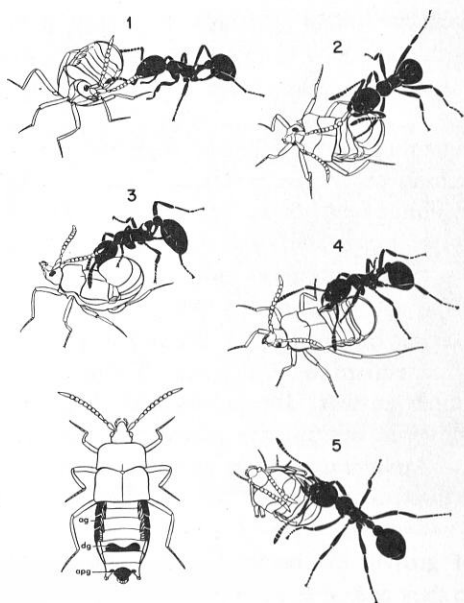


FIG. 16. Behavioral interactions between the beetle *Ateomes pubicollis* (white) and the ant *Myrmica laevinodis* (black) during the adoption process. (1 and 2) The beetle antennates and presents its appeasement glands (apg) to the ant. (3) After licking the ant moves around and licks the adoption glands (ag). (4) The beetle unrolls its abdomen and the ant picks the beetle up by the bristles associated with the adoption glands. (5) The ant carries the beetle into the nest; the beetle assumes a typical transportation posture. (From Hölldobler, 1969.)

suppress aggressive behavior. The ant is attracted next by a second series of glands along the lateral margins of the abdomen. The beetle now lowers its abdomen in order to permit the ant to approach. The glandular openings are surrounded by bristles. These are grasped by the ant and used to carry the beetle into the brood chamber. By experimentally occluding the openings of the glands, it could be shown that the secretion is essential for successful adoption. For this reason I have come to label them *adoption glands*. Thus, the adoption of the adult beetle, like that of the larva, depends on chemical communication. Again it is most probable that an imitation of a species-specific pheromone is involved (Hölldobler, 1970a).

Before leaving the *Formica* nest the *Ateomes* beetle must obtain enough food to enable it to survive the migration to the *Myrmica* nest. This it obtains by begging from the ants. The begging behavior is essentially the same toward both *Formica* and *Myrmica*. The beetle attracts the ant's attention by rapidly drumming on it with its antennae. Using its maxillae and forelegs it taps the mouthparts of the ant, thus inducing regurgitation (Fig. 17). As noted previously, the ants themselves employ a similar mechanical stimulation of the mouthparts to

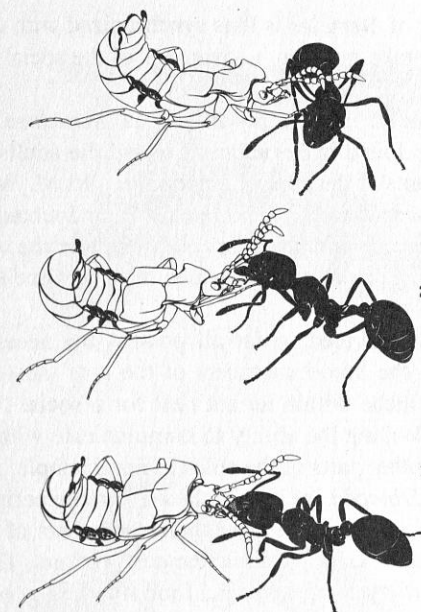


FIG. 17. The myrmecophilous beetle *Ateomes pubicollis* soliciting regurgitation in its host ant *Myrmica laevinodis*. (1) the beetle gains the attention of a worker ant by tapping it with its antennae and forelegs. (2) then the beetle stimulates the labium of the ant thereby releasing regurgitation (3). (From Hölldobler, 1970a.)

obtain food from one another. It is thus clear that *Ateomes* is able to obtain food by imitating these simple tactile food-begging signals.

