

Chapter 19

COMMUNICATION IN SOCIAL HYMENOPTERA

Bert Hölldobler

Introduction

The truly social (eusocial) Hymenoptera include all ant species and the more highly organized bees and wasps. Wilson (1971), following Michener's definition, characterizes eusocial insects as follows:

These insects can be distinguished as a group by their common possession of three traits: individuals of the same species cooperate in caring for the young; there is a reproductive division of labor, with more or less sterile individuals working on behalf of fecund individuals; and there is an overlap of at least two generations in life stages capable of contributing to colony labor, so that offspring assist parents during some period of their life.

The complex social life within the insect society depends on the efficiency of many different forms of communication, involving a diversity of visual, mechanical, and chemical cues. The basic social activities, such as gathering food, caring for offspring, defense against enemies, establishing dominance orders, searching for new nest sites, and territorial behavior, are regulated by the precise transmission of these signals in time and space.

Sex Communication

Males and females of social insects, no less than those of solitary insects, must communicate in order to find each other. We should therefore expect the most basic patterns of communication during courtship. Unfortunately, however, we have almost no information concerning which signals regulate sexual behavior in social wasps; and only recently have some of the signals involved during the nuptial flights and mating behavior in ants been analyzed.

In the carpenter ants (*Camponotus herculeanus*) it has been demonstrated that the nuptial flights of both sexes are 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 too (Hölldobler and Maschwitz, 1965). Falke (1968) found six different compounds in the secretions of the male mandibular glands of *Camponotus herculeanus*, five of which he could identify: methyl-6-methylsalicylate, 3,4-dihydro-8-hydroxy-2-methylisocoumarin, 2,4-dihydroxy-acetophenone, cholesterol, and 7-hydroxy-phthalide. None of these

compounds released the swarming behavior in females. Perhaps the synchronization pheromone is identical with the sixth, not yet chemically identified substance. Recently, Brand et al. (1973) also found methyl-6-methylsalicylate and 3,4-dihydro-8-hydroxy-2-methylisocoumarin in the mandibular glands of males of *C. herculeanus* and *C. ligniperda*.

The mechanisms by which the males and females are attracted to one another after they have left the nest, as well as those controlling copulatory behavior, have remained unknown for most ant species. Haskins and Whelden (1965) described behavioral patterns of ergatoid *Rhytidoponera metallica* that suggest that these individuals attract males by chemical means. The wingless worker-females wait outside their nest for males from other nests for mating. They typically exhibit a "calling behavior," in which the abdomen is elevated to a slanting position, the sting is slightly extruded, and the last intersegmental membranes are dorsally extended (Fig. 1). Presumably the females discharge sex pheromones by which they attract males and stimulate copulatory behavior (Hölldobler and Haskins, unpublished). Buschinger (1968) described similar behavioral patterns of virgin *Harpagoxenus sublaevis*, and Kanno and Johnson (1969) found circumstantial evidence for the existence of a female sex pheromone in *Formica montana* and *F. pergandei*.

Recently, we succeeded for the first time in locating the morphological origin of and in bioassaying a female sex pheromone in *Xenomyrmex floridanus*, the first such discovery for the ants as a whole (Hölldobler, 1971a). During the nuptial flight the males are strongly attracted to the females. When different glandular substances were tested, it was found that poison gland secretions of the females function as sex pheromones. The males gather on sticks contaminated with poison gland secretion and even try to copulate

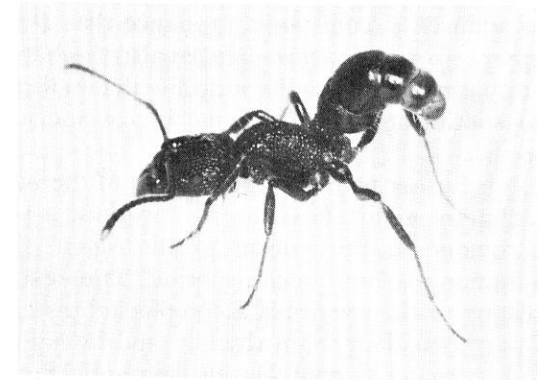


Fig. 1. Ergatoid female of *Rhytidoponera metallica* in calling posture.

with the stick. If a female was contaminated with poison gland secretion she was highly attractive to the males, even before she had left the nest for the nuptial flight. Buschinger (1972a) demonstrated that in *Harpagoxenus sublaevis* the sex pheromone also originates from the poison gland.

Courtship in pharaoh's ant (*Monomorium pharaonis*) is regulated by several signals. First the males are chemically attracted and stimulated by a pheromone that originates from the Dufour's gland and the bursa pouches of the females. Males that are sexually stimulated by the pheromone attempt to copulate with any object of a suitable size (in particular, females, separated gasters of females, other males, and dummies out of filter paper: Hölldobler and Wüst, 1973). For a successful copulation, however, it is necessary that the female provides additional signals, such as touching the male with her antennae or presenting her gaster to him (Petersen and Buschinger, 1971; Hölldobler and Wüst, 1973).

These examples demonstrate that it is not unusual for myrmicine ant species to produce sex pheromones in one of their sting glands. In-

deed, Buschinger (1971a, 1971b, 1972a, 1972b) has adduced circumstantial evidence that *Dorymyrmex pacis* and *Leptothorax kutteri* also discharge a sex pheromone from the sting and that in those two species at least the signal is not species-specific.

It is further true that the females of the harvesting ant genus *Pogonomyrmex* produce a sex pheromone in the poison gland. Again, the pheromone is not species-specific. The sexual isolation of the species is accomplished instead by particular daily flight rhythms and by highly localized mating arenas. During the nuptial flight period the males from many different nests in the environment assemble at certain places (~50 m X 80 m in size) and stay there for up to six days. Every day during a short, specific period the females arrive at these arenas. By discharging the sex pheromone they stimulate mating behavior in the males. After mating they take off again, and only when they land a second time, often hundreds of meters from the mating arena, do they begin excavating soil to found a new colony (Hölldobler, unpublished).

Mating in bumblebees is regulated by visual and chemical cues. Schremmer (1972) reports that males of *Bombus confusus* select striking signposts on which they rest and from which they fly after any object that roughly resembles a female bumblebee. The mating behavior in other bumblebee species, such as *Bombus terrestris*, *B. pratorum*, and *B. lucorum*, is still more elaborate. Individual males of these species establish chemically marked flight routes by depositing spots of odorous secretions at intervals along the route (Frank, 1941; Haas, 1946). The height and location of these flight paths differ from species to species (Haas, 1949a, 1949b; Bringer, 1973); in addition the scents seem to be species-specific. According to Haas (1949a, 1949b, 1952) and Kullenberg (1956), males as well as females are attracted by these marking pheromones. When virgin females venture close enough, males rec-

ognize them by a specific female pheromone. This queen odor is also important for inducing copulatory behavior in the males (Free, 1971).

There is some uncertainty concerning the anatomical source of the marking pheromones. Haas (1952) found that the secretions originate from the mandibular glands, and this has been generally accepted by other investigators (Kullenberg, 1956; Stein, 1963; Bergström et al., 1968). Later, however, Kullenberg et al. (1973) reported that movie analyses of the marking behavior of the male bumblebees and refined dissecting methods have revealed that the pheromone is not produced in the mandibular glands but rather in the cephalic portion of the labial glands. If this is correct we probably have to assume that the major component of the marking secretions of *B. terrestris*, identified by Bergström et al. (1967) as 2,3-dihydrofarnesol, was not extracted, as reported, from the mandibular glands but from the labial glands. Calam (1969) has identified the main components in extracts of the heads of males of five other *Bombus* species and found them all different. Similar results were obtained by Kullenberg et al. (1970), who found that the marking pheromones differ among thirteen species of *Bombus* and six species of *Psithyrus*. Even within the species *B. lucorum* Bergström et al. (1973) discovered two forms in which the males clearly differ in their main cephalic volatile compounds. The "dark" form contains ethyl dodecanoate whereas the "blonde" form contains ethyl tetradec-cis-9-enoate as their main components. It is likely that these two varieties are in fact distinct sibling species. However, how far these chemical differences are effective as prezygotic isolating mechanisms remains to be tested by behavioral experiments.

In the honeybee *Apis mellifera* chemical communication plays a major role in regulating reproductive behavior. During the mating period drones usually assemble in large numbers in

"congregation places." Every year the same localities are visited for this purpose (Ruttner and Ruttner, 1965, 1968, 1972). The specific cues by which these assembling areas are detected by the drones is still a mystery. No evidence exists that pheromones are involved, although Gerig (1972) recently reported that extracts from the heads of males attract flying males once they have arrived at the congregation places. When a virgin female appears, she is immediately pursued by a "swarm" of males. Multiple mating is commonplace in the honeybees.

The behavioral physiology of chemical communication between queens and drones was first studied by Gary (1962, 1963). Noting that drones do not respond to queen pheromones inside the hive, but do respond to virgin queens during the mating flights, Gary suspended virgin queens approximately 10–20 m high on helium-filled balloons and stationary towers. Such exposed queens were highly attractive to drones, which approached and even mated with them. A bioassay was then developed to determine the chemical cues of the attractiveness of the queens to drones. It turned out that the attraction pheromone originates from the mandibular glands of the queen. The primary active compound was identified as 9-oxo-2-decenoic acid, although the total mixture of the mandibular gland secretions was more attractive than pure 9-oxo-2-decenoic acid. These results have been confirmed by Pain and Ruttner (1963), who utilized Gary's bioassay with slight modifications. Butler and Fairey (1964) identified 9-hydroxydec-2-enoic acid as a second attractive compound in the mandibular gland secretions of honeybee queens, although Blum et al. (1971b) found that this substance did not release attraction in honeybee drones.

From these results it can be concluded that the mandibular gland substance of queens contains the sex pheromone and that its most effective component is 9-oxo-2-decenoic acid.

Circumstantial evidence, however, indicates that there may be additional chemical signals involved during mating behavior in honeybees. Morse et al. (1962) extirpated the mandibular glands from virgin queens, but still a small group of these treated queens mated successfully. Butler (1971) suggests that at least in close range, additional pheromones from the abdominal tergites or the Koschnevnikov's gland in the sting chamber stimulate copulation behavior. It may well be that the main function of the mandibular gland pheromones is a long-distance attractant, while in close range additional signals become important. The sex pheromone of *Apis* is not species-specific. Receptor physiological investigations as well as behavioral observations have revealed that drones of *Apis mellifera* are attracted not only by queens of their own species but also by the mandibular gland secretions of *Apis cerana* and *Apis florea* (Butler et al., 1967; Ruttner and Kaissling, 1968). For further information the reader is referred to a recent review by Gary (1974).

Worker-Queen Communication

The division of labor in reproductive and nonreproductive castes is regulated by a variety of communicative signals. A honeybee society is constantly informed of the presence of their queen by chemical cues. Queen pheromones were found to originate from the queen's mandibular glands and were named by Butler (1954a) "queen substance." Its major component was identified independently by Callow and Johnston (1960) and by Barbier and Lederer (1960) as 9-oxodec-trans-2-enoic acid. As reported above, this substance functions outside the hive as the queen's sex pheromone. Although inside the hive the males are not responsive to the queen substance, this pheromone strongly affects the physiology and behavior of worker bees. More than a dozen other com-

pounds of the mandibular gland secretions have been chemically identified, most of which remain unknown in function.

While stationary or slowly moving, the nest queen of a honeybee colony is usually surrounded by approximately eight to ten worker bees, the so-called court. Butler (1973) describes the forming of a court as follows:

What seems to happen is that some of the household bees moving around the brood nest—the only place in an undisturbed colony where queen rearing occurs—happen to meet the queen, or to get within a few millimeters of her. The bees that do so, react in one of three ways: They ignore her, or they appear to be actually repelled by her and move rapidly away, or they join her “court” and stay with her for a period varying from a few seconds to half-an-hour or even more. Some of the bees that join a queen’s “court” seem strongly stimulated by her and immediately begin examining her body with their antennae and often lick it too. If the queen moves and they lose contact with her, they often examine with their antennae the comb where she has been, apparently seeking some substance with which she contaminated it. Those that find her again usually examine and, perhaps, lick her. It seems probable that such bees are actively seeking queen substances.

In an attempt to analyze the communicative mechanism that leads to the court formation, Gary (1961a, 1961b) confined a queen in a cage with one wall made out of wire gauze. Many workers gathered at this wall. When a similar test was performed with a queen whose mandibular gland had been removed, only a few workers assembled at the cage. In contrast, however, Velthuis (1970a) reported that uncaged queens continued to attract workers even if their mandibular glands had been extirpated. Butler et al. (1973) conducted an additional series of experiments and confirmed that the scent of a mated laying queen as well as that of synthetic 9-oxo-2-decenoic acid cause an accumulation of workers on the cage, and that fewer workers gathered on the cage if the queen’s mandibular

gland had been removed. However, when the queen remained uncaged so that the workers could touch her, workers continued to assemble around a stationary queen, even when the mandibular gland had been extirpated. Since it could be shown that the heads of those queens still contained traces of 9-oxodecenoic acid, it is assumed that this major component of the queen substance releases the court formation. Yet it cannot be completely ruled out that additional unidentified substances, produced in other parts of the queen, such as the abdomen, may also be involved (Velthuis, 1970a). In any case it seems to be clear that in an undisturbed colony workers are attracted to their queen only over very short distances (Butler et al., 1973).

The effect of the queen pheromones can be tested by removing the queen from the colony. Shortly afterward the workers move around excitedly while showing increased fanning behavior. If the queen is not replaced within forty-eight hours, the workers begin construction of queen cells, in which new queens can be produced. This sequence suggests that the presence of a mated laying queen inhibits the rearing of new queens. And, indeed, Butler and Gibbons (1958) demonstrated that queen rearing can be inhibited even in the absence of a queen, merely by exposing the colony to queen substance extracted from the mandibular glands of mated, laying queens. Again there is some circumstantial evidence that additional pheromones, originating from the queen’s abdomen, may contribute to this inhibitory process (Velthuis, 1970b).

The queen not only inhibits the production of new queens but also suppresses the ovary development of worker bees. When kept without a queen some workers undergo ovarian development. De Groot and Voogd (1954) and Voogd (1955) demonstrated that this growth can be prevented by exposing them to the queen substance. Queen rearing by workers and the devel-

opment of their ovaries can be inhibited without the workers themselves having direct contact with a queen, provided these individuals have access to other workers that have recently been with a queen (Butler, 1954a; Pain, 1961). The precise mechanisms of transmission of the inhibitory signals is still very little understood. According to recent results of Velthuis (1972) it seems likely that a worker in contact with a queen becomes contaminated with traces of queen substance and probably transfers these pheromones when it contacts other worker bees. It is now suggested that the inhibitory effect is transmitted via the sensory channel and not via the alimentary channel, as previously assumed by Butler (1954a). This assumption is supported by the fact that some chemoreceptors on the antennae have been found to respond specifically to 9-oxo-2-decenoic acid (Beetsma and Schoonhoven, 1966; Kaisling and Renner, 1968).

By a variety of experiments it has been demonstrated that free movement of the queen over the brood combs is necessary to ensure an effective distribution of the inhibitory substances. This indicates that the queen herself actively takes part in distributing her queen substance and thereby suppresses the fertility of her daughters and the rearing of young queens.

Older queens tend to fail to inhibit queen rearing because their colonies have become too large or because the mobility of the old queen and the production of queen substance have decreased. This, in turn, leads either to a superseding of the old queen by a young queen or the preparation by the colony for reproductive swarming, during which the old queen leaves with a group of workers to start a new colony. During swarming the major component of the queen substance, 9-oxo-decenoic acid, again plays an important role: it is the main signal by which the workers are kept close to their queen, and it also releases the clustering behavior around the queen after she has settled. Accord-

ing to Butler and Simpson (1967) a second component of the queen’s mandibular gland secretions, the less-volatile 9-hydroxydecenoic acid, may function as an additional signal for tight clustering.

We have seen that 9-oxodecenoic acid serves many purposes: outside the hive it functions as a sex pheromone and as a powerful attractant during swarming behavior; inside the nest it is the most important signal for the social regulation of reproductive behavior in honeybees.

Honeybee societies are strictly monogynous. As just pointed out, the old queen leaves the nest with a swarm of workers before the young queens emerge. Since two or more queens do not tolerate one another it seems reasonable that eclosing and freshly hatched queens signal their presence. Indeed, Hansson (1945) found that young queens continuously exchange “quacking” and “piping” sounds. When he played the recorded sound back, he got a piping answer from a hatched queen and a quacking answer from queens that were still in their cells but close to eclosion. It appears plausible that this sound communication prevents premature emergence of a young queen before the older queen has left the hive. Hansson’s experiments, however, have shown that the sound signals alone do not completely suppress the hatching of a young queen. Simpson and Cherryl (1969) report that piping sounds are also produced during swarming behavior. It was even possible to initiate swarming in honeybees by playing the piping sounds back to a colony. Of course, after the swarm has left the nest with the older queen, the absence of these piping sounds would indicate that the way is free for the eclosion of another queen.

Whereas it is apparent that only the substrate-borne vibrations of the sounds are perceived by the bees, there remains some confusion about the physical properties of the sounds. According to Hansson the frequency of the piping sounds averages 435–493 cycles per

sec and the quacking sounds about 323 cycles per sec. Wenner (1962b) apparently was not aware of Hansson's work when he published pretty much the same biological findings. Contrary to Hansson, however, he characterized the piping sound with 1,300 cycles per sec and the quacking sound with 2,500 cycles per sec. Wenner also reported that only the piping sound, and not the quacking sound, released an answer in the young queens.

Besides these chemical and acoustical signals involved in communication between the castes, there exists at least one form of indirect communication between the workers and their queen. Workers are able to determine the sex of their queen's offspring by the size of the cells that they build. The queen lays unfertilized eggs in large hexagonal cells, out of which males develop; but the fertilized eggs, which she lays in small hexagonal cells, develop into workers. Koeniger (1970a, 1970b) was able to demonstrate experimentally that the queen measures the width of the cell with her front legs before she lays an egg. Thus the workers communicate to their queen via the cell size what kind of egg she should lay.

The mechanisms of communication between the castes has not been analyzed as well for other species of social Hymenoptera as it has been for honeybees. Some findings indicate that bumblebee queens produce a pheromone comparable to the honeybee's queen substance (Röseler, 1967, 1970). For more detailed information the reader is referred to Michener (1974). In ants only circumstantial evidence of the presence of special queen pheromones has been adduced (Stumper, 1956; Bier, 1958; Lange, 1958; Hölldobler, 1962; Watkins and Cole, 1966; Brian and Blum, 1969; Brian, 1970).

In some social wasps, such as *Vespa crabro* or *Vespa orientalis*, workers tend to form a court around their queen resembling that of honeybees. If the wasp queen is removed, a conspicuous unrest breaks out in the workers, but they

immediately calm down again after the queen has been returned. Also, the development of the workers' ovaries is inhibited when a queen is present. All these observations strongly suggest that the wasp queens produce a queen substance. Indeed, Ikan et al. (1969) were able to isolate a substance from head extracts that showed in bioassays the effects of a queen substance. They identified it as δ -n-hexadecalactone.

In the more primitive social wasps, such as *Polistes*, dominance orders are established by certain overt behavioral patterns instead of by chemical signals. When the colony is founded by several females, only one of them becomes the queen, and the others become workers. As Pardi (1940, 1948) and Pardi and Cavalcanti (1951) first demonstrated, the egg-laying queen dominates the other females through her larger size and more aggressive behavior, which is mostly expressed through ritualized aggressive posturing. The dominant individual stands somewhat higher than the subordinate one, while the latter crouches and lowers its antennae. Pardi (1948) found that there is a correlation between the development of the ovaries and the position in the dominance order: females with the largest ovaries were also the most dominant ones. Similar dominance orders have been found in related genera such as *Mischocyttarus* (Jeanne, 1972) (Fig. 2). For more information on the establishment of dominance hierarchies and the evolution of queen control the reader is referred to Wilson (1971: 299–305), Evans and Eberhard (1970), and Spradbery (1973).