Finally we can reflect on the significance of host changing as seen in the beetle *Ateomes*. There are good reasons for believing *Ateomes* first evolved myrmecophilic relationships with *Formica*. We can hypothesize that the ancestral *Ateomes* beetles hatched in *Formica* nests in the autumn and then dispersed, returning to other *Formica* nests only to overwinter. This pattern is seen in *Lomechusa* today (Wasmann, 1915; Hölldobler, 1972). However, in the *Formica* nest brood keeping ceases during the winter, and consequently social food flow is reduced. In contrast, the *Myrmica* colony maintains brood keeping throughout the winter. Thus, in *Myrmica* nests, larvae and nutrient from the social food flow are both available as high-grade food sources to the myrmecophiles. These observations, coupled with the fact that the beetles are sexually immature when they hatch, suggest why it is advantageous for the beetle to overwinter in *Myrmica* nests. In the *Myrmica* nest gametogenesis proceeds, and when spring comes, the beetles are sexually mature. They then return to the *Formica* nest to mate and lay their eggs. At this time the *Formica* are just beginning to raise their own larvae and the social food flow is again optimal. The

life cycle and behavior of *Atemeles* is thus synchronized with that of its host ants in such a manner as to take maximum advantage of the social life of each of the two species.

The North American staphylinid myrmecophile *Xenodusa* has a similar life history. The larvae are found in *Formica* nests and the adults overwinter in the nests of the carpenter ants of the genus *Camponotus*. W. M. Wheeler (1911) first discovered this fact more than 50 years ago. It is undoubtedly significant that *Camponotus*, like *Myrmica*, maintains larvae throughout the winter. It may well be that the host-changing behavior of *Xenodusa* has the same significance as that discussed in *Atemeles*.

The myrmecophiles described so far all possess the necessary repertoire to enable them to live in the brood chambers of the ants' nests. These chambers constitute the optimal niche within an ant nest for a social food-flow parasite. Other myrmecophiles lacking the ability to communicate with their hosts to this degree tend to occupy other parts of the colony. For example, staphylinid beetles of the European genus *Dinarda* are usually found in more peripheral chambers of *Formica sanguinea*. It is also in the peripheral chambers of the nest that food exchange occurs between the foragers and the nest workers. Thus, at this site the *Dinarda* are able to participate in the social food flow. They obtain food in three ways. Occasionally they insert themselves between two workers exchanging food and literally snatch the food droplet from the donor's mouth. They also use a simple begging behavior in order to obtain food from returning food-laden foragers. The beetle approaches an ant and touches its labium surreptitiously. This usually causes the ant to regurgitate a small droplet of food. The ant, however, immediately recognizes the beetle as an alien and commences to attack it. At the first sign of hostility the beetle raises its abdomen and offers the ant the appeasement secretion. The secretion is quickly licked up by the ant, and almost immediately the attack ceases. During this brief interval the beetle makes its escape. Other groups of staphylinid beetles, for example, those of the genus *Pella*, live outside the nest on the garbage dumps or along the trails of the ants. Such myrmecophiles have evidently not developed any of the interspecific communication signals that would permit them to live inside the nest chambers. They do, however, possess and use the abdominal "appeasement glands" when attacked by the ants.

Some of the myrmecophiles prey on ants. For example, *Pella laticollis* lives near the trail of *Lasius fuliginosus* and hunts ants. When attacked by the ants it quickly provides the appeasement secretions. Then, it uses the moment's pause to jump on the back of the ant and to kill her by a bite between the head and thorax. The beetle next drags the ant away from the trail and devours it (Hölldobler, Möglich, and Maschwitz, unpublished observations).