Alarm Communication

When a rapid exchange of information is crucial for the survival of a society, specialized, behaviorally very active signals are needed. The social insects are rich in such systems.

Like many solitary insects, social insects also

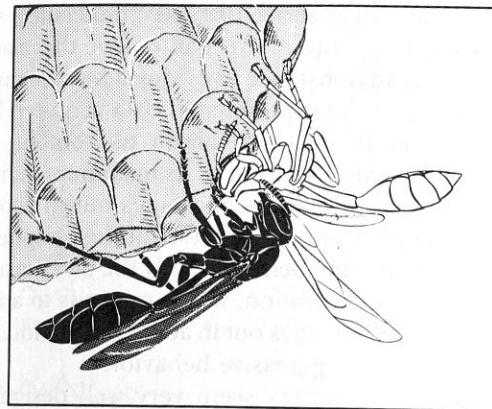


Fig. 2. Domination behavior in *Mischocyttarus drewseni*. The dominating wasp (black) is violently mauling the thorax of the subordinate with her mandibles. The subordinate is responding with an extremely submissive posture: head down against the nest surface, abdomen raised, and wings spread. (From R. L. Jeanne, 1972.)

use chemicals to repel predators. In social insects, however, defensive reactions are closely connected with alarm communication, and quite often both substances serve both functions. In many cases the discharge of alarm pheromones and defensive substances is accompanied by characteristic body movements and postures (Fig. 3). The species of *Formica* spray mixtures of formic acid and Dufour's gland 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 abdomens 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 (Goetsch, 1953), *Solenopsis fugax* and *Monomorium pharaonis* (Hölldobler, 1973b), and many other myrmicine species.

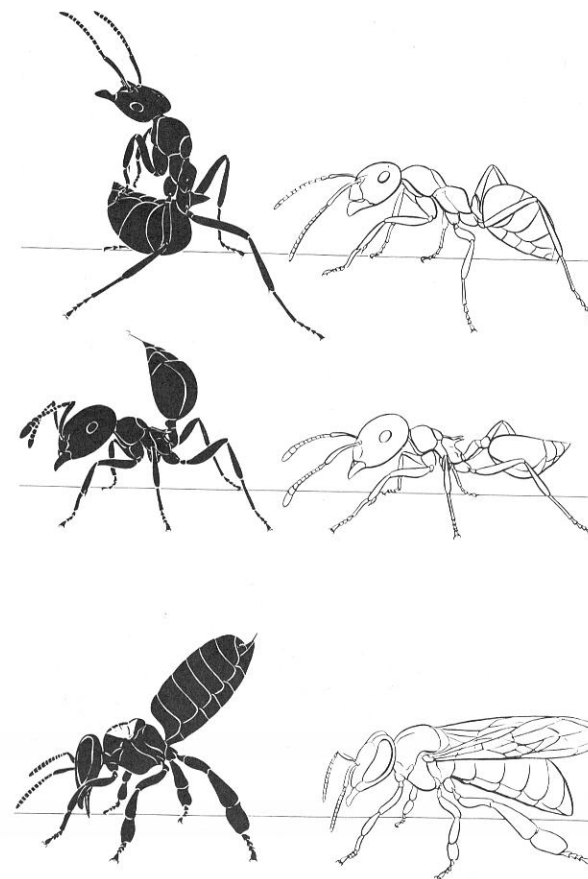


Fig. 3. The alarm-defense behavior (black) is contrasted with the normal posture (white). Top: *Formica polycetena*; middle: *Crematogaster ashmeadi*; bottom: *Apis mellifera*. (From Hölldobler, 1970b.)

In addition to some early reports by Goetsch, Sudd's (1957b) observations on the pharaoh ant (*Monomorium pharaonis*) were among the first on chemical alarm communication. Workers of this species react with escape behavior when a nest mate is crushed nearby. Wilson (1958) and Butenandt, Linzen, and Lindauer (1959) carried out the first experimental investigations on alarm pheromones in ants. Butenandt et al. worked with the leaf cutter ant *Atta sexdens* while Wilson studied the harvester ant *Pogonomyrmex badius*. In

both species workers discharge a strong-smelling substance from the mandibular glands (the morphological location of various pheromone glands is illustrated in Fig. 4) if they perceive some kind of threatening stimulus. McGurk et al. (1966) identified this alarm pheromone of *P. badius* 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/cc by moving toward the odor source. The total capacity of the

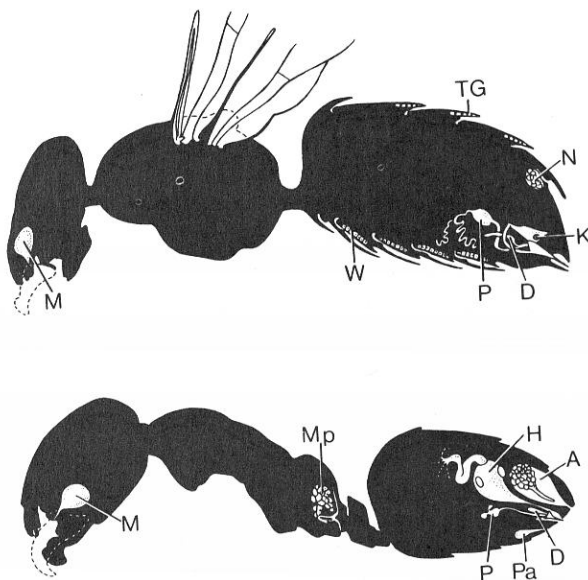


Fig. 4. Pheromone gland system of the honeybee *Apis mellifera* and the dolichoderine ant *Iridomyrmex humilis*. A = anal gland, D = Dufour's gland, H = hindgut, K = Koschnevnikov's gland, M = mandibular gland, Mp = metapleural gland, N = Nassanoff's gland, P = poison gland, Pa = Pavan's gland, TG = tergal glands (presumably scent glands), W = wax glands. (Based on Ribbands, 1953; Pavan and Ronchetti, 1955; Renner and Baumann, 1964; Wilson, 1971.)

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 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 concentration, 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-lived, 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. 5) 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/cc. The quantity of these substances altogether 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 nest mates 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 expanded in subterranean nests. Also in this species, as in *P. badius*, the signal fades out rather quickly unless reinforced by other alarming ants.

Undecane, one of the alarm substances identified by Regnier and Wilson in the Dufour's gland of *Acanthomyops* has also been found in a number of other formicine species (Bernardi et al., 1967; Regnier and Wilson, 1969; Bergström

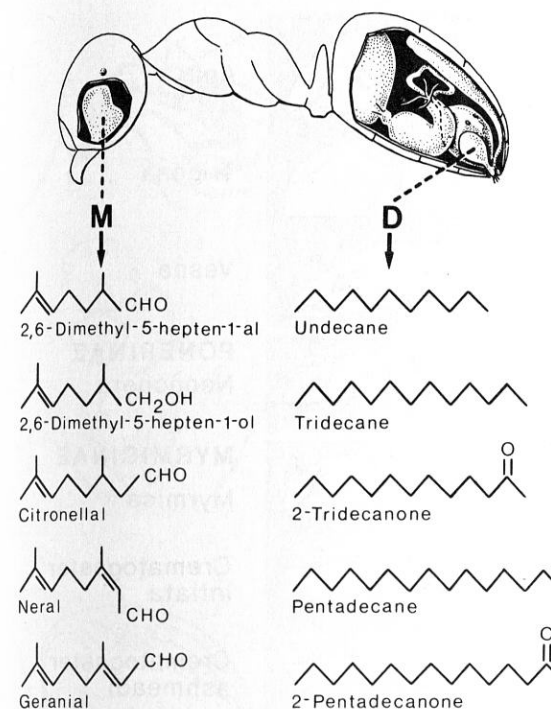


Fig. 5. Substances found in the mandibular gland and Dufour's gland of the ant *Acanthomyops claviger*. Undecane and the mandibular gland substances function both as defensive substances and as alarm substances. D = Dufour's gland, M = mandibular gland. (After Regnier and Wilson, 1968.)

and Löfquist, 1968, 1970, 1972, 1973). This indicates that alarm pheromones are not very species-specific. Indeed, using extracellular single-cell recordings, Dumpert (1972) found that the cells of the sensilla trichodea curvata on the antennae of *Lasius fuliginosus* react to twelve alarm substances produced by species of three different ant subfamilies. But Dumpert also found that some single cells of the sensilla trichodea curvata react most specifically to undecane, the alarm pheromone of *L. fuliginosus*. These results demonstrate that the relative specificity of alarm pheromones among different genera and subfamilies, revealed by behavioral

experiments (Maschwitz, 1964), is probably achieved at the level of the central nervous system and not at the receptor level. It is therefore premature to speculate about the specificity of certain alarm pheromone receptors merely on the basis of behavioral specificity tests (Amoore et al., 1969; Blum et al., 1971). However, it should also be stressed that electrophysiological investigations alone are equally insufficient in proving the behavioral specificity of certain signals.

Nevertheless the efficiency of an alarm pheromone seems to depend on certain structural characteristics. Blum et al. (1966) tested a series of forty-nine ketones on *Iridomyrmex pruinosus* to find the relationship between chemical structure and alarm-inducing power. The natural alarm pheromone is 2-heptanone. By increasing the number of carbon atoms from three to thirteen 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 to 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 responses from the workers and showed excellent properties as alarm substances. As mentioned above, the main component of the natural alarm substances is undecane, a C_{11} -alkane.

These findings lead to the assumption that in most cases the size of a molecule is more important than a specific structure. Bossert and Wilson (1963) predicted that most alarm substances in social insects would have between five and ten carbon atoms and a molecular weight between 100 and 200. They speculated that this would be the ideal size of a molecule to meet the special

requirements for an efficient chemical alarm communication. In fact, most of the alarm pheromones identified so far fall into these categories.

However, there are a few exceptions to this rule of a relative structural nonspecificity. Riley, Silverstein, and Moser (1974a, 1974b) 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 Wilson, 1971; Gabba and Pavan, 1970; Pain, 1973; Blum, 1974). Most of them are ketones, aldehydes, acids, or hydrocarbons. They are produced in a variety of exocrine glands (Fig. 6). In summarizing the behavioral results we 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 that this advantage 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, and when the young workers eclose to adults, they function in the raiders' nest as brood tenders, nest builders, and 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 decyl acetate,

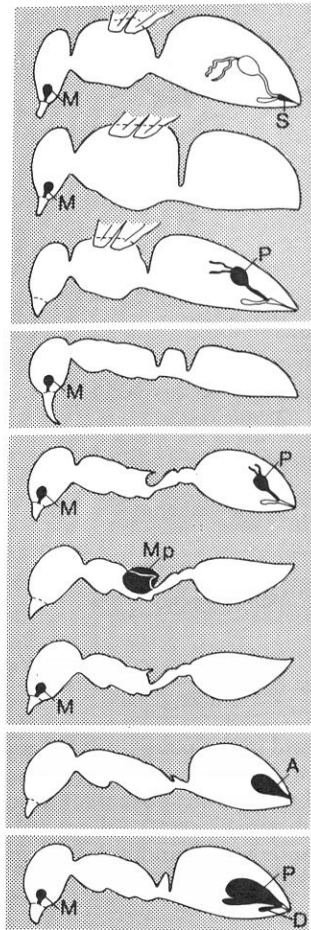


Fig. 6. Alarm pheromone glands in bees, wasps, and ants. A = anal gland, D = Dufour's gland, M = mandibular gland, Mp = metapleural gland, P = poison gland, S = sting chamber. (Based on Maschwitz, 1964, 1974; Duffield and Blum, 1973; Blum, 1966a.)

dodecyl acetate, and tetradecyl acetate as principal components of the glandular substances. One *F. subintegra* worker contains the relatively enormous amount of 700 μg of these substances. During the slave raids the raider ants discharge these substances upon encountering prey workers and apparently stimulate nest mates to join them in the fighting. In addition

Apis

Trigona

Vespa

PONERINAE

Neoponera

MYRMICINAE

Myrmica

Crematogaster
inflata

Crematogaster
ashmeadi

DOLICHODERINAE

Tapinoma

FORMICINAE

Formica

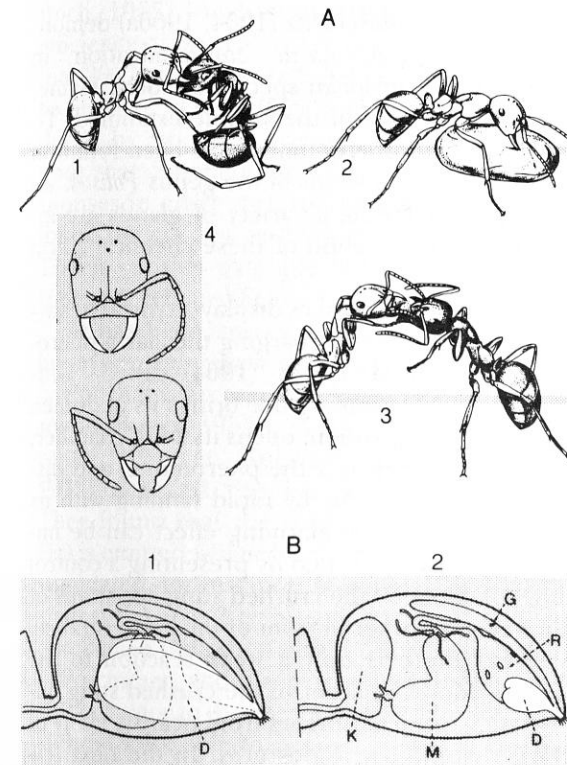


Fig. 7. A: 1. A worker of the slave raider ant *Polyergus rufescens* (left) attacks a slave ant *Formica fusca* (right). 2. The slave raider carries a pupa of *F. fusca* homeward. 3. A *Polyergus* worker is fed by a *F. fusca* slave ant, which has eclosed from a captured pupa. 4. The saber-shaped mandibles 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; based in part on Regnier and Wilson, 1971.)

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 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 remove the pupae. This grotesque exaggeration of a communication signal, resulting in misleading the society, is a fantastic analogy to the human propaganda technique. For this reason Regnier and Wilson called these substances "propaganda pheromones."

In addition to these pheromones, other modes of alarm communication have been discovered. Markl (1965, 1967, 1968, 1970) found that in leaf cutting ants (*Atta cephalotes* and *Acromyrmex octospinosus*) workers stridulate whenever they are prevented from moving freely, for instance, when they fight with workers of a neighboring colony or when they are trapped under sand after a cave-in of their nest. Nest mates are attracted by these stridulatory sounds from as far away as 8 cm. When the sound is emitted by a buried ant, the attracted workers begin to dig where the sound is loudest, and in a few seconds the trapped ant is rescued. The sounds are produced by special stridulatory organs. The posterior rim of the postpetiolar tergite acts as a scraper, while a field of parallel ridges at the anterior end of the first tergite of the gaster functions as the file. Markl was able to demonstrate that the ants respond only to vibrations conducted through the soil. Whereas the airborne stridulatory sounds extend far into the ultrasonic with a maximum between 20 and 60 kHz, the intensity spectrum of the soil-conducted vibrations does not contain frequencies above 6 to 8 kHz, with the intensity maximum concentrated around 3 kHz. The ants perceive the vibrations with receptors in the legs. Markl found that receptors of the forelegs are four to five times as sensitive as those of the middle and hind legs. It is also interesting to note that small workers are considerably more sensitive than the big soldier ants to the substrate-borne vibrations.

Since many ant species possess stridulatory organs, it can be expected that this kind of communication is more common than was previously assumed (Markl, 1973). But there are other kinds of vibrational warning and alarm signals in ants that are only little studied. In *Camponotus herculeanus*, for example, we observed that the sexual castes, especially the males that tend to leave the nest too early for the nuptial flight, are summoned back into the nest by workers by means of rapid oscillatory jerking movements (Hölldobler, 1965; Hölldobler and Maschwitz, 1965). A similar "warning" behavior has been observed in other species, such as *Lasius niger* and *L. alienus*.

In many arboreal ant species (*Camponotus*, *Polyrhachis*, *Hypoclinea*, *Dolichoderus*) vibrational jerking movements of workers can be readily observed when the nest is disturbed. Markl and Fuchs (1972) analyzed the signals produced by some of these movements in *Camponotus herculeanus* and *C. ligniperda*. They found that the ants actually rap on the substrate by hitting the ground alternately with the mandibles and the gaster. The hits follow in series of two to three, sometimes up to seven, with intervals of about 50 msec. These signals, which propagate in solid wood, have an intensity spectrum reaching from 100 Hz to 10 kHz and an energy maximum at 4–5 kHz. Circumstantial evidence indicates that one of the major biological functions of the sounds is to amplify or to modify the effect of other attack-releasing stimuli and alarm signals.

Finally, in the primitive Australian ponerine ant *Amblyopone australis*, we observed a remarkable vibrational alarm communication behavior that is apparently entirely transmitted by tactile contacts between nest mates; in this system substrate-borne vibrations could not be recorded (Hölldobler et al., unpublished).

In spite of these recent discoveries on mechanical alarm communication, it is still fair to say that chemical communication plays the major role in alarming and alerting behavior in social

Hymenoptera. Maschwitz (1964, 1966a) demonstrated chemical alarm communication in twenty-three European species of social Hymenoptera, nearly all of the sample examined. To date, no alarm pheromones have been found in bumblebees or in wasps of the genus *Polistes*. As illustrated in Fig. 6, a variety of glands are involved in the secretion of these chemical alarm signals.

As in ants, honeybees display a typical behavioral pattern when discharging the alarm pheromones, which Maschwitz (1964) called "Giftsterzeln." The alarming bee brings its abdomen into a slanting position, opens its sting chamber, from which it releases the pheromone, and dispenses it into the air by rapid fanning with its wings (Fig. 3). The alarming effect can be impressively demonstrated by presenting a control odor followed by the crushed sting apparatus of a honeybee worker in front of the hive entrance. Whereas there is only a weak reaction to the control odor, the scent of the crushed sting immediately attracts workers from nearby, many of which assume alarm postures. In the next few minutes more than a hundred workers sometimes rush out of the hive. As Maschwitz (1964) demonstrated, the pheromone alone does not release aggression; additional cues characterizing an enemy are necessary to focus the defensive attack.

Although these experiments clearly indicate that the glandular source of the alarm pheromones is associated with the sting apparatus, the precise origin of the pheromones is not yet known. The main chemical component is isoamyl acetate (Boch et al., 1962). The first investigations were carried out with *Apis mellifera*; since then Morse et al. (1967) found the same alarm pheromone in *A. florea*, *A. cerana*, and *A. dorsata*. Maschwitz (1964) demonstrated that honeybee workers produce a second alarm pheromone in their mandibular glands. This substance has been identified as 2-heptanone (Shearer and

Boch, 1965). Boch et al. (1970) compared the efficiency of both alarm pheromones and found that 20–70 times more 2-heptanone is necessary to elicit an alarm effect comparable to that induced by isopentyl acetate. It is interesting to note that 2-heptanone also releases alarm responses in other *Apis* species, even though it is found only in *Apis mellifera* (Morse et al., 1967). This is another example of the general lack of species-level specificity in alarm pheromones.

It has been known for some time that the honeybee *Apis cerana* shows a social defense behavior that is accompanied by a peculiar hissing sound (Butler, 1954b; Sakagami, 1960). Only recently, however, Koeniger and Fuchs (1972, 1973) analyzed this behavior experimentally. They found that the short hissing sound (700 Hz) is emitted whenever the hive is mechanically stimulated, for instance, by shaking or knocking against the hive. The hissing is transmitted from one bee to the other with a transmission speed of 25 cm/sec, and it remarkably reduces aggressive behavior in the bees. Using Asiatic bears, the authors were able to demonstrate that the hissing sound of a bee colony functions as an effective acoustic repellent against large predators, and it is speculated that the bees might mimic the defensive hissing sounds of snakes, which are very common in the habitat of *Apis cerana*.

Multiple Functions of Alarm Signals

As just noted, alarm communication is closely meshed with defensive behavior. Not only are the behavioral patterns frequently identical but often the same substances function as both defensive secretions and alarm messengers. Maschwitz (1964) was able to show that in *Formica* species formic acid is used as a powerful defensive secretion, but its smell also effectively alarms nest mates, although this is not the case in *Acanthomyops claviger* (Regnier and Wilson, 1968). The myrmicine ants *Crematogaster* pro-

duce 2-hexenal in their mandibular glands (Bevan et al., 1961; Blum et al., 1969). This substance is the major component of the alarm pheromone but it also has a remarkable defensive power. As can be seen from Fig. 6, glands that produce alarm pheromones are associated with mandibles or the sting apparatus, morphological features that play a major role in aggressive and defensive behavior.

There seem to be a few exceptions to this rule: Sudd (1962) claims that the strong odor of the African stink ant (*Paltothyreus tarsatus*) originates from the metapleural gland and that this secretion functions as an alarm pheromone. The evidence, however, is not convincing, especially since Casnati et al. (1967) identified dimethyldisulfide and dimethyltrisulfide in the mandibular gland secretions of *P. tarsatus*. These secretions apparently serve as defensive substances and also as chemical alarm signals (Crewe and Fletcher, 1974). In *Crematogaster inflata* the metapleural gland is remarkably enlarged. Maschwitz (1974) found that the workers use the sticky substance as a defensive secretion and that in addition the fluid releases alarm behavior. In most of the other ant species, however, workers produce acidic secretions in the metapleural glands. For instance, the main component of the secretions of the leaf cutter ant *Atta sexdens* is phenylacetic acid. Since these secretions effectively suppress bacterial growth, it is believed that their main function is to suppress microorganisms in the interior of the nest (Maschwitz et al., 1970; Maschwitz, 1974).

The response behavior to the alarm signal varies in different groups and castes of the society, and it varies in time and space. 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. Wilson (1958) showed that the alarm pheromone of the harvester ant *Pogonomyrmex badius* releases a variety of reactions. At low concentration it merely attracts nest mates, and in high concentration it releases aggressive behavior. If the high concentration persists the attracted workers start to dig where the concentration is highest. It was demonstrated that this signal elicits rescue behavior in *Pogonomyrmex*, for instance, if workers are buried under sand after a cave-in of their nest.

Circumstantial evidence shows that *Camponotus socius* uses low concentrations of formic acid, its major alarm-defensive secretion, to fortify its recruitment signals (Hölldobler, 1971c). Similarly the poison gland secretion of *Pogonomyrmex* is not only a defensive secretion but also a strong attractant. When an enemy is stung it is simultaneously marked with this attractant; thus more workers aim their attacks toward it. In other circumstances, however, the same substance functions as a very effective recruitment signal by which nest mates are attracted and guided to newly discovered food sources (Hölldobler and Wilson, 1971).

In stingless bees (Meliponinae), no less than in ants, alarm pheromones often have a double function. All alarm pheromones in this group appear to originate from the mandibular glands (Blum et al., 1970), and, as will be shown in the next section, often function also as trail pheromones.

Multiple functions of alarm pheromones are also known in honeybees. Morse (1972) has shown that the alarm pheromone (isopentyl acetate) released near queens in a swarm, causes a remarkable decrease of the discharge of the attractive Nassenoff gland pheromone. It has been speculated that bees use this inhibition as a mechanism to reject a foreign queen from a swarm. Simpson (1966) and Butler (1966) report that the mandibular gland secretion (2-hepta-

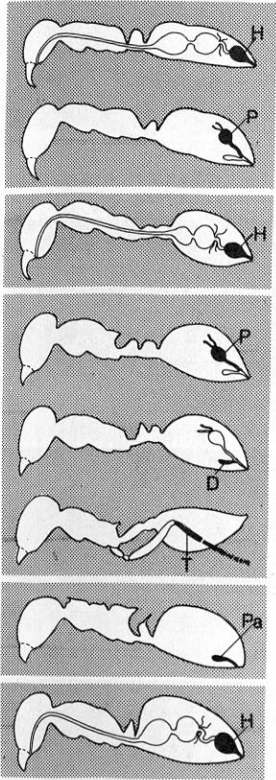
none) of honeybees, which can also serve as an alarm pheromone, has a strong repellent effect on foraging bees. Indeed, Nunez (1967) gave experimental evidence that honeybee foragers mark exhausted food sources with a repellent signal. It is most likely that this signal is identical with 2-heptanone.

Recruitment Communication

Although advanced social insects must alarm nest mates when danger threatens, it is of equal importance for them to transmit information about newly discovered food sources or better nesting sites. The rapid retrieval of food and the fast emigration to a better nest require an effective communication system.

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 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, which led to the discovery of a number of trail pheromone glands in different taxonomic groups of ants (Fig. 8).

Wilson's analyses (1962) also revealed for the first time the organization of chemical mass communication in fire ants. It was found that the



PONERINAE

Termiteopone

Leptogenys

DORYLINAE

Neivamyrmex

MYRMICINAE

Tetramorium

Solenopsis

Crematogaster

DOLICHODERINAE

Monacis

FORMICINAE

Lasius

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. (Based on Wilson, 1959a; Wilson and Pavan, 1959; Hangartner and Bernstein, 1964; Watkins, 1964; Blum and Ross, 1965; Blum, 1966b; Leuthold, 1968b; Fletcher, 1971.)

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 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 are stimulated to leave the nest. This 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 (1969a) 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 (Fig. 9).

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 nest mate 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*

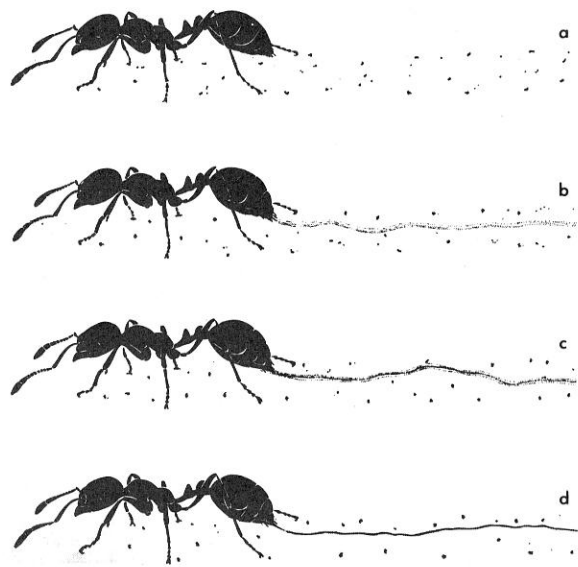


Fig. 9. A worker of the fire ant *Solenopsis geminata* running over a sooted glass plate and laying an odor trail from the extruded sting. a. If the food source is poor, the worker leaves only the tracks made by its feet on the glass plate. b.–d. The better the food source the more intense is the track made by the extruded sting. (From Hölldobler, 1970b, based on Hangartner, 1969c.)

venestula, *C. emeryi* (Wilson, 1959b), *Leptothorax acervorum* (Dobrzanski, 1966), and *Bothroponera tessierinoda* (Maschwitz et al., 1974b; Hölldobler et al., 1973). Until recently, however, nothing has been learned about the precise nature of the signals involved.

The analyses of the signals by which tandem running is organized in the myrmicine 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 nest mates. Then it turns around and raises the gaster into a slanting position. Simultaneously, the sting is exposed and a droplet of a light liquid is

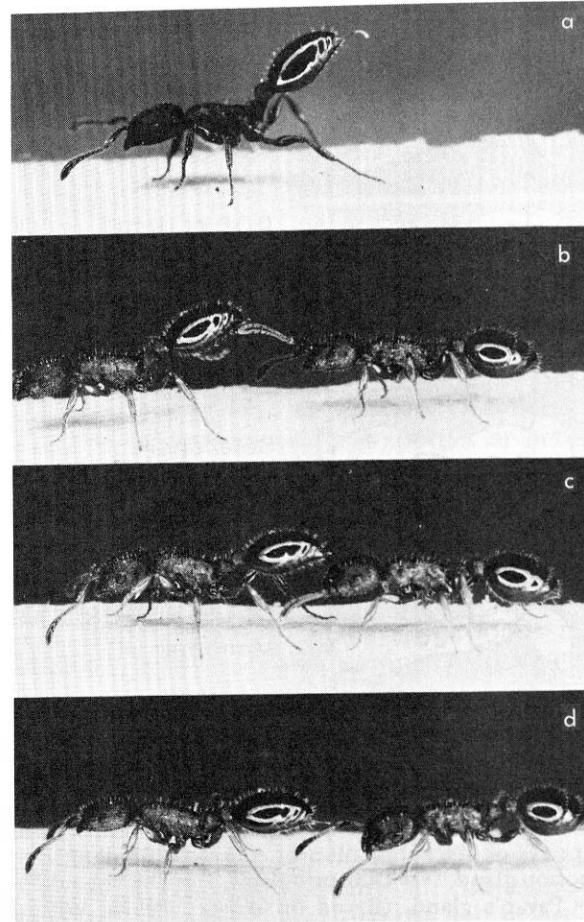


Fig. 10. Behavioral exchange of signals leading to tandem running in *Leptothorax acervorum*. a. A recruiting worker assumes the calling position. A nest mate arrives and touches the gaster b. and hind legs c. of the calling ant with its antennae. d. The calling ant lowers its gaster, and tandem running starts. The sting of the recruiting ant remains extruded, but is not dragged over the surface. (From Möglich et al., 1974b.)

extruded (Fig. 10). Nest mates are attracted by this calling behavior. When the first ant arrives at the calling ant, it touches it on the hind legs or gaster with its antennae, and tandem running starts. The recruiting ant leads the nest mate to the newly discovered food source. During tan-

dem running the leader ant lowers its gaster, but its sting remains extruded. It is not dragged over the surface, however, as in those ant species that lay chemical trails from their stings. The follower keeps close antennal contact with the leader, continuously touching its hind legs and gaster. Whenever this contact is interrupted, for example, when the follower accidentally loses the 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 the same 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 on the hind legs or the 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 those bearing secretions of the Dufour's gland. Further experiments revealed that the poison gland substance not only functions as a calling pheromone but also 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. Gastres 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 hind legs (Leuthold, 1968b; Fletcher and Brand, 1968), all other myrmicine species generate the trail pheromone from one of the sting glands (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 leading 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 (p. 419) it has recently been demonstrated that in several myrmicine species the pheromones originate from the sting glands (Hölldobler, 1971a; Hölldobler and Wüst, 1973; Buschinger, 1972a). It is interesting to note that in species in which wingless ergatoids attract males for mating, for example, *Harpagoxenus sublaevis* (Buschinger, 1971b), the females display sexual calling behavior apparently identical to the tandem-calling behavior 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). 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 evolved (Hölldobler et al., 1974; Möglich et al., 1974a).

In *C. 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-termed fast runs, which are interrupted by food exchange and grooming. After several regurgitations, the recruiter ant now performs brief food offerings while facing nest mates head on. During one recruitment performance such "rituals" were observed to be repeated three to sixteen times. Apparently this behavior keeps nest mates 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. But 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 nest mates 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 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 to recruit nest mates 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 in recruitment to food sources. As Fig. 11 depicts, this is indeed the case. When facing the nest mate head on, the recruiter grasps it on the mandibles and pulls it forward heavily. Shortly afterward it loosens its grip, turns completely around, and presents its gaster to the nest mate. If the nest mate responds by touching the recruiting ant's gaster or hind legs, tandem running starts. This behavioral sequence is very stereotyped and is regularly employed when nest mates are invited to follow the signaler to a new nest. We have therefore 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 that the recruiting ant keeps a firm grip when turning around. The nest mate is thereby slightly lifted, a movement that apparently causes it to fold its legs tightly to its body and roll its gaster underneath. In this posture it is carried to the target area (Fig. 12). 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 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 organizational level of recruitment communication in formicine ants, "group recruitment."

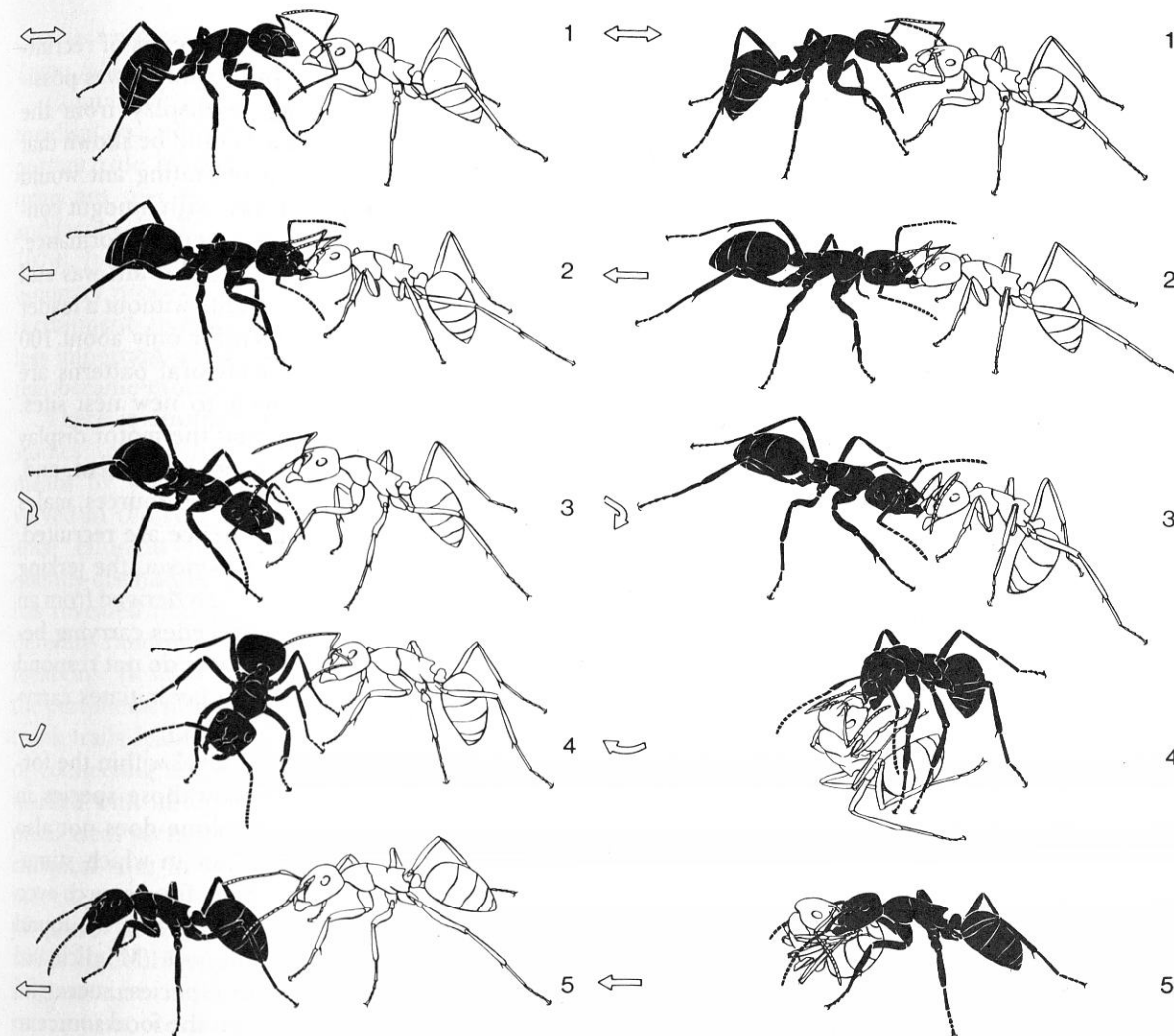


Fig. 11. Invitation behavior to tandem running in *Camponotus sericeus*. 1. The recruiter (black) approaches a nest mate (white) and displays a jerking behavior for about 2–3 sec. 2. The recruiting ant grasps the nest mate at the mandibles and pulls it at a distance of about 2–20 cm. 3. The recruiter loosens its grip and 4. turns around 180°. 5. The recruiter presents its gaster to the nest mate. The nest mate contacts the gaster and hind legs of the leader ant, then tandem running starts. The arrows indicate the direction of the movements. (From Hölldobler et al., 1974.)

Fig. 12. Behavioral sequences that initiate carrying behavior. 1. The recruiter ant (black) approaches a nest mate (white) and displays a jerking behavior for 2–3 sec. 2. The recruiter grasps the nest mate at the mandibles and pulls it a distance of about 2–20 cm. 3. When the recruiter turns it holds the nest mate with a firm grip; the nest mate is thereby slightly lifted. 4. The nest mate folds its legs and antennae tightly to its body and rolls its 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.)

In this case one ant recruits about five to thirty nest mates 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). Because of its apparent intermediate stage between the tandem-running technique and the chemical mass communication, a detailed experimental analysis of this recruitment behavior was considered most desirable.

Working with *Camponotus socius*, I found that scouts set chemical signposts 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 recruitment effect. Inside the nest the recruiting ant faces its nest mates head on and performs a "waggle" display (Fig. 13). The vibrations with head and thorax last 0.5–1.5 sec with 6–12 strokes/sec. Nest mates 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 demon-

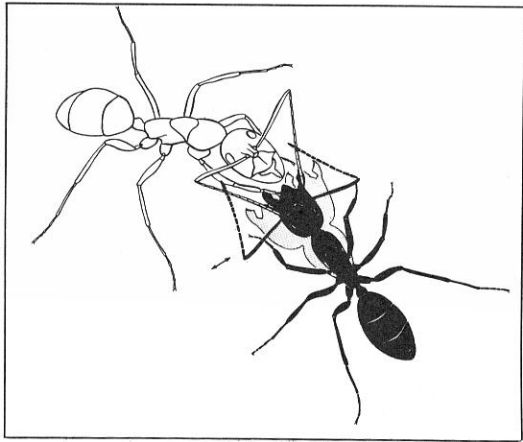


Fig. 13. Schematic illustration of the "waggle" movement of a recruiting ant (black) (*Camponotus socius*) upon encountering a nest mate. Arrow indicates the to-and-fro direction of the movement. (From Hölldobler, 1971c.)

strated 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 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 for 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 that precedes carrying behavior. Indeed, when nest mates 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 does not also 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, nest mates rush out and follow the trail to the food source without being guided by the recruiting ant. From here it is only a small step to chemical mass communication, where the trail pheromone alone releases a recruitment effect and where the outflow of foragers is controlled by the amount of pheromone discharged. This

case is represented among the formicines by *Lasius fuliginosus* (Hangartner, 1967).

Cumulative studies have made clear that motor displays and mechanical signals play an important role in recruitment communication in many ant species (see also Sudd, 1957a; 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 as the chemical recruitment system became more sophisticated.

There is another important result of these studies that provides a clue 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, the peripheral nest borders, garbage dumps, and trunk trails leading to permanent food sources or connecting two nest entrances are especially marked with hindgut material. 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; Hölldobler, unpublished). 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 was then transformed into a more specific orienting and stimulating signal used during recruitment behavior.

The specificity of trail pheromones in ants varies considerably. 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 the leaf cutting ant *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. Moser and Blum (1963) and 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 pheromones of many formicine species (except for that from *L. flavus*), its own trail could be understood by none of the other species tested. Huwyler et al. (1973) 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*) that 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*.

A similar partial specificity of trail pheromones has been reported from other genera, such as *Eciton* (Torgerson and Akre, 1970) and *Monomorium* (Blum, 1966b). 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), whereas poison gland secretions release only a very weak trail-following response. These contradictory findings cannot be explained easily. In summarizing all these results we can say that although trail pheromones of ants are by no means strictly species-specific, they are generally more specific than alarm pheromones.