Along the trails of *Lasius fuliginosus* are also to be found the nitidulid beetle *Amphotis marginata*. Acting as "highwaymen" in the ant world, these beetles

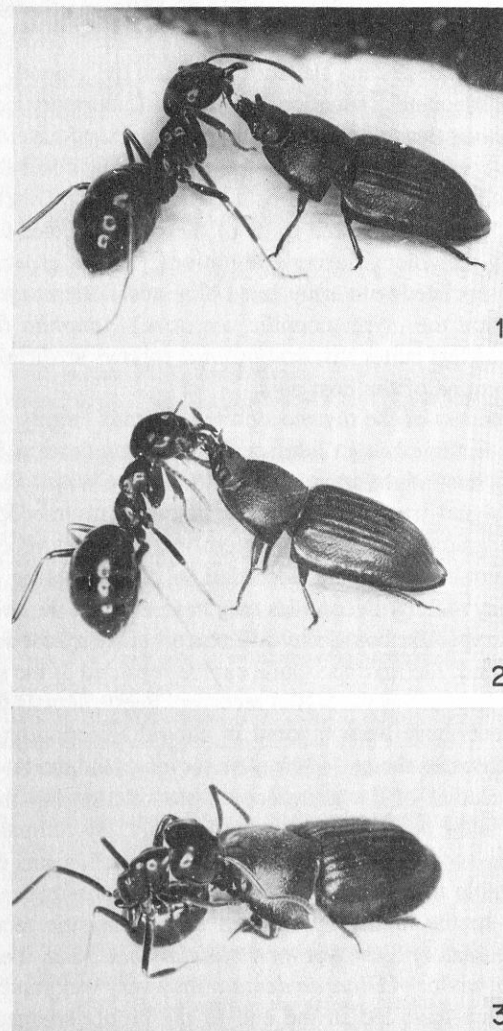


Fig. 18. The nitidulid beetle *Amphotis marginata* waits in ambush on the foraging trails of *Lasius fuliginosus* for food-laden workers. By stimulating the ant's mouthparts (1) the beetle causes it to regurgitate crop contents (2). The robbed ant frequently reacts aggressively, but passive defense (3) enables the armored beetle to weather the attack. (From Hölldobler, 1971b.)

successfully stop and obtain food from ants returning to the nest. Ants that are heavily laden with food are most easily deceived by the beetles' simple begging behavior. Soon after the beetle begins to feed, however, the ant realizes it has been tricked and attacks the beetle. The beetle then is able to defend itself simply by retracting its appendages and flattening itself on the ground. This mechanism gives the beetle adequate protection (Fig. 18). Laboratory experiments have shown that *Amphotis* locates the nests and the trails of *Lasius fuliginosus* by recognizing host-specific odors and the trail pheromones laid down by the ants (Hölldobler, 1968; Hölldobler, unpublished observations). Other myrmecophiles also utilize the chemically marked trails of their host species to locate the host nests or to follow the colony during emigrations. This is especially true for the myrmecophiles associated with army ants (Akre and Rettenmeyer, 1968). Moser (1964) reported that the myrmecophilic cockroach *Attaphila fungicola*, which lives in nests of the leaf cutter ant, *Atta texana*, follows artificial trails composed of the trail pheromone of the host ants.

In short, the success of the myrmecophiles depends largely on their ability to communicate with their hosts. Interspecific communication between a myrmecophile and its host might arise in evolution in two ways. First, we can think of the ant as a signal transmitter and the potential myrmecophile as a signal receiver. By the gradual evolutionary modification of its receptor system and behavior, the myrmecophile has succeeded in discriminating the transmitter's signals. In this way the myrmecophiles may have evolved the ability to recognize the odors of their specific hosts, the difference between host adults and larvae, and so forth. Second, the myrmecophile can be regarded as the signal transmitter and the potential host ant as the signal receiver. Beetle signals that induce social behavior in the ants have been favored in natural selection and very gradually improved. In both cases the ant's behavior serves as the model which the beetle mimics. The evolution of the myrmecophilous relationship therefore involves adaptive change in the potential myrmecophile only. By comparative analyses of the interspecific associations and communication mechanisms of closely related species it is possible to reconstruct a picture of the possible evolutionary pathways which led to the highly specialized social parasitic relationships in ant societies. The predatory behavior of *Pella laticollis* and the more primitive myrmecophilic behavior of *Dinarda dentata* may very well represent early evolutionary steps which have led in the end to the highly adapted myrmecophilic behavior of *Atemeles* and *Lomechusa*.

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