Among different ant species the persistency 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 honeydew plants) the trail pheromones are more persistent. Hangartner (1967) studied the physical nature of the relatively high persistency of the chemical trails in *Lasius fuliginosus* and found that in this species the persistency 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 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 a long-lived component (Moser and Silverstein, 1967).

This leads us to another important function of chemical trails in ants. As 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 foraging grounds. This has recently been demonstrated for species of the myrmicine harvesting ant genus *Pogonomyrmex*.

Workers of *Pogonomyrmex* lay chemical trails with poison gland secretions to recruit nest mates to new rich seed falls (Hölldobler and Wilson, 1970). These recruitment pheromones are relatively short-lived. However, laboratory and field experiments 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). 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 the 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.

In a recent analysis (Hölldobler, 1974) it was demonstrated that trunk trails used by *Pogonomyrmex barbatus* and *P. rugosus* during foraging and homing have the effect of avoiding aggressive confrontations between neighboring colonies of the same species. They channel the mass of foragers of hostile neighboring nests in divergent directions, after which each ant pursues its individual foraging exploration. This system subtly partitions the foraging grounds and allows a much denser nest-spacing pattern than does a foraging strategy without trunk trails, such as that employed by *P. maricopa*.

It is interesting to note that honeybees and wasps also use relatively persistent chemical orientation cues to locate the nest entrance (Butler et al., 1969, 1970). Apparently these species deposit the chemical signposts with footprints. It

cannot be excluded that ants also employ the footprint technique for setting auxiliary chemical orientation cues. In fact, I frequently observed that foragers of *Pogonomyrmex* rub their legs over the abdominal tip before they leave the nest; an even more striking version of this behavior occurs in the slave-raiding ant *Polyergus* just before and during slave raids (Hölldobler, unpublished). Moreover, Torgerson and Akre (1970) have shown that workers of the army ants *Eciton hamatum*, which lay trails with hindgut contents, are able to set weak footprint trails after their gasters have been removed. Finally, Leuthold (1968b) provided circumstantial evidence that workers of *Crematogaster ashmeadi* can deposit chemical footprints without exhibiting the typical trail-laying behavior involving the hindlegs.

Chemical strategies during foraging also play an important role in interspecific competition among ants. I found that the subterranean species *Solenopsis fugax*, commonly called the thief ant, lays odorous trails in the tunnels leading into the brood chambers of neighboring ant species. The recruitment trail pheromone originates from the Dufour's gland. More important, however, is the fact that *Solenopsis*, when preying on the foreign brood, discharges a highly effective and long-lasting repellent substance from the poison gland. This material prevents brood-keeping ants from defending their own larvae against the predators. A very similar chemical offense is used by pharaoh ants (*Monomorium pharaonis*). In addition to the recruitment pheromone originating from the Dufour's gland, a repellent substance is discharged from the poison gland that enables the *Monomorium* to compete successfully with other ant species at the same food sources (Hölldobler, 1973b).

Very little is known about recruitment communication in social wasps. Hase's (1935) observations on *Polybia atra* indicate that this species alerts nest mates when a food source has been found. Similar observations were made by Lindauer (1961) on *Polybia scutellaris*, and Naumann

(1970) got very good observational evidence that *Protopolybia pumila* conducts a sort of "departure dance," which stimulates nest mates to fly out for foraging. Although Kalmus (1954) claims that *Paravespula germanica* and *P. vulgaris* do not alert nest mates to new food sources, Maschwitz et al. (1974a) provided experimental evidence proving recruitment communication in these species. The main signal seems to be the scent of the food.

In sum, it appears on the basis of limited evidence that in at least some wasp species scouts have the ability to alert nest mates when new food sources are found, but these individuals do not transmit directional information about the food source.

A similar simple system of communication about food sources is possessed by bumblebees (*Bombus*). In these relatively primitive forms, social facilitation seems to occur after a successful forager has returned to the colony. Odors from the food source, clinging to the body of the scout bee, apparently provide some information about the food source (Free, 1970b).

Workers of some species of meliponine bees (stingless bees) employ a similar primitive recruitment communication. Kerr and Esch (1965) report that in *Trigona silvestris* an increasing number of bees fly out and search for food when a forager returns to the nest carrying a characteristic odor with the food. Lindauer and Kerr (1958, 1960) and Esch (1967b) studied the different organizational levels of recruitment communication in stingless bees and found a variety of recruitment techniques of increasing complexity.

In *Trigona droryana*, returning foragers alert nest mates by a buzzing sound and a characteristic zigzag run inside the hive; however, no information about the direction and distance of the food source is transmitted. A similar communication behavior has been found in *T. muelleri*, *T. jaty*, and *T. araujoii*. The next higher organizational level is represented by *Trigona* (*Scaptotrigona*)

trigona) *postica*. Recruiting bees are clearly able to transmit directional information about the food source in the following way: When a scout bee discovers a food source it usually makes several trips between the food and the nest. Then it begins to set chemical signposts at two-meter intervals on its way back to the nest, using a marking substance that originates from the mandibular glands. Having laid a chemical trail from the food source to the nest, the scout conducts zigzag runs and emits characteristic sounds, which apparently alert the nest mates and induce them to follow the scout along the trail to the food source. During one such guiding flight a bee can lead more than fifty recruited nest mates to the target area. Lindauer and Kerr proved that the trail pheromone alone is not enough to elicit trail-following behavior in newcomers. A guide bee is necessary to lead the recruits to the food source. Only after the newcomers have been led along the trail, do they follow the trail back and forth on their own.

There seems to exist some degree of specificity in these chemical orientation trails. *Trigona xanthotricha* follows trails of *T. postica*, but not vice versa. Neither *T. postica* nor *T. spinipes* follow each other's trails (Kerr et al., 1963). Blum et al. (1970) identified neral and geranial as major compounds of the mandibular gland secretions of *Trigona subterranea* and provided circumstantial evidence that these substances constitute the effective trail pheromone. Recently Kerr et al. (unpublished; cited in Blum, 1974) succeeded in inducing trail-following behavior in *T. spinipes* along an artificial trail of 2-heptanol, one of the major compounds in the mandibular gland secretions of this species. It is interesting to note here that a propaganda-pheromone technique has also been discovered in stingless bees comparable to that used by slave raiding ants (see p. 429). Stejskal (1962) observed that the robber bee *Lestrimelitta limao* lays chemical trails from its own nest to the host species' nests with mandibu-

lar gland secretions. Blum (1966a) identified citral as the major trail pheromone, and later (Blum et al., 1970) found that when citral is introduced into colonies of the hosts *Trigona* or *Melipona*, the behavior of these bees is completely disrupted; in particular the victims seem unable to launch a defense.

In general, meliponine recruits evidently have to be alerted before they follow a chemical trail. Lindauer and Kerr (1958) provided the first experimental proof that sounds, emitted by recruiting bees, constitute the important triggering signal. Lindauer (1961) described the decisive experimental procedure as follows:

We divided the beehive into two compartments with a board. Through a sliding door at the entrance hole we could direct the marked collector bees into either one or the other compartment. After a fairly long feeding interval, we allowed a single scout to come to a known feeding place and could now establish that when we allowed her to return into compartment A she would also alert her colleagues in compartment B. In another experiment we combined two colonies in a single box, separated only by a wire screen. Now we could observe that the humming of a single collector bee of colony A would also alert novices of colony B. The result of the experiments was negative, however, when we padded the floor with foam rubber. The latter result indicates that the receptor mechanism for these humming sounds is not really hearing, but the vibrational sense. It thus seems to be proved that the humming of the collector bees has an alerting effect.

All species of *Trigona* studied produce such alerting sounds. A comparative investigation, however, revealed that the sounds of *Melipona* are more sophisticated. No odor trails are known in the genus *Melipona*, but the duration of the sounds produced by returning foragers varies directly with the distance to the food source (Kerr and Esch, 1965; Esch, 1967a). Thus the sounds not only alert nest mates but may also convey some information about the distance of the food source. Indeed, foragers of *Melipona quadrfasciata* that visited a nearby feeding station

could be induced to fly out again to visit the station when a tape recording of their own sounds was played back to them (Esch, 1967a). However, it must be mentioned that this experiment worked only if the feeding station was not too far away. Furthermore, only experienced worker bees responded. In addition to this alerting and distance-indicating signal, recruiting bees of *Melipona* guide hive mates in a striking zigzag flight toward the food source. These guiding flights last only 30–50 meters, after which the followers usually lose contact with the leader bee. However, after twenty to thirty repetitions of such guiding flights, the recruited bees try to find the target area on their own. In some species, for example, *Melipona seminigra*, the guiding flights are even shorter, only 10–20 m in length.

Recruitment Communication in *Apis*

CHEMICAL SIGNALS

The celebrated "dance language" in honeybees is probably the most sophisticated and most thoroughly studied communication behavior in the animal kingdom. However, it should not be overlooked that chemical signals also play an important role in the recruitment communication of these insects. The chemical signals interact with the dance language, and when they are described separately from it, as will now be done, the reader should keep in mind that the separation is artificial.

Karl von Frisch, who was the first to understand the bees' dance language, also discovered that honeybees employ a variety of chemical cues in recruitment communication. As early as 1923 he demonstrated that environmental odors, such as floral scents, play an important role during the recruitment process. It seems that floral scents in particular are carried on the body surface of scout bees when they return to the hive, where, together with the taste of the nectar offered in

regurgitation, it informs nest mates about the nature of the newly discovered food source. Bees that have already had a successful experience with a similar food source often become alerted by the familiar odor. Ribbands (1954, 1955a, 1955b) showed that some of these individuals are stimulated by the scents alone to fly out and search for food.

In addition to the environmental odors, pheromones are used during the recruitment of nest mates to certain target areas. As early as 1902 Sladen described "Sterzel"-behavior (chemical calling behavior) in honeybees. In many circumstances—for example, when bees attempt to attract lost foragers home to the hive or during swarming to a new nesting site—they bring their abdomen into a slanting position and by everting the Nassanoff's gland discharge an attraction pheromone, while simultaneously fanning their wings vigorously, thus accelerating the distribution of the pheromone (Renner, 1960) (Fig. 14). In 1923 von Frisch found that also during foraging worker bees discharge the Nassanoff gland secretions at feeding dishes containing highly concentrated sugar water. He found that more recruits arrive at a feeding station where scout bees were allowed to discharge the pheromone than at control stations where the

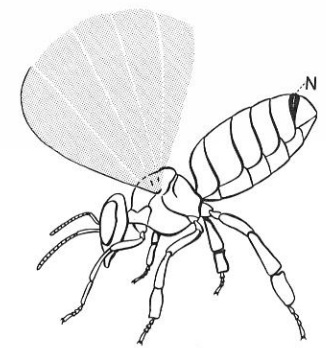


Fig. 14. A honeybee worker of *Apis mellifera* showing a recruitment calling posture with the Nassanoff gland exposed and fanning with the wings.

scout bees' scent organs had been sealed off. More recently Free and Williams (1970) pointed out that the role of the Nassanoff gland secretion as a recruitment signal is especially important during recruitment to new water sources. Since water is, in contrast to most of the natural food sources, all but scentless, it is more important to mark it so that it will be found. Indeed, bees commonly discharge the Nassanoff gland secretions after they have thoroughly inspected a new water source.

The Nassanoff gland opens dorsally between the last two abdominal tergites. Boch and Shearer (1962, 1964) identified geraniol, nerolic, and geranic acids as major compounds of the secretions, and their bioassays indicate that the mixture of these compounds is the attracting stimulus. In addition, Weaver et al. (1964) found citral to be a potent component, even though this substance constitutes only a minor fraction (Butler and Calam, 1969).

DANCE COMMUNICATION

Von Frisch and his students described a variety of different dance forms conducted by honeybees in the hive (see von Frisch, 1967a). In the following brief account I will concentrate on the two most important dance patterns employed to alert and recruit nest mates to certain target areas.

When a scout bee of *Apis mellifera* discovers a new rich food source, say, about 15 m from the hive, she flies home, enters the hive, and regurgitates food to several nest mates. After several trips back to the food source she finally starts to conduct the "round dance" (Fig. 15), which von Frisch describes as follows:

With swift tripping steps the forager bee runs in a circle, of such small diameter that for the most part only a single cell lies within it. She runs about over the six adjacent cells, suddenly reversing direction and then turning again to her original course, and so on. Between two reversals there are often one or two com-



Fig. 15. The round dance of *Apis mellifera*. The recruiting worker (black) dances the figure indicated by the arrows. Stimulated nest mates follow closely. (Based on von Frisch, 1967a.)

plete circles, but frequently only three-quarters or half of a circle. The dance may come to an end after one or two reversals, but 20 and more reversals may succeed one another; correspondingly, at times the dance lasts scarcely a second and at others often goes on for minutes. During dances of long duration the center of movement may shift gradually over the breadth of several cells. After the round dance has ended, food often is distributed again at this or some other place on the comb and the dance is then resumed; this performance may even be repeated thrice or (rarely) oftener. The dance ends unexpectedly as it began, and after a short period of cleaning and "refueling" the bee rushes hastily to the hive entrance and takes off on the next foraging flight.

The round dance contains no directional or distance information about the food source. It merely alerts and stimulates nest mates to fly out and search for the newly discovered food source. However, the alerted bees perceive the odor of the nearby source by antennating the dancer,

and they also receive taste samples. These cues enable them to find the particular source. As von Frisch has shown, the better the food source the more vigorous, long lasting, and lively are the dances, and, in turn, the more bees are recruited to the food source. Although some of these parameters are difficult to measure, there exists good observational evidence that they increase with the quality of the food, for instance, the sugar concentration of the bait (Lindauer, 1948; Boch, 1956).

If the distance between feeding place and hive increases from 25 m to 100 m the round dance gradually changes into the "waggle dance" (Fig. 16), and at distances greater than 100 m the round dance is finally completely re-

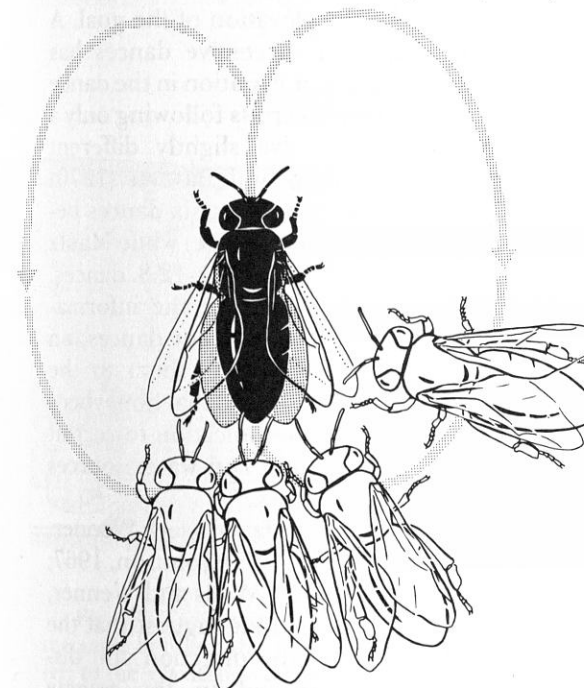


Fig. 16. The waggle dance of *Apis mellifera*. The recruiting worker (black) dances the figure indicated by the arrows. During the straight run it waggles vigorously with its body. The dancing bee is closely followed by stimulated nest mates. (Based on von Frisch, 1967a.)

placed by the waggle dance. Von Frisch (1967a) describes the waggle dance as follows:

In the typical tail-wagging dance the bee runs straight ahead for a short distance, returns in a semi-circle to the starting point, again runs through the straight stretch, describes a semicircle in the opposite direction, and so on in regular alternation. The straight part of the run is given particular emphasis by a vigorous wagging of the body. This results from rapid rhythmic sidewise deflections of the whole body that are greatest at the tip of the abdomen and least at the head. The axis about which the sidewise oscillation is to be envisaged lies close before the bee's head and perpendicular to the substrate. The movement to and fro is repeated 13–15 times in a second.

Like the round dance the waggle dance announces the find of a new profitable food source, the kind of food (by odor and taste samples), and the productivity of the food (by vigor and liveliness of the dances). But, unlike the round dances, the waggle dances in addition transmit information about the distance and the compass direction of the target area. Alerted bees follow the dancing bee with close antennal contact, and thereby receive this information. The straight run seems to be the most important part of the waggle dance figure. Not only do the alerted bees pay closest attention to this part of the dance but also its features are most closely correlated with the specific distance and direction of the target area.

The greater the distance to the food source the longer the duration of the straight run. The straight run, however, is characterized not only by the vigorous wagging of the abdomen. Esch (1961, 1964) and Wenner (1962a) found that during the straight run, the dancer also emits a buzzing sound the duration of which is exactly the same as that of the straight run. Esch produced circumstantial evidence that the duration of the buzzing, which the follower bees perceive with their antennae and legs, is the most important distance-indicating cue. Occasionally, for

example when the sugar concentration is low, recruiters conduct "silent" dances. Of 15,000 such dances observed by Esch, none succeeded in recruiting bees to the food source. The next question is: How does the dancer estimate the distance between the hive and the food source? Strong circumstantial evidence exists that the bees use the amount of energy consumed on the flight to the food source as a measure of the distance. For instance, if a bee has to fly to the food against a head wind, the distance she indicates in the dance is longer than the actual one. The same is true if the bee is somehow hindered by an artificial weight or some tinfoil mounted on her thorax to increase air resistance during her flight to the food. It is important to note that only one way is measured—only the energy required to fly to the food source is indicated in the dance.

As noted, the waggle dance contains not merely information about the distance of a food source but also the direction in which the recruits have to fly. If the weather is very warm and many bees are assembled outside the hive, one can frequently observe foragers regurgitating their crop contents even before they enter the hive; they also dance on a horizontal surface in front of the nest entrance under the open sky. In those cases the straight run of the dance always points in the direction of the food source. The dancing bee maintains the same angle relative to the sun as on the flight from the hive to the feeding place. In a series of ingenious experiments, von Frisch demonstrated that the bee orients just as well relative to the polarized light of the blue sky. When, however, the sky is completely clouded or the horizontal platform is placed in the dark, the dancers are disoriented and do not indicate a specific direction.

Inside the hive, where it is completely dark, the bees are therefore forced to use another cue to orient their dances. Now they dance on the vertical surface of the combs and translate the

solar angle (azimuth) into the gravitational angle. The dancer changes the angle of the straight run with respect to the sun to an angle with respect to gravity. If the food source is located, say, 40° left of the sun, the dancing bee will orient its straight run at an angle of 40° to the left of the vertical. When the bee dances straight up, it is indicating a food source located on a straight line toward the sun. Similarly, if the scout dances straight down it means the goal is located in the opposite direction. In this way the scout is able to indicate any direction in the 360° around the nest (Fig. 17). However, she cannot signal "upward" or "downward" with reference to space outside the hive. Thus the hive mates are informed about the azimuthal angle and the distance but not about the elevation of the goal. A comparative analysis of successive dances has shown that there is a minor variation in the dance components. Therefore recruits following only a single dance would receive slightly different messages. However, Esch and Bastian (1970) found that recruits follow at least six dances before they fly out to the food source, while Mautz (1971) found them following 6.9–12.8 dances. Apparently the recruits integrate the information they receive from the different dances, an operation that accurately directs them to the goal. Lindauer (1955) discovered that honeybees employ waggle-dance communication to recruit nest mates not only to food and water sources but also to new nesting sites.

Wenner and his associates (see Wenner, 1967; Wenner et al., 1967, 1969; Johnson, 1967; Johnson and Wenner, 1970; Wells and Wenner, 1973) claimed new results that suggest that the bees do not understand the direction and distance information contained in the waggle dance. According to their hypothesis the recruited bees find their way to the food source entirely by means of other cues, such as odors. Their criticism of von Frisch's experiments in part reflects their incomplete interpretation of

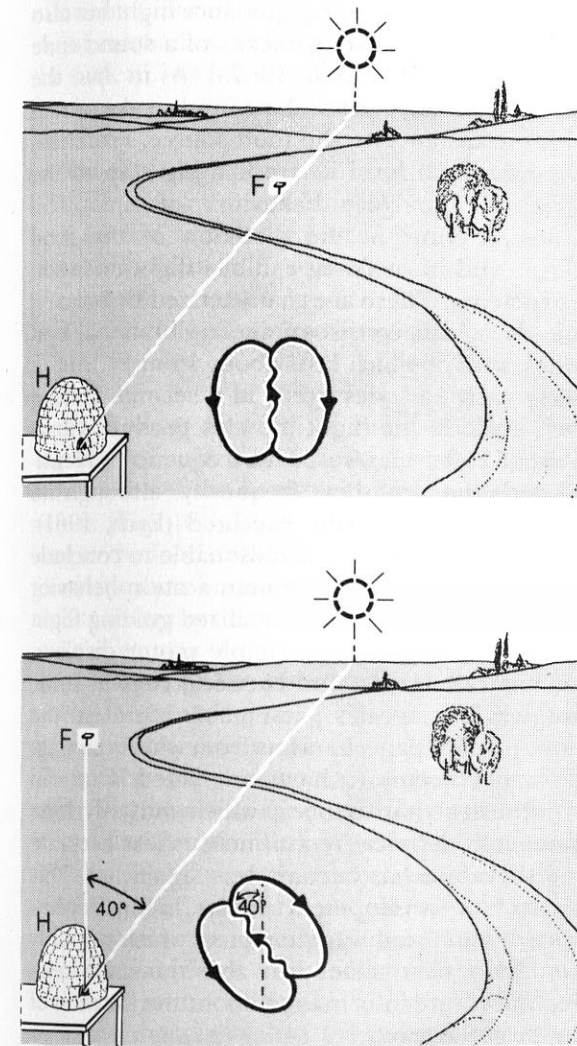


Fig. 17. Two examples illustrating the transfer of the angle between the sun, food source (F), and hive (H) to the gravitational dimension. Above: The food source is located in the direction of the sun; the straight waggle run of the dancing figure on the vertical comb points straight up. Below: The food source is located 40° to the left of the line drawn from the hive to the sun; therefore, the dancing bee orients its straight waggle run in an angle 40° to the left of the vertical line on the comb.

earlier, extensive literature. Although they criticized von Frisch's control experiments as being insufficient to prove direction and distance communication in honeybees, their own experiments were far more seriously lacking in controls. For a critical evaluation of this controversy see von Frisch (1967b, 1968), Wilson (1971), Lindauer (1971), Michener (1974), Gould (1975), Gould et al. (1970), and Griffin (see this volume, p. 27). On the positive side, the skepticism of Wenner and his associates has stimulated new investigations by other research groups. New techniques and more-rigorous control experiments were applied, which finally led to the full confirmation of von Frisch's results.

The most important progress in the study of the honeybees' dance communication has very recently been achieved by Gould (1974, 1975). He succeeded in causing a "natural dummy" to dance and was thereby able to misdirect recruits into areas other than those where the feeding station was located. For the design of his experiments Gould exploited the following findings: (1) Von Frisch (1962) had reported that the honeybees tend to interpret a bright light in the hive as the sun and will orient their dances to it rather than to gravity. (2) Lindauer and Schricker (1963) demonstrated that bees with their ocelli painted over are far less sensitive to light. On this basis Gould argued:

When a light of an appropriate brightness is used, foragers with painted ocelli will ignore the light and dance with respect to gravity, while untreated bees both dance and interpret dances as though the light were the sun. If the bees utilize the distance and direction information in the dance, it should be possible for ocelli-painted foragers to recruit bees to specific but incorrect locations.

Indeed, by this kind of experimentation, Gould demonstrated that a significant number of recruits used the false information about distance and direction transmitted by the dancing bee and

arrived at the checkpoint but not at the feeding station.

EVOLUTIONARY ASPECTS OF DANCE COMMUNICATION

The search by von Frisch and his associates for more-elementary forms of communication in other bee species, including stingless bees, has resulted in the reconstruction of the possible evolution that led to the highly sophisticated dance language in the honeybee *Apis mellifera*. Boch (1957) demonstrated that even within the species *A. mellifera* there exist considerable variations in the dance language. Different geographical races communicate with different "dialects." For instance, in *A. mellifera carnica* the round dance changes to the waggle dance when the goal is about 85 m from the hive, whereas in *A. mellifera nigra* and *A. mellifera intermissa* this occurs at distances of about 65 m and in *A. mellifera fasciata* at only 12 m.

Lindauer (1956) studied dance communication in other *Apis* species. Probably the closest relative to *A. mellifera* is *A. indica*. It also nests in dark crevices, and like *A. mellifera* it translates the azimuthal angle into a gravitational angle on a vertical surface. However, the waggle dance is performed even when the goal is as close as 2 m from the nest. The giant honeybee (*Apis dorsata*) nests in the open under a rock or in a tree. Foragers dance on the vertical comb, but they need the sun or the blue sky to orient their waggle dance. The dwarf honeybee (*Apis florea*) also nests in the open. It communicates by the waggle dance but only performs on a horizontal platform. If it is forced to dance on a vertical surface, it either stops dancing or becomes disoriented. Obviously this species is not able to translate the azimuthal angle into the gravitational angle.

This brings us back to the stingless bees, discussed on p. 441–43. In the most advanced species, such as *Melipona quadrifasciata* and *M. merillae*, foragers not only show the direction to

the goal by a short zigzag guidance flight but also indicate the distance by means of a sound code (Esch et al., 1965; Esch, 1967a). As in *Apis*, the duration of these particular sounds is correlated with the distance to the food source. From this organizational level it is not a big step to the "symbolic guidance behavior" of *Apis*. The honeybee runs in the direction of the food source and in so doing exhibits flight-intention movements. These are characterized by buzzing sounds, which consist of short vibrational episodes, one of which lasts about 15 msec. About thirty such episodes occur in a second. During each episode the flight muscles produce vibrations of 250 cycles/sec. This frequency is identical with the wing-beat frequency, although no wing stroke is actually executed (Esch, 1961). From these findings it is reasonable to conclude that the waggle-dance communication behavior in honeybees is a highly ritualized guiding flight to the target area. The simple motor displays, mechanical signals, and chemical cues of some stingless bee species presumably represent the more primitive mechanisms from which the waggle dance seems to have originated. One can hypothesize that in bees, which must fly long distances, chemical recruitment is less accurate and therefore has become less significant. This led to the development of the highly sophisticated, ritualized waggle dance, which not only stimulates nest mates but also transmits relatively accurate information about the location of the target area.

Communication during Trophallaxis

Wilson (1971) defines trophallaxis as the "exchange of alimentary liquids among colony members and guest organisms either mutually or unilaterally. In stomodeal trophallaxis the material originates from the mouth; in proctodeal trophallaxis it originates from the anus." Trophallaxis plays a central role in the social orga-

nization of most species of social insects. It is the major mechanism by which food is distributed in the society; but in addition it functions to transfer specific pheromones from one individual to another.

Usually trophallaxis is initiated by specific communication stimuli. Montagner (1966, 1967) studied the signals involved during food exchange between adults of the social wasps *Vespula* (*Paravespula*) *germanica* and *V. (P.) vulgaris*. He found that the soliciting wasp initiates regurgitation in a prospective donor by a series of tactile signals. When the begging wasp has approached the nest mate head-on, she lowers her body slightly, turns her head sideways, and strokes the mouthparts of the donor with her antennae and palpi (Fig. 18). This stimulation continues as long as the food exchange goes on. When regurgitation comes to an end, the donor pushes its antennae against the mandibles of the beggar, and the contact is interrupted.

Montagner describes a social hierarchy among the adults by which dominant individuals apparently receive more food than they give. The mother queen is on top of the hierarchical order, virgin queens are dominant over their sisters, and within the worker group there appears to exist a dominance relationship expressed by certain subtle behavioral patterns. For instance, a dominant worker does not lower its body when it solicits food from a subordinate. Occasionally, it even steps on the donor, stroking intensively with its antennae against the mouthparts of the subordinate and thereby "forcing" it to regurgitate its crop contents.

There also exists a reciprocal food exchange between wasp adults and larvae. Du Buyson (1903) and Janet (1903) were the first to describe the larval secretions of *Polistes* and *Vespula* as sweet substances. Roubaud (1911) suggested that larvae induce brood-tending behavior in adult wasps by offering them these secretions, and W. M. Wheeler (1918) finally proposed the

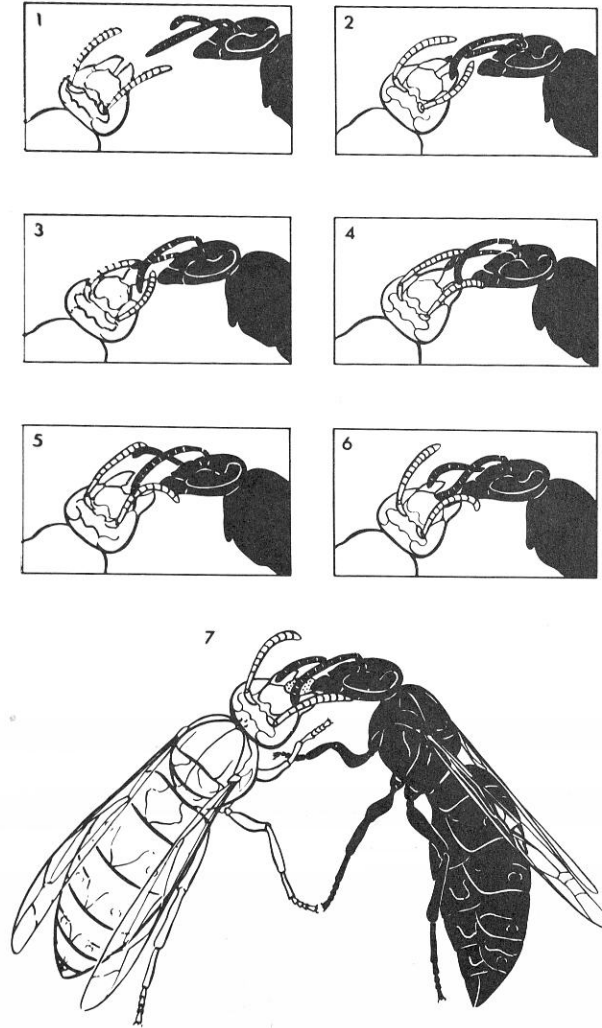


Fig. 18. The initiation of regurgitation between two workers of the wasp *Vespula* (*Paravespula*) *germanica*. 1., 2. The solicitor on the right approaches the donor and places the tips of her flexible antennae on the donor's lower mouthparts. 3. The donor responds by closing her antennae onto those of the solicitor, who then begins gently to stroke her antennae up and down over the lower mouthparts 4–7. If this interaction continues, the donor will begin to regurgitate, and the solicitor will be able to feed. (From Wilson, 1971, based on Montagner, 1966.)

term "trophallaxis" for this kind of reciprocal food exchange.

Usually wasp larvae give away these liquids, which are secreted from the saliva glands, as soon as they are stimulated by very unspecific tactile signals. Maschwitz (1966b) analyzed the larval salivary secretions of *Vespula* (*Paravespula*) *germanica* and found it to be an 8.9 percent sugar solution (trehalose and glucose). Amino acids, proteins, and proteolytic enzymes and small amounts of uric acid and ammonia are also present in the larval saliva secretions. Maschwitz provided convincing evidence that these larval secretions are used by workers as an energy source, especially when they are prevented from making foraging trips during bad weather and on other occasions. Thus the larvae can function as living storage containers.

According to Montagner's findings (1963, 1964) *Vespula* males obtain most of their food by milking larvae. Their "awkward" begging behavior toward adult workers solicits but little food; thus they depend heavily on larval secretions. Ikan et al. (1968) and Ishay and Ikan (1969), working with *Vespa orientalis*, confirmed Maschwitz's results and discovered in addition what Wilson (1971) has called "a biochemical division of labor." *Vespa orientalis* adults are apparently unable to digest proteins. Only larvae are capable of gluconeogenesis and convert proteins, which they are fed by workers, partly to carbohydrates, such as glucose, fructose, and sucrose, and return them to the adults during trophallaxis. This division of labor is not universal, however, because in other wasp species, such as *Vespula germanica*, proteolytic enzymes have been detected in the midguts of larvae and adults (Spradbery, 1973).

Trophallaxis is highly variable among species of bees and is most elaborately developed in the honeybees *Apis*. Michener (1974) describes a typical food exchange between forager and nest-worker in honeybees as follows:

When a forager with a crop full of nectar arrives in the nest, she promptly approaches a receiver head-on, opens her mandibles, and regurgitates a drop of nectar onto the slightly projected base of her proboscis (upper surface of prementum and stipites), the rest of which remains folded back under the head. The receiver then extends her proboscis and, with the tip of it, takes nectar from the drop. Meanwhile the antennae of both bees are in continual stroking motion, an activity that probably keeps the two bees properly oriented for the transfer.

Montagner and Pain (1971), with the aid of high-speed motion picture analysis, recently described the movement of the antennae during the trophallactic act in more detail. Free (1956, 1959) studied the releasing stimuli of trophallactic behavior in honeybees with a series of ingenious dummy experiments. He was able to demonstrate that the head with antennae is clearly superior to any other part of the body in releasing the solicitation of food-offering behavior. If the antennae are removed, the dummy becomes less effective, but the effectiveness can be restored by inserting artificial antennae made of wire. In addition, odor seems to play a major role: heads belonging to nest mates were more effective as trophallactic releasers than those belonging to members of another colony. Free also found that a begging bee releases regurgitation in a nest mate by thrusting its proboscis between the mouthparts of a prospective donor.

The "eagerness" with which hive workers accept the crop load from a recruiting forager indicates to the forager the food need of the colony and may in fact determine whether the forager starts to recruit nest mates to the food source by dancing. A similar communication mechanism is applied during the "air conditioning" process in a beehive. Even if the outside temperature rises to more than 70°C, the internal temperature of the hive remains about 35°C. This is achieved by an increased evaporation of water.

Water is carried into the hive and distributed on cells in tiny droplets. Droplets are deposited particu-

larly at the entrance of the open brood cells. At the same time a large number of bees can be seen hanging over the brood cells and continuously extending their proboscises back and forth. Each time they do this they press a drop of water from their mouths and spread it with the proboscis into a film, which has a large evaporating surface. When the water evaporates, the proboscis is retracted again and a new droplet spread out. [Lindauer, 1971]

This air-conditioning behavior is regulated by a highly organized division of labor. Only experienced bees function as water collectors; they give their water loads to the nest workers, which then spread the water around. However, the water collectors' activity has to be adjusted to the needs inside the hive, which in turn depends on the temperature. In other words, there has to be a sort of thermostat that turns the cooling system on or off. Lindauer (1954) discovered that this consists of a relatively simple "feedback" communication process.

Let us assume that water collecting is still in progress and the foragers are to be informed whether or not there is need for more water. To transmit this information the hive bees make use of the short moment when they have contact with the collectors; this is during water delivery at the entrance hole. As long as overheating exists, the home-coming foragers are relieved of their burden with great greed, three or four bees at once may rush up to a collector and suck from her the extruded water droplet. This stormy begging informs the collector bee that there is a pressing need for more water. When the overheating begins to subside, however, the hive bees show less interest in the water collectors. The latter now have to run around in the hive themselves, trying to find somewhere a bee that will relieve them of at least part of the water load. The delivery in such cases takes much more time, of course. This rejecting attitude contains the message "Water needs fulfilled," and the water collecting will thus stop, even though the collectors themselves have not been at the brood nests to experience the changed temperature situation. [Lindauer, 1971]

Lindauer could convincingly demonstrate that in honeybees "this delivery time is in fact an accurate gauge of water demand."

In ants the development of trophallactic food exchange is highly variable. In most of the species of the two more-primitive subfamilies Myrmecinae and Ponerinae, trophallaxis is either completely lacking or only poorly developed. The rate of trophallactic food exchange can be measured quantitatively by labeling the food with radioactive tracers (Gösswald and Kloft, 1956, 1960; Wilson and Eisner, 1957). Many species of the subfamilies Aneuretinae, Dolichoderinae, Formicinae, and Myrmicinae show a relatively high food-exchange rate (Wilson and Eisner, 1957). In a few other species, however, trophallaxis apparently has become irrelevant with the development of very specialized feeding habits. Examples of these specialized groups include the harvesting ants and fungus-growing ants.

The rate of food exchange depends also on several environmental and physiological factors, such as temperature, humidity, and nutritional status, as well as on the size and social structure of the group (Kneitz, 1963; Lange, 1967). The radioactive tracer technique allows the direction of social food flow to be determined; it can further be used to identify which castes and age groups are participating. Lange (1967), for instance, discovered that in *Formica* species the flow of protein food is directed preferentially toward young workers and queens, whereas carbohydrates are more evenly distributed in the colony. In most species only female castes regurgitate food to other members of the society. In carpenter ants (*Camponotus herculeanus* and *C. ligniperda*) young males also take an active part in the social food distribution (Hölldobler, 1966). In these species the males live in the nest an unusually long time (more than nine months) before departing for the nuptial flight. During the first phase of their adult life especially, they receive large amounts of food from the workers. This intake apparently enables them to complete their spermatogenesis and to build up a rich fat

body. It seems reasonable that during this period the males do not block the social food flow but rather participate actively in the social food distribution.

Foragers usually carry liquid food into the nest in their crops (foregut) and regurgitate part of the contents to individual nest mates (Fig. 19). There is strong circumstantial evidence that during trophallaxis secretions from the labial gland and postpharyngeal gland are also passed from one individual to the other. Recent results by Markin (1970) indicate that in the Argentine ant *Iridomyrmex humilis* secretions from the postpharyngeal gland are preferentially fed to queens and small larvae.

The social food flow in an ant society is organized by a variety of signals. Queen pheromones and specific cues by which young workers and brood are identified probably regulate the directed food flow. In addition certain behavioral patterns and tactile signals play a major role during trophallactic food exchange. Several attempts have been made to analyze these signals in ants (Kloft, 1959; Wallis, 1961; Hölldobler, 1966; Lenoir, 1972a, 1972b). Recently we applied high-speed motion picture analyses (200–450 f/sec), which, together with the facts already



Fig. 19. Schematic drawing illustrating the food flow from the crop (right) of the donor ant to the soliciting ant (left). K = crop, M = midgut, R = hindgut. (From Hölldobler, 1973c.)

known, enabled us to synthesize a fairly complete picture of the food exchange behavior in *Formica* (Hölldobler, 1970a, 1973c).

The behavioral patterns of the donor and the solicitor are exceedingly different. Workers returning to the nest with a heavily filled crop approach nest mates head-on, with their mandibles wide open and their labia extended. If this results in a mouth-to-mouth contact and the labium of the food-offering ant is only slightly touched, regurgitation occurs instantly. If the food-carrying ant does not find a nest mate ready to accept the food, she will regurgitate a food droplet even without any tactile stimulation. After she has held it for a while between her mandibles, she will finally scrape it off on the ground or a wall of the nest chamber.

According to Wallis (1961), in about 90 percent of the cases the initiative during food-exchange behavior comes from the soliciting worker. The solicitor first antennates an approaching ant, and as soon as both ants stand head-on, the beggar conducts rapid strokes with its forelegs while simultaneously continuing to antennate the other ant's head (Fig. 20). The more intense the begging behavior the more precisely are the strokes of the forelegs aimed toward the mouthparts of the donor. Motion pictures taken from the underside clearly demonstrate that in these cases the strokes hit the labium of the donor. Indeed, these tactile signals seem to release regurgitation. The donor opens the mandibles, extrudes the labium, and regurgitates crop contents. Frequently, stroking with the forelegs ceases as soon as the food begins to flow. Nevertheless, the beggar continues to touch the head and to palpate the mouthparts of the donor with its maxillae. The donor, on the other hand, keeps its antennae folded backward, and only when the regurgitation comes to an end does it move them closer to the beggar's head. Often the beggar then provides another series of strokes with its forelegs, which may induce a sec-

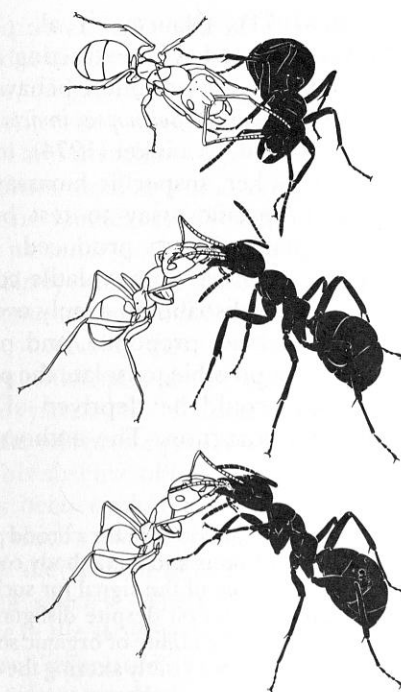


Fig. 20. Three behavioral steps that generally characterize trophallactic food exchange in the ant *Formica sanguinea*. Above: The begging ant (white) antennates a prospective donor ant. Middle: The solicitor stimulates the labium of the donor with its forelegs while continuing its antennation. This leads to regurgitation of crop contents by the donor. Below: As the crop of the donor gradually empties, the tendency to regurgitate crop contents weakens. The donor raises its forelegs and finally exhibits its own begging movements. This usually terminates the trophallactic food exchange. (From Hölldobler, 1973c.)

ond phase of regurgitation. But when the donor finally raises its forelegs and even conducts begging strokes, the trophallactic contact usually breaks up. These observations suggest that besides the other stimuli, the tactile stimulation of the mouthparts releases regurgitation in food-laden ants. This inference was confirmed experimentally. Ants with a full crop could be induced to regurgitate crop contents by artificially stimulating them at the labium.

Trophallactic relations exist not only between adults but also between larvae and adults. In species of the subfamilies Ponerinae, Myrmicinae, and Formicinae, especially, larvae stimulated by touch discharge small quantities of liquid, which are then readily licked up by the workers (Le Masne, 1953; Maschwitz, 1966b). Maschwitz found relatively high concentrations of amino acids but no carbohydrates in the stomodeal contents of larvae of *Tetramorium caespitum*. Wüst (1973) demonstrated that the stomodeal secretions originate from the labial gland. She found that the labial glands of *Monomorium pharaonis* contain amino acids and proteins, but no carbohydrates. Ant larvae also discharge a clear liquid from the anal region. Le Masne (1953) speculates that these substances originate from the Malpighian tubules and contain waste products. Wüst was able to show that the proctodeal substances are discharged from the rectal bladder and that they contain mainly amino acids. Wüst also provided experimental evidence that these larval secretions can play an important role in the "social food household" of an ant colony. In *Leptothorax curvispinosus*, these larval secretions seem to constitute the main food of the queens (Wilson, 1974).

Brood-Adult Communication

The preceding section presented a few examples of behavioral interactions between larvae and adults in the social Hymenoptera. I will now discuss some signals that have been found to regulate communication between brood and adults.

The fourth- and fifth-instar larvae of hornets (*Vespa crabro* and *V. orientalis*) produce sounds by extending and contracting their bodies rhythmically and thereby scraping their mandibles across the carton wall of the cells. Investigations by Schaudinischky and Ishay (1968) and Ishay and Landau (1972) indicate that these sounds may

function as a "food-begging" signal. When the sounds were recorded and played back through a vibrator attached to an empty cell, workers oriented toward the cell and attempted to feed it. According to Ishay and Schwartz (1973), the sound frequencies produced by worker-, queen-, and male-larvae differ from one another. The same authors found species differences in the larval sounds of *V. orientalis* and *V. crabro*. In studying thermoregulation in the nests of hornets, Ishay and Ruttner (1971) discovered that female adults tend to warm older pigmented pupae, even when they are placed outside the nest. Ishay (1972) provided evidence that these pupal wasps emit a pheromone that not only attracts the adults but also evokes warming behavior.

Brooding behavior is also induced by chemical signals in young queens of the bumblebee species *Bombus vosnesenskii* and *B. edwardsii* by chemical signals. Heinrich (1974) demonstrated that in this case the pheromone apparently does not originate from the brood but is deposited onto the brood clump by the queen. The scent guides the queen and subsequently the workers to the site where the brood is located and induces them to provide warming behavior.

Although not much is known about brood-adult communication in honeybees, there is circumstantial evidence that honeybee workers can smell their larvae. Free (1967) has demonstrated that the odor of the brood alone causes honeybee workers to forage for pollen. Further, it has been shown that honeybee workers distinguish not only between worker larvae and male larvae (Haydak, 1958) but also between worker larvae and queen larvae (Woyke, 1971). The cues employed are still unknown.

Ants lick and tend their brood constantly. Numerous observations indicate that this intimate relationship between nurses and brood is based on chemical communication (Watkins and Cole, 1966; Hölldobler, 1965, 1967; Schneirla,

1971; Wilson, 1971). Glancey et al. (1970) claimed to have succeeded in extracting larval pheromones that release adoption behavior in adult ants from larvae of *Solenopsis invicta* (= *S. saevissima*). Walsh and Tschinkel (1974), unable to duplicate the rather unspecific bioassay, developed a more specific assay to test brood-recognition signals. They produced good evidence that in *S. invicta* a nonvolatile contact brood pheromone is distributed evenly over the whole cuticle of larvae, prepupae, and pupae. Although it was not possible to isolate the pheromone, the pupae could be deprived of their attractiveness by extraction. The authors concluded:

There exists substantial evidence for a brood pheromone. The retrieval of skins and larval body contents on blotter, the persistence of the signal for such long periods after death (72 hours) despite disfigurement of the larval cuticle and the ability of organic solvents to destroy the signal without visibly altering the cuticle are compelling evidence for a pheromone.

I can fully confirm these results by my own independent investigations with *Camponotus ligniperda* (Hölldobler, 1965) and *Formica sanguinea* (Hölldobler, unpublished). In these species I found nonvolatile chemical components, attractive to adult ants, on the pupa's skin. I have circumstantial evidence that these pupal pheromones are at least in part contained in the exuvial liquid. During eclosion of the pupa the pheromones seem to stimulate nurse ants to aid the young in the eclosion process.

This result leads us to the formulation of another important problem. Ant larvae, pupae, and young callow workers can easily be transferred from one colony to another, often even from one species to another (K. Hölldobler, 1948; Plateaux, 1960; Hölldobler, 1967). After a certain age, however, adult workers are no longer accepted by foreign colonies. If, as is generally assumed, the colony odor is caused by the

absorption of a specific mixture of environmental odorants into the cuticle, it is not clear why larvae, pupae, and callow workers should not carry the odor of the colony in which they are raised and therefore be just as subject to aggression from members of a foreign colony as their older nest mates are. To explain these contradictions we can hypothesize that in the brood stages the colony odor is masked by the brood-tending pheromones, which are not colony-specific. It is also conceivable that these pheromones have a high position in a hierarchical order of a pheromone system and "dominate" any other colony-specific odorous cues (Hölldobler, 1973a).

This absence of brood discrimination has actually been exploited by many social parasitic ants, which conduct so-called slave raids, during which they rob brood of closely related neighboring species. When these kidnapped pupae eclose in the slave raiders' nest, the young workers are "imprinted" with the odor of their captors' colony and in the future behave in a hostile manner toward their real sisters, who have remained behind in their mutual mother's nest. The assumption of a high position of the brood pheromone in a pheromone system would also imply that the *Q/K* ratio, i.e., the ratio of pheromone molecules released to the response-threshold concentration (Bossert and Wilson, 1963), should be very low. A high *Q/K* would saturate the nest with the dominant signal, and colony odors and other chemical signals would become almost ineffective. Indeed, the observations that the brood pheromones are nonvolatile and are effective only in very close ranges support this speculation.

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. Different species of myrmecophiles occupy different sites within an ant colony. Some live along the trails of the ants, some 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*. *L. 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 Wasmann's observations, made sixty 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 up and try

to make contact with the ant's head. If they succeed they tap the ant's labium with their own mouthparts (Fig. 21). This apparently releases regurgitation of food by the ant. The ant larvae beg for food in much the same way, but less intensely.

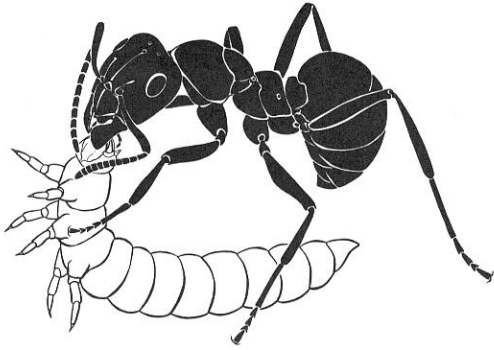


Fig. 21. Food-begging behavior of the larva of the myrmecophilous beetle *Ateomes pubicollis*. (From Hölldobler, 1967.)

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 receive. 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 demon-

strated 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 had to be shellac-free. Furthermore, it was possible to show that after all the secretions were extracted 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 that 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 given 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. *Ateomes* 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 spring return to a *Formica* nest to breed (Wasmann, 1910; Hölldobler, 1970a). The fact that the adult beetle is tolerated and fed in the nests of ants belonging to two different subfamilies suggests that it is able to communicate efficiently in two different "languages."

The *Ateomes* 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 *Ateomes* 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 the other species present and locate their nests. Laboratory experiments have revealed that they identify the *Myrmica* nests by specific odors. Wind-borne 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 five sequential steps depicted in Fig. 22. First the beetle taps the ant lightly with its antennae and raises the tip of its abdomen toward the ant. The latter structure contains what I call the "appeasement glands." The secretions of these glands, which are immediately licked up by the

ant, seem to 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, which 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 the ant with its antennae. Using its maxillae and forelegs it touches the mouthparts of the ant, thus inducing regurgitation (Fig. 23). As noted previously, the ants themselves employ a similar mechanical stimulation of the mouthparts to 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 con-

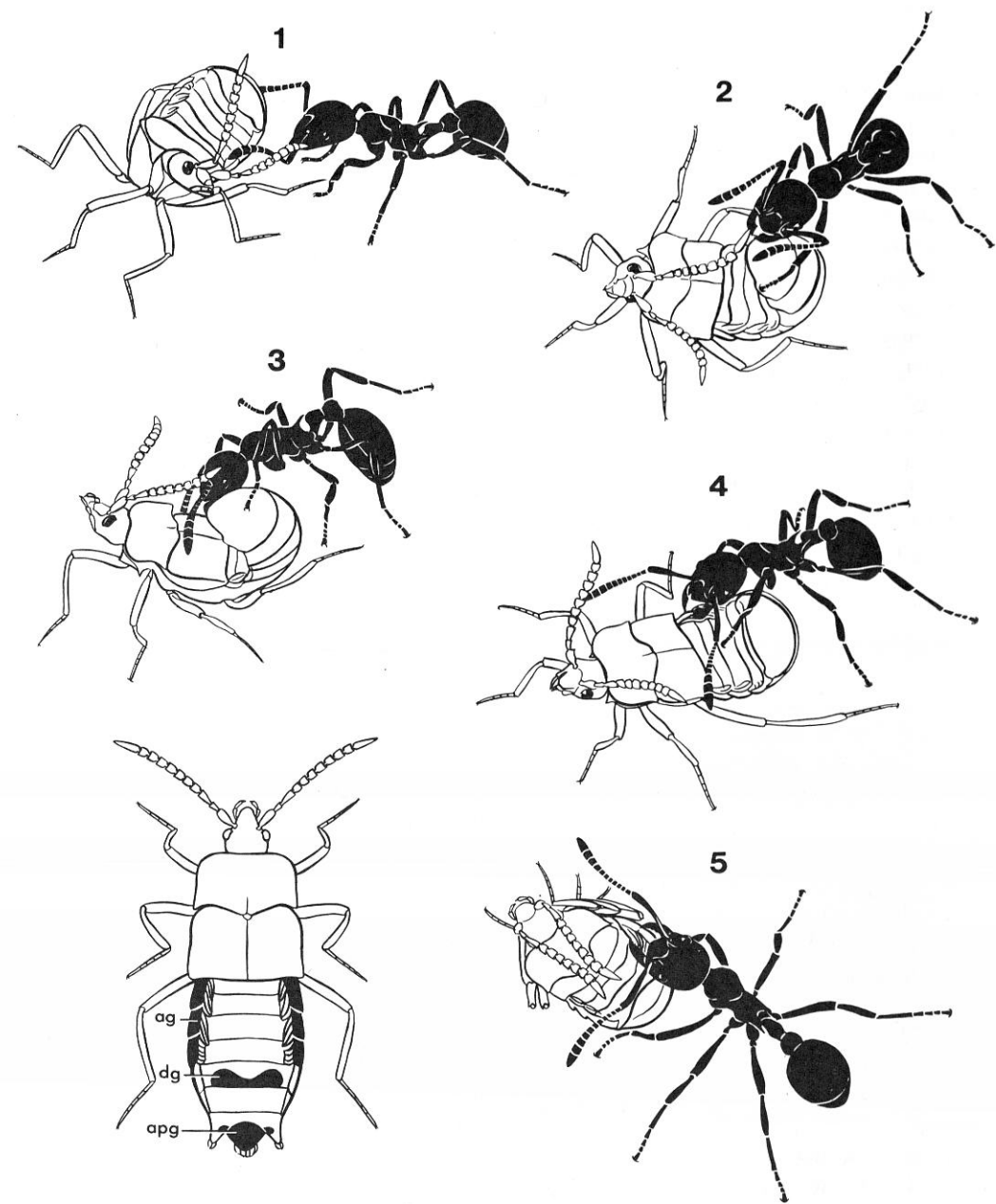


Fig. 22. Behavioral interactions between the beetle *Ateleles pubicollis* (white) and the ant *Myrmica laevinodis* (black) during the adoption process. 1., 2. The beetle antennates to the ant. 3. After licking, the ant moves around and licks the adoption glands (ag). 4. The

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.)

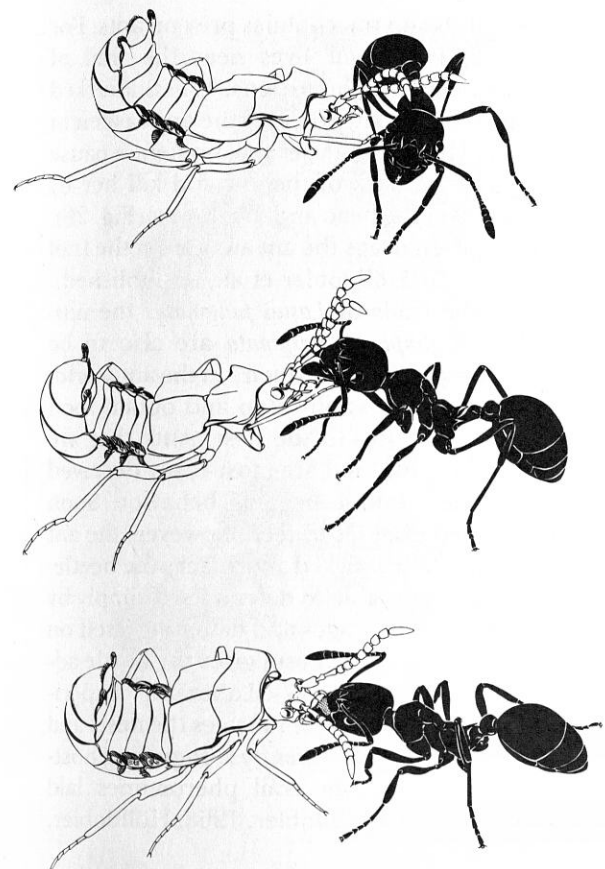


Fig. 23. The myrmecophilous beetle *Ateleles pubicollis* soliciting regurgitation in its host ant *Myrmica laevinodis*. Above: The beetle gains the attention of a worker ant by tapping it with its antennae and forelegs. Middle: The beetle then stimulates the labium of the ant, thereby releasing regurgitation (bottom). (From Hölldobler, 1970a.)

trast, 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 *Ateleles* 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). 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 *Ateleles*.

All the myrmecophiles described so far possess the necessary repertoire to enable them to live in the brood chambers of the ants' nests. These chambers constitute the optimal niche in an ant colony for a social food-flow parasite. Other myrmecophiles, which lack 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*, where food exchange occurs between the foragers and the nest workers. It is here that *Dinarda* is 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 (Fig. 24). 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 (Fig. 25). This usually causes the ant to regurgitate a small droplet of food. The ant,

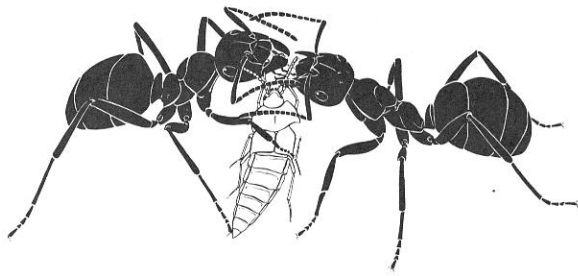


Fig. 24. The myrmecophilous beetle *Dinarda dentata* inserts itself between two ant workers exchanging food. (From Hölldobler, 1973a.)

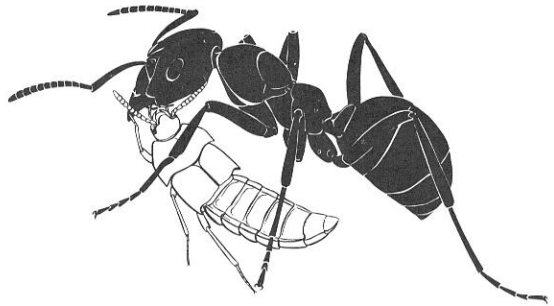


Fig. 25. The beetle *Dinarda dentata* approaches a food-laden ant and touches its labium surreptitiously. This usually causes the ant to regurgitate a small droplet of food. (From Hölldobler, 1973a.)

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, which 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. However, it uses the moment's pause to jump on the back of the ant and kill her by biting between the head and the thorax (Fig. 26). The beetle then drags the ant away from the trail and devours it (Hölldobler et al., unpublished).

Along the trails of *Lasius fuliginosus* the nitidulid beetle *Amphotis marginata* are also to be found. Acting as "highwaymen" in the ant world, these beetles 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. 27). Laboratory experiments showed 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).

Other myrmecophiles also utilize the chemically marked trails of their host species to locate

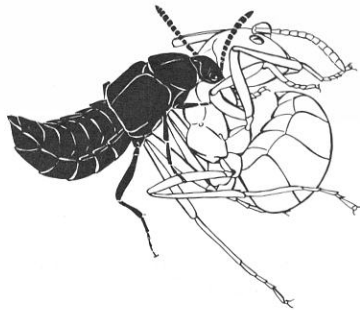


Fig. 26. The predatorial beetle *Pella laticollis* jumps on the back of the ant *Lasius fuliginosus* and kills her by a bite between the head and the thorax.

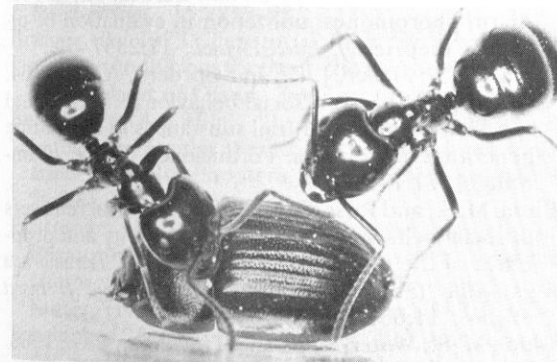
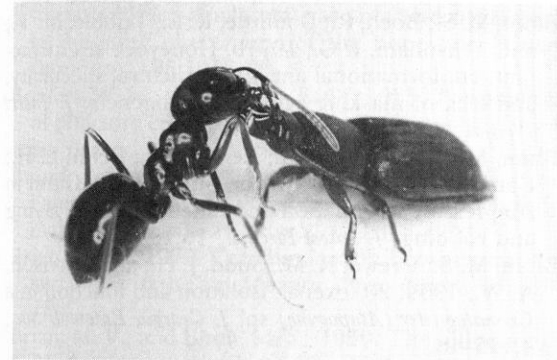
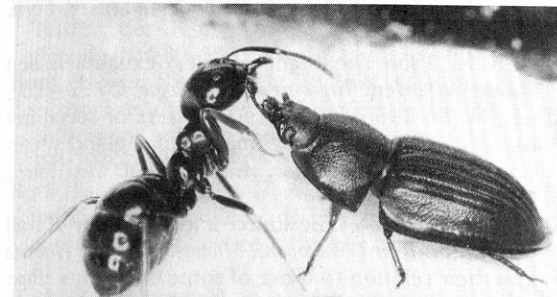


Fig. 27. The nitidulid beetle *Amphotis marginata* waits in ambush on the foraging trails of *Lasius fuliginosus* for food-laden workers. By stimulating the ant's mouthparts (top) the beetle causes it to regurgitate crop contents (middle). The robbed ant frequently reacts aggressively, but passive defense (bottom) enables the armored beetle to weather the attack. (From Hölldobler, 1971b.)

the host nests or to follow the colony during migrations. 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 laid down with 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 that 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 that 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 that have led in the end to the highly adapted myrmecophilic behavior of *Atemeles* and *Lomechusa*.

References

- Akre, R. D., and Rettenmeyer, C. W., 1968. Trail-following by guests of army ants (Hymenoptera: Formicidae: Ecitonini). *J. Kansas Entomol. Soc.*, 41:165-74.
- Amoore, J. E.; Palmieri, G.; Wanke, E.; and Blum, M. S., 1969. Ant alarm pheromone activity: correlation with molecular shape by scanning computer. *Science*, 165:1266-69.
- Barbier, J., and Lederer, E., 1960. Structure chimique de la substance royale de la reine d'abeille (*Apis mellifica* L.). *C. R. Acad. Sci. (Paris)*, 250:4467-69.
- Beetsma, J., and Schoonhoven, L. M., 1966. Some chemosensory aspects of the social relations between the queen and the worker in the honeybee. *Proc. Kon. ned. Acad. Wet.*, ser. C, 69:643-47.
- Bergström, G.; Kullenberg, B.; and Stållberg-Stenhagen, S., 1973. Studies on natural odoriferous compounds, VII: recognition of two forms of *Bombus lucorum* L. (Hymenoptera, Apidae) by analysis of the volatile marking secretions from individual males. *Chemica Scripta*, 3. Preprint, pp.1-9.
- Bergström, G.; Kullenberg, B.; Stållberg-Stenhagen, S.; and Stenhagen, E., 1968. Studies on natural odoriferous compounds, II: identification of a 2,3-dihydrofarnesol as the main component of the marking perfume of the male bumble-bees of the species *Bombus terrestris* L. *Arkiv Kemi*, 28:453-69.
- Bergström, G., and Löfquist, J., 1968. Odour similarities between the slave-keeping ants *Formica sanguinea* and *Polyergus rufescens* and their slaves *Formica fusca* and *Formica rufibarbis*. *J. Insect Physiol.*, 14:995-1011.
- Bergström, G., and Löfquist, J., 1970. Chemical basis for odour communication in four species of *Lasius* ants. *J. Insect Physiol.*, 16:2353-75.
- Bergström, G., and Löfquist, J., 1972. Similarities between the Dufour's gland secretions of the ants *Camponotus ligniperda* (Latr.) and *Camponotus herculeanus* (L.). *Ent. scand.*, 3:225-38.
- Bergström, G., and Löfquist, J., 1973. Chemical congruence of the complex odoriferous secretions from Dufour's gland in three species of ants of the genus *Formica*. *J. Insect Physiol.*, 19:877-907.
- Bernardi, C.; Cardani, D.; Ghiringhelli, D.; Selva, A.; Baggini, A.; and Pavan, M., 1967. On the components of secretion of mandibular glands of the ant *Lasius (Dendrolasius) fuliginosus*. *Tetrahedron Letters*, 40:3893-96.
- Bevan, C. W. L.; Birch, A. J.; and Caswell, H., 1961. An insect repellent from black cocktail ants. *J. Chem. Soc.*, part 1:488.
- Bier, K. H., 1958. Die Regulation der Sexualität in den Insektenstaaten. *Ergebnisse der Biologie*, 20:97-126.
- Blum, M. S., 1966a. Chemical releasers of social behavior, VIII: citral in the mandibular gland secretion of *Lestrimelitta limao*. *Ann. Entomol. Soc. Amer.*, 59:962-64.
- Blum, M. S., 1966b. The source and specificity of trail pheromones in *Termitopone*, *Monomorium* and *Huberia* and their relation to those of some other ants. *Proc. Roy. Entomol. Soc. (London)*, 41:155-60.
- Blum, M. S., 1974. Pheromonal sociality in the hymenoptera. In: *Pheromones*, M. C. Birch, ed. Amsterdam: North-Holland Publishing Co., pp.223-49.
- Blum, M. S.; Boch, R.; Doolittle, R. E.; Tribble, M. T.; and Traynham, J. G., 1971b. Honeybee sex attractant: conformational analysis, structural specificity, and lack of masking activity of congeners. *J. Insect Physiol.*, 17:349-64.
- Blum, M. S.; Crewe, R. M.; Kerr, W. E.; Keith, L. H.; Garrison, A. W.; and Walker, M. M., 1970. Citral in stingless bees: isolation and function in trail laying and robbing. *J. Insect Physiol.*, 16:1637-48.
- Blum, M. S.; Crewe, R. M.; Sudd, J. H.; and Garrison, A. W., 1969. 2-Hexenal: isolation and function in a *Crematogaster (Atopogyne)* sp. *J. Georgia Entomol. Soc.*, 4:145-48.
- Blum, M. S.; Doolittle, R. E.; and Beroza, M., 1971a. Alarm pheromones: utilization in evaluation of olfactory theories. *J. Insect Physiol.*, 17:2357-61.
- Blum, M. S.; Moser, J. C.; and Cordero, A. D., 1964. Chemical releaser of social behavior II. Source and specificity of the odor trail substances in four attine genera (Hymenoptera: Formicidae). *Psyche (Cambridge)*, 71:1-7.
- Blum, M. S., and Ross, G. N., 1965. Chemical releasers of social behaviour, V: source, specificity and properties of the odour trail pheromone of *Tetramorium guineense* (F.) (Formicidae, Myrmicinae). *J. Insect Physiol.*, 11:857-68.
- Blum, M. S.; Water, S. L.; and Traynham, J. G., 1966. Chemical releasers of social behavior, VI: the relation of structure to activity of ketones as releasers of alarm for *Iridomyrmex pruinosus* (Roger). *J. Insect Physiol.*, 12:419-27.
- Blum, M. S., and Wilson, E. O., 1964. The anatomical source of trail substances in formicine ants. *Psyche (Cambridge)*, 71:28-31.
- Boch, R., 1956. Die Tänze der Bienen bei nahen und fernen Trachtquellen. *Z. vergl. Physiol.*, 38:136-67.

- Boch, R., 1957. Rassenmassige Unterschiede bei den Tänzen der Honigbiene (*Apis mellifica*). *Z. vergl. Physiol.*, 40:289-320.
- Boch, R., and Shearer, D. A., 1962. Identification of geraniol as the active component in the Nasanoff pheromone of the honeybee. *Nature (London)*, 194:704-706.
- Boch, R., and Shearer, D. A., 1964. Identification of nerolic and geranic acids in the Nasanoff pheromone of the honeybee. *Nature (London)*, 202:320-21.
- Boch, R.; Shearer, D. A.; and Petrasovits, A., 1970. Efficacies of two alarm substances of the honeybee. *J. Insect Physiol.*, 16:17-24.
- Boch, R.; Shearer, D. A.; and Stone, B. C., 1962. Identification of iso-amylacetate as an active compound in the sting pheromone of the honeybee. *Nature (London)*, 195:1018-20.
- Bossert, W. H., and Wilson, E. O., 1963. The analysis of olfactory communication among animals. *J. Theoret. Biology*, 5:443-69.
- Brand, J. M.; Duffield, R. M.; McConnell, J. G.; and Fales, H. M., 1973. Caste-specific compounds in male carpenter ants. *Science*, 179:388-89.
- Brian, M. V., 1970. Communication between queens and larvae in the ant *Myrmica*. *Anim. Behav.*, 18:467-72.
- Brian, M. V., and Blum, M. S., 1969. The influence of *Myrmica* queen head extracts on larval growth. *J. Insect Physiol.*, 15:2213-23.
- Bringer, B., 1973. Territorial flight of bumble bee males in coniferous forest on the northernmost part of the island of Öland. *Zoon*, suppl. 1, pp.15-22.
- Buschinger, A., 1968. "Locksterzeln" begattungsbereiter ergatoide Weibchen von *Harpagoxenus sublaevis* Nyl. (Hymenoptera, Formicidae). *Experientia*, 24:297.
- Buschinger, A., 1971a. Weitere Untersuchungen zum Begattungsverhalten sozialparasitischer Ameisen (*Harpagoxenus sublaevis* Nyl. und *Doromyrmex pacis* Kutter, Hym. Formicidae). *Zool. Anz.*, 187:184-98.
- Buschinger, A., 1971b. "Locksterzeln" und Kopula der sozialparasitischen Ameise *Leptothorax kutteri* Buschinger (Hym. Form.). *Zool. Anz.*, 186:242-48.
- Buschinger, A., 1972a. Giftdrüsensekret als Sexualpheromon bei der Ameise *Harpagoxenus sublaevis*. *Naturwissenschaften*, 59:313-14.
- Buschinger, A., 1972b. Kreuzung zweier sozialparasitischer Ameisenarten, *Doromyrmex pacis* Kutter und *Leptothorax kutteri* Buschinger (Hym. Formicidae). *Zool. Anz.*, 189:169-79.
- Butenandt, A.; Linzen, B.; and Lindauer, M., 1959. Über einen Duftstoff aus der Mandibeldrüse der Blattschneiderameise *Atta sexdens rubropilosa* Forel. *Arch. Anat. Microscop. Morphol. Exper.*, 48:13-19.
- Butler, C. G., 1954a. The method and importance of the recognition by a colony of honeybees (*A. mellifera*) of the presence of its queen. *Trans. Roy. Entomol. Soc. London*, 105:11-29.
- Butler, C. G., 1954b. *The World of the Honeybee*. London: Collins.
- Butler, C. G., 1966. Mandibular gland pheromone of worker honeybees. *Nature (London)*, 212:530.
- Butler, C. G., 1971. The mating behavior of the honeybee (*Apis mellifera*) L. *J. Entomol.*, 46:1-11.
- Butler, C. G., 1973. The queen and the "spirit of the hive." *Proc. Roy. Ent. Soc. (London)*, 48:59-65.
- Butler, C. G., and Calam, D. H., 1969. Pheromones of the honeybee: the secretion of the Nasanoff gland of the worker. *J. Insect Physiol.*, 15:237-44.
- Butler, C. G.; Calam, D. H.; and Callow, R. K., 1967. Attraction of *Apis mellifera* drones by the odours of the queens of two other species of honeybees. *Nature (London)*, 213:423-24.
- Butler, C. G.; Callow, R. K.; Koster, C. G.; and Simpson, J., 1973. Perception of the queen by workers in the honeybee colony. *J. Apicult. Res.*, 12:159-66.
- Butler, C. G., and Fairley, E. M., 1964. Pheromones of the honeybee: biological studies of the mandibular gland secretion of the queen. *J. Apicult. Res.*, 3:65-67.
- Butler, C. G.; Fletcher, D. J. C.; and Watler, D., 1969. Nest-entrance marking with pheromones by the honeybee *Apis mellifera* L., and by a wasp *Vespa vulgaris* L. *Anim. Behav.*, 17:142-47.
- Butler, C. G.; Fletcher, D. J. C.; and Watler, D., 1970. Hive entrance finding by honeybee (*Apis mellifera*) foragers. *Anim. Behav.*, 18:78-91.
- Butler, C. G., and Gibbons, D. A., 1958. The inhibition of queen rearing by feeding queenless worker honeybees (*A. mellifera*) with an extract of "queen substance." *J. Insect Physiol.*, 2:61-64.
- Butler, C. G., and Simpson, J., 1967. Pheromones of the queen honeybee (*Apis mellifera*) which enable her workers to follow her when swarming. *Proc. Roy. Ent. Soc. (London)*, ser. A, 42:149-54.
- Calam, D. H., 1969. Species and sex-specific compounds from the heads of male bumble bees (*Bombus* spp.). *Nature (London)*, 221:856-57.
- Callow, R. K., and Johnston, N. C., 1960. The chemical constitution and synthesis of queen substance of honeybees (*Apis mellifera*). *Bee World*, 41:152-53.

- Carthy, J. D., 1950. Odour trails of *Acanthomyops fuliginosus*. *Nature* (London), 166:154.
- Carthy, J. D., 1951. The orientation of two allied species of British ants, II: odour trail laying and following in *Acanthomyops (Lasius) fuliginosus*. *Behaviour*, 3:304-18.
- Casnati, G.; Ricca, A.; and Pavan, M.; 1967. Sulla secrezione difensiva della glandole mandibolari di *Paltothyreus tarsatus* (Fabr.). *Chim. Ind. (Milan)*, 49:57-61.
- Crewe, R. M., and Fletcher, D. J. C., 1974. Ponerine ant secretions: the mandibular gland secretions of *Paltothyreus tarsatus* Fabr. *J. Entomol. Soc. Sth. Afr.*, 37:291-98.
- Dobrzanski, J., 1966. Contribution to the ethology of *Leptothorax acervorum* (Hymenoptera: Formicidae). *Acta Biol. Exp. (Warsaw)*, 26:71-78.
- du Buysson, R., 1903. Monographie de Guêpe ou *Vespa*. *Ann. Soc. Entomol. France*, 72:260-88.
- Duffield, R. M., and Blum, M. S., 1973. 4-Methyl-3-heptanone: identification and function in *Neoponera villosa* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Amer.*, 66:1357.
- Dumpert, K., 1972. Alarmstoffrezeptoren auf der Antenne von *Lasius fuliginosus* (Latr.) (Hymenoptera, Formicidae). *Z. vergl. Physiol.*, 76:403-25.
- Esch, H., 1961. Über die Schallerzeugung beim Werbetanz der Honigbiene. *Z. vergl. Physiol.*, 45:1-11.
- Esch, H., 1964. Beiträge zum Problem der Entfernungsweisung in den Schwänzeltänzen der Honigbienen. *Z. vergl. Physiol.*, 48:534-46.
- Esch, H., 1967a. Die Bedeutung der Lauterzeugung für die Verständigung der stachellosen Bienen. *Z. vergl. Physiol.*, 56:199-220.
- Esch, H., 1967b. The evolution of bee language. *Scientific American*, 216:96-104.
- Esch, H., and Bastian, J. A., 1970. How do newly recruited honeybees approach a food site? *Z. vergl. Physiol.*, 68:175-81.
- Esch, H.; Esch, I.; and Kerr, W. E.; 1965. An element common to communication of stingless bees and to dances of honeybees. *Science*, 149:320-21.
- Evans, H. E., and Eberhard, M. J. West, 1970. *The Wasps*. Ann Arbor: University of Michigan Press. 265pp.
- Falke, J., 1968. Substanzen aus der Mandibeldrüse der Männchen von *Camponotus herculeanus*. Diss. University of Heidelberg.
- Fletcher, D. J. C., 1971. The glandular source and social functions of trail pheromones in two species of ants (*Leptogenys*). *J. Entomol.*, ser. A, 46:27-37.
- Fletcher, D. J. C., and Brand, J. M., 1968. Source of the trail pheromone and method of trail laying in the ant *Crematogaster peringueyi*. *J. Insect Physiol.*, 14:783-88.
- Frank, A., 1941. Eigenartige Flugbahnen bei Hummelmännchen. *Z. vergl. Physiol.*, 28:467-84.
- Free, J. B., 1956. A study of stimuli which release the food begging and offering response of worker honeybees. *Brit. J. Anim. Behav.*, 4:94-101.
- Free, J. B., 1959. The transfer of food between the adult members of a honeybee community. *Bee World*, 40:193-201.
- Free, J. B., 1967. Factors determining the collection of pollen by honeybee foragers. *Anim. Behav.*, 15:134-44.
- Free, J. B., 1970b. The flower constancy of bumblebees. *J. Anim. Ecol.*, 39:395-402.
- Free, J. B., 1971. Stimuli eliciting mating behavior of bumblebee (*Bombus bratorum*) males. *Behaviour*, 40:55-61.
- Free, J. B., and Williams, J. H., 1970. Exposure of the Nasanov gland by honeybees (*Apis mellifera*) collecting water. *Behaviour*, 37:286-90.
- Frisch, K. von, 1923. Über die "Sprache" der Bienen, eine tierpsychologische Untersuchung. *Zool. Jb. (Physiol.)*, 40:1-186.
- Frisch, K. von, 1962. Über die durch Licht bedingte "Missweisung" bei den Tänzen im Bienenstock. *Experientia*, 18:49-53.
- Frisch, K. von, 1965. *Tanzsprache und Orientierung der Bienen*. Berlin: Springer-Verlag.
- Frisch, K. von, 1967a. *The Dance Language and Orientation of Bees*. Cambridge: Belknap Press of Harvard University Press.
- Frisch, K. von, 1967b. Honeybees: do they use direction and distance information provided by their dancers? *Science*, 158:1072-76.
- Frisch, K. von, 1968. The role of dance in recruiting bees to familiar sites. *Anim. Behav.*, 16:531-33.
- Gabba, A., and Pavan, M., 1970. Researches on trail and alarm substances in ants. In: *Communication by Chemical Signals*, J. W. Johnston, D. G. Moulton, and A. Turk, eds. New York: Appleton-Century-Crofts, pp.161-203.
- Gary, N. E., 1961a. Mandibular gland extirpation in living queen and worker honeybees (*Apis mellifera*). *Ann. ent. Soc. Amer.*, 54:529-31.
- Gary, N. E., 1961b. Queen honeybee attractiveness as related to mandibular gland secretion. *Science*, 133:1479-80.

- Gary, N. E., 1962. Chemical mating attractants in the queen honey bee. *Science*, 136:773-74.
- Gary, N. E., 1963. Observations of mating behavior in the honeybee. *J. Apicult. Res.*, 2:3-13.
- Gary, N. E., 1974. Pheromones that affect the behavior and physiology of honeybees. In: *Pheromones*, M. C. Birch, ed. Amsterdam: North-Holland Publishing Co., pp.200-21.
- Gerig, L., 1972. Ein weiterer Duftstoff zur Anlockung der Drohnen von *Apis mellifica* (L.). *Z. angew. Entomol.*, 70:286-89.
- Glancey, B. M.; Stringer, C. E.; Craig, C. H.; Bishop, P. M.; and Martin, B. B.; 1970. Pheromone may induce brood tending in the fire ant, *Solenopsis saevissima*. *Nature* (London), 226:863-64.
- Goetsch, W., 1953. *Vergleichende Biologie der Insektenstaaten*. Leipzig: Geest u. Portig K. G. 482pp.
- Gösswald, K., and Kloft, W., 1956. Untersuchungen über die Verteilung von radioaktiv markiertem Futter im Volk der kleinen Roten Waldameise (*Formica rufopratensis minor*). *Waldhygiene*, 1:200-202.
- Gösswald, K., and Kloft, W., 1960. Neuere Untersuchungen über die sozialen Wechselbeziehungen im Ameisenvolk, durchgeführt mit Radio-Isotopen. *Zool. Beitr.*, 5:519-56.
- Gould, J. L., 1974. Honey bee communication: misdirection of recruits by foragers with covered ocelli. *Nature* (London), 252:300-301.
- Gould, J., 1975. Honey bee recruitment: the dance-language controversy. *Science*, 189:685-93.
- Gould, J. L.; Henerey, M.; and MacLeod, M. C.; 1970. Communication of direction by the honeybee. *Science*, 169:544-54.
- Groot, A. P. de, and Voogd, S., 1954. On the ovary development in queenless workerbees (*Apis mellifera* L.). *Experientia*, 10:384-85.
- Haas, A., 1946. Neue Beobachtungen zum Problem der Flugbahnen bei Hummelmännchen. *Z. Naturforsch.*, 1:596-600.
- Haas, A., 1949a. Arttypische Flugbahnen von Hummelmännchen. *Z. vergl. Physiol.*, 31:281-307.
- Haas, A., 1949b. Gesetzmässiges Flugverhalten der Männchen von *Psithyrus silvestris* Lep. und einiger solitärer Apiden. *Z. vergl. Physiol.*, 31:671-83.
- Haas, A., 1952. Die Mandibeldrüse als Duftorgan bei einigen Hymenopteren. *Naturwissenschaften*, 39:484.
- Hangartner, W., 1967. Spezifität und Inaktivierung des Spurpheromons von *Lasius fuliginosus* Latr. und Orientierung der Arbeiterinnen im Duftfeld. *Z. vergl. Physiol.*, 57:103-36.
- Hangartner, W., 1969a. Trail laying in the subterranean ant *Acanthomyops interjectus*. *J. Insect Physiol.*, 15:1-4.
- Hangartner, W., 1969c. Structure and variability of the individual odor trail in *Solenopsis* (Formicidae). *Z. vergl. Physiol.*, 62:111-20.
- Hangartner, W., and Bernstein, S., 1964. Über die Geruchspur von *Lasius fuliginosus* zwischen Nest und Futterquelle. *Experientia*, 20:392-93.
- Hangartner, W.; Reichson, J.; and Wilson, E. O.; 1970. Orientation to nest material by the ant *Pogonomyrmex badius* (Latreille). *Anim. Behav.*, 18:331-34.
- Hansson, A., 1945. Lauterzeugung und Lautauffassungsvermögen der Bienen. *Opuscula Entomol.*, suppl. 6, pp.1-124.
- Hase, A., 1935. Über den "Verkehr" am Wespennest, nach Beobachtungen an einer tropischen Art. *Naturwissenschaften*, 23:780-83.
- Haskins, C. P., and Whelden, R. M., 1965. "Queenless" worker sibship, and colony versus population structure in the formicid genus *Rhytidoponera*. *Psyche*, (Cambridge), 72:87-112.
- Haydak, M. H., 1958. Do the nurse honeybees recognize the sex of the larvae? *Science*, 127:1113.
- Heinrich, B., 1974. Pheromone induced brooding behavior in *Bombus vosnesenskii* and *B. edwardsii* (Hymenoptera: Bombidae). *J. Kansas Entomol. Soc.*, 47:396-404.
- Hingston, R. W. G., 1929. *Instinct and Intelligence*. New York: Macmillan Co.
- Hölldobler, B., 1962. Zur Frage der Oligogynie bei *Camponotus ligniperda* Latr. und *Camponotus herculeanus* L. (Hym. Formicidae). *Z. angew. Entomol.*, 49:337-52.
- Hölldobler, B., 1965. Das soziale Verhalten der Ameisenmännchen und seine Bedeutung für die Organisation der Ameisenstaaten. Diss., University of Würzburg. 122pp.
- Hölldobler, B., 1966. Futterverteilung durch Männchen im Ameisenstaat. *Z. vergl. Physiol.*, 52:430-55.
- Hölldobler, B., 1967. Zur Physiologie der Gast-Wirt-Beziehungen (Myrmecophilie) bei Ameisen, I: Das Gastverhältnis der *Atemeles*- und *Lomechusa*-Larven (Col. Staphylinidae) zu *Formica* (Hym. Formicidae). *Z. vergl. Physiol.*, 56:1-21.
- Hölldobler, B., 1968. Der Glanzkafer als "Wegelagerer" an Ameisenstrassen. *Naturwissenschaften*, 55:397.
- Hölldobler, B., 1969. Orientierungsmechanismen des Ameisengastes *Atemeles* (Coleoptera, Staphylinidae) bei der Wirtssuche. *Zool. Anz.*, suppl. 33, pp.580-85.
- Hölldobler, B., 1970a. Zur Physiologie der Gast-Wirt-

- Beziehungen (Myrmecophilie) bei Ameisen, II: Das Gastverhältnis der imaginalen *Atemeles pubicollis* Bris (Col. Staphylinidae) zu *Myrmica* und *Formica* (Hym. Formicidae). *Z. vergl. Physiol.*, 66:215–50.
- Hölldobler, B., 1970b. Chemische Verständigung im Insektenstaat. *Umschau*, 70:663–69.
- Hölldobler, B., 1971a. Sex pheromone in the ant *Xenomyrmex floridanus*. *J. Insect Physiol.*, 17:1497–99.
- Hölldobler, B., 1971b. Communication between ants and their guests. *Scientific American*, 224:86–93.
- Hölldobler, B., 1971c. Recruitment behavior in *Camponotus socius* (Hym. Formicidae). *Z. vergl. Physiol.*, 75:123–42.
- Hölldobler, B., 1971d. Homing in the harvester ant *Pogonomyrmex badius*. *Science*, 171:1149–51.
- Hölldobler, B., 1972. Verhaltensphysiologische Adaptationen an ökologische Nischen in Ameisennestern. *Verh. Dtsch. Zool. Ges.*, 65:137–44.
- Hölldobler, B., 1973a. Zur Ethologie der chemischen Verständigung bei Ameisen. *Nova Acta Leopoldina*, 37:259–92.
- Hölldobler, B., 1973b. Chemische Strategie beim Nahrungserwerb der Diebsameise (*Solenopsis fugax* Latr.) und der Pharaoameise (*Monomorium pharaonis* L.). *Oecologia*, 11:371–80.
- Hölldobler, B., 1973c. *Formica sanguinea* (Formicidae): Futterbetteln. *Encyclopaedia Cinematographica*, E 2.
- Hölldobler, B., 1974. Home range orientation and territoriality in harvesting ants (*Pogonomyrmex*). *Proc. Nat. Acad. Sci. (U.S.A.)*, 71:3274–77.
- Hölldobler, B., and Maschwitz, U., 1965. Der Hochzeitsschwarm der Rossameise *Camponotus herculeanus* L. (Hym. Formicidae). *Z. vergl. Physiol.*, 50:551–68.
- Hölldobler, B.; Möglich, M.; and Maschwitz, U., 1973. *Bothroponera tessarinoda* (Formicidae): Tandemlauf beim Nestumzug. *Encyclopaedia Cinematographica* (E 2040/1973), 3–14.
- Hölldobler, B.; Möglich, M.; and Maschwitz, U., 1974. Communication by tandem running in the ant *Camponotus sericeus*. *J. Comp. Physiol.*, 90:105–27.
- Hölldobler, B., and Wilson, E. O., 1970. Recruitment trails in the harvester ant *Pogonomyrmex badius*. *Psyche* (Cambridge), 77:385–99.
- Hölldobler, B., and Wüst, M., 1973. Ein Sexualpheromon bei der Pharaoameise *Monomorium pharaonis* (L.). *Z. Tierpsychol.*, 32:1–9.
- Hölldobler, K., 1948. Über ein parasitologische Problem: Die Gastpflege der Ameisen und die Symphilieinstinkte. *Z. Parasitenkunde*, 14:3–26.
- Huwyler, S.; Grob, K.; and Viscontini, M., 1973. Identifizierung von sechs Komponenten des Spurpheromons der Ameisenart *Lasius fuliginosus*. *Helvetica Chimica Acta*, 56:976–77.
- Ikan, R.; Bergmann, E. D.; Ishay, J.; and Gitter, S., 1968. Proteolytic enzyme activity in the various colony members of the oriental hornet, *Vespa orientalis* F. *Life Sciences*, 7:929–34.
- Ikan, R.; Gottlieb, R.; Bergmann, E. D.; and Ishay, J., 1969. The pheromone of the queen of the oriental hornet, *Vespa orientalis*. *J. Insect Physiol.*, 15:1709–12.
- Ishay, J., 1972. Thermoregulatory pheromones in wasps. *Experientia*, 28:1185–87.
- Ishay, J., and Ikan, R., 1969. Gluconeogenesis in the oriental hornet *Vespa orientalis* F. *Ecology*, 49:169–71.
- Ishay, J., and Landau, E. M., 1972. *Vespa* larvae send out rhythmic hunger signals. *Nature* (London), 237:286–87.
- Ishay, J., and Ruttner, F., 1971. Thermoregulation im Hornisennest. *Z. vergl. Physiol.*, 72:423–34.
- Ishay, J., and Schwartz, A., 1973. Acoustical communication between the members of the oriental hornet (*Vespa orientalis*) colony. *J. Acoust. Soc. Amer.*, 63:640–49.
- Janet, C., 1903. *Observations sur les guêpes*. Paris: C. Nand. 85pp.
- Jeanne, R. L., 1972. Social biology of the neotropical wasp *Mischocyttarus drewseni*. *Bull. Mus. Comp. Zool. Harvard*, 144:63–150.
- Johnson, D. L., 1967. Honeybees: Do they use direction information contained in their dance maneuver? *Science*, 155:844–47.
- Johnson, D. L., and Wenner, A. M., 1970. Recruitment efficiency in honeybees: studies of the role of olfaction. *J. Apicult. Res.*, 9:13–18.
- Kaissling, K. E., and Renner, M., 1968. Antennale Rezeptoren für Queen substance und Sterzelduft bei der Honigbiene. *Z. vergl. Physiol.*, 59:357–61.
- Kalmus, H., 1954. Finding and exploitation of dishes of syrup by bees and wasps. *Brit. J. Anim. Behav.*, 2:136–39.
- Kannowski, P. B., and Johnson, R. L., 1969. Male patrolling behavior and sex attraction in ants of the genus *Formica*. *Anim. Behav.*, 17:425–29.
- Kerr, W. E., and Esch, H., 1965. Comunicacao entre as abelhas sociais brasileiras e sua contribuicao para o entendimento da sua evolucao. *Ciencia e Cult.* (Sao Paulo), 17:529–38.
- Kerr, W. E.; Ferreira, A.; and DeMattos, N. S., 1963. Communication among stingless bees: additional data (Hymenoptera, Apidae). *J. N. Y. Entomol. Soc.*, 71:80–90.
- Kloft, W., 1959. Versuch einer Analyse der trophobi-

- otischen Beziehungen von Ameisen zu Aphiden. *Biol. Zentralbl.*, 78:863–70.
- Kneitz, G., 1963. Tracerversuche zur Futterverteilung bei Waldameisen. *Symp. Gen. Biol. Ital.* (Pavia), 12:38–50.
- Koeniger, N., 1970a. Über die Fähigkeit der Bienenkönigin (*Apis mellifica*) zwischen Arbeiterinnen und Drohnzellen zu unterscheiden. *Apidologie*, 1:115–42.
- Koeniger, N., 1970b. Factors determining the laying of drone and worker eggs by the queen honeybee. *Bee World*, 51:166–69.
- Koeniger, N., and Fuchs, S., 1972. Kommunikativ Schallerzeugung von *Apis cerana* Fabr. im Bienenvolk. *Naturwissenschaften*, 59:169.
- Koeniger, N., and Fuchs, S., 1973. Sound production as colony defense in *Apis cerana* Fabr. *Proc. Seventh Congr. IUSSI*, London, pp.199–204.
- Kullenberg, B., 1956. Field experiments with chemical sexual attractants on aculeate Hymenoptera males. *I. Zool. Bidrag Upsala*, 31:253–54.
- Kullenberg, B.; Bergström, G.; Bringer, B.; Carlberg, B.; and Cederberg, B., 1973. Observations on scent marking by *Bombus* Latr. and *Psithyrus* Lep. males (Hym. Apidae) and localization of site of production of the secretion. *Zoon*, suppl. 1, pp.23–30.
- Kullenberg, B.; Bergström, G.; and Stållberg-Stenhagen, S., 1970. Volatile components of the cephalic marking secretion of male bumble bees. *Acta Chemica Scand.*, 24:1481–83.
- Lange, R., 1958. Der Einfluss der Königin auf die Futterverteilung im Ameisenstaat. *Naturwissenschaften*, 45:196.
- Lange, R., 1967. Die Nahrungsverteilung unter den Arbeiterinnen des Waldameisenstaates. *Z. Tierpsychol.*, 24:513–45.
- Le Masne, G. M., 1952. Les échanges alimentaires entre adultes chez la fourmi *Ponera eduardi* Forel. *C. R. Acad. Sci. (Paris)*, 235:1549–51.
- Le Masne, G. M., 1953. Observations sur les relations entre le couvain et les adultes chez les fourmis. *Ann. Sci. Nat.*, 15:1–56.
- Lenoir, M. A., 1972a. Note sur le comportement de sollicitation chez les ouvrières de *Myrmica scabrinodis* Nyl. (Hymenoptères, Formicidae). *C. R. Acad. Sci. (Paris)*, 274:705–707.
- Lenoir, M. A., 1972b. Sur la rôle de l'odorat dans le compartement de sollicitation chez les ouvrières de *Myrmica scabrinodis* Nyl. (Hymenoptères, Formicidae). *C. R. Acad. Sci. (Paris)*, 274:906–908.
- Leuthold, R. H., 1968a. Recruitment to food in the ant *Crematogaster ashmeadi*. *Psyche* (Cambridge), 75:334–50.
- Leuthold, R. H., 1968b. A tibial gland scent-trail and trail-laying behavior in the ant *Crematogaster ashmeadi* Mayr. *Psyche* (Cambridge), 75:233–48.
- Lindauer, M., 1948. Über die Einwirkung von Duft- und Geschmacksstoffen sowie anderer Faktoren auf die Tänze der Bienen. *Z. vergl. Physiol.*, 31:348–412.
- Lindauer, M., 1954. Temperaturregulierung und Wasserhaushalt im Bienenstaat. *Z. vergl. Physiol.*, 36:391–432.
- Lindauer, M., 1955. Schwarmbienen auf Wohnungssuche. *Z. vergl. Physiol.*, 37:263–324.
- Lindauer, M., 1956. Über die Verständigung bei indischen Bienen. *Z. vergl. Physiol.*, 38:521–57.
- Lindauer, M., 1961. *Communication among Social Bees*. Cambridge: Harvard University Press.
- Lindauer, M., 1971. The functional significance of the honeybee waggle dance. *Amer. Nat.*, 105:89–96.
- Lindauer, M., and Kerr, W. E., 1958. Die gegenseitige Verständigung bei den stachellosen Bienen. *Z. vergl. Physiol.*, 41:405–34.
- Lindauer, M., and Kerr, W. E., 1960. Communication between the workers of stingless bees. *Bee World*, 41:29–41, 65–71.
- Lindauer, M., and Schricker, B., 1963. Über die Funktion der Quellen bei den Dämmerungsflügen der Honigbienen. *Biol. Zbl.*, 82:721–25.
- Markin, G. P., 1970. Food distribution within laboratory colonies of the Argentine ant, *Iridomyrmex humilis* (Mayr). *Ins. Soc.*, 17:127–57.
- Markl, H., 1965. Stridulation in leaf-cutting ants. *Science*, 149:1392–93.
- Markl, H., 1967. Die Verständigung durch Stridulationssignale bei Blattschneiderameisen, I: Die Biologische Bedeutung der Stridulation. *Z. vergl. Physiol.*, 57:299–330.
- Markl, H., 1968. Die Verständigung durch Stridulationssignale bei Blattschneiderameisen, II: Erzeugung und Eigenschaften der Signale. *Z. vergl. Physiol.*, 60:103–50.
- Markl, H., 1970. Die Verständigung durch Stridulationssignale bei Blattschneiderameisen, III: Die Empfindlichkeit für Substratvibrationen. *Z. vergl. Physiol.*, 69:6–37.
- Markl, H., 1973. The evolution of stridulatory communication in ants. *Proc. Seventh Congr. IUSSI* (London), pp.258–65.
- Markl, H., and Fuchs, S., 1972. Kopfsignale mit Alarmfunktion bei Rossameisen (*Camponotus*) (For-

- micidae, Hymenoptera). *Z. vergl. Physiol.*, 76:204-25.
- Maschwitz, U., 1964. Gefahrenalarmstoffe und Gefahrenalarmierung bei sozialen Hymenopteren. *Z. vergl. Physiol.*, 47:596-655.
- Maschwitz, U., 1966a. Alarmsubstances and alarm behavior in social insects. *Vitamins and Hormones*, 24:267-90.
- Maschwitz, U., 1966b. Das Speichelsekret der Wespenlarven und seine biologische Bedeutung. *Z. vergl. Physiol.*, 53:228-52.
- Maschwitz, U., 1974. Vergleichende Untersuchungen zur Funktion der Ameisenmetathorakaldrüse. *Oecologia*, 16:303-10.
- Maschwitz, U.; Beier, W.; Dietrich, J.; and Keidel, W.; 1974a. Futterverweigerung bei Wespen der Gattung *Paravespula*. *Naturwissenschaften*, 61, 506.
- Maschwitz, U.; Hölldobler, B.; and Möglich, M.; 1974b. Tandemlaufen als Rekrutierungsverhalten bei *Bothroponera tessierina* Forel (Formicidae, Ponerinae). *Z. Tierpsychol.*, 35:113-23.
- Maschwitz, U.; Koob, K.; and Schildknecht, H.; 1970. Ein Beitrag zur Funktion der Metathorakaldrüse der Ameisen. *J. Insect Physiol.*, 16:387-404.
- Mautz, D., 1971. Der Kommunikationseffekt der Schwänzelantenne bei *Apis mellifica carnica* (Pollm.). *Z. vergl. Physiol.*, 72:197-220.
- McGurk, D. J.; Frost, J.; Eisenbraun, E. J.; Vick, K.; Drew, W. A.; and Young, J.; 1966. Volatile compounds in ants: identification of 4-methyl-3-heptanone from *Pogonomyrmex* ants. *J. Insect Physiol.*, 12:1435-41.
- Michener, C. D., 1974. *The Social Behavior of Bees*. Cambridge: The Belknap Press of Harvard University Press.
- Möglich, M., and Hölldobler, B., 1974. Social carrying behavior and division of labor during nest moving. *Psyche* (Cambridge), 81:219-36.
- Möglich, M., and Hölldobler, B., 1975. Communication and orientation during foraging and emigration in the ant *Formica fusca*. *J. Comp. Physiol.*, 101:275-88.
- Möglich, M.; Hölldobler, B.; and Maschwitz, U.; 1974a. *Camponotus sericeus* (Formicidae): Tandemlauf beim Nestumzug. *Encyclopaedia Cinematographica* E 2039/1974, pp.3-18.
- Möglich, M.; Maschwitz, U.; and Hölldobler, B.; 1974b. Tandem calling: a new kind of signal in ant communication. *Science*, 186:1046-47.
- Montagner, H., 1963. Étude préliminaire des relations entre les adultes et le couvain chez les guêpes sociales du genre *Vespa*, au moyen d'un radioisotope. *Insectes Soc.*, 10:153-66.
- Montagner, H., 1964. Étude du compartement alimentaire et des relations trophallactique des mâles au sein de la société des guêpes, au moyen d'un radioisotope. *Ins. Soc.*, 11:301-16.
- Montagner, H., 1966. Le mécanisme et les conséquences des compartements trophallactiques chez les guêpes du genre *Vespa*. Thesis, University of Nancy.
- Montagner, H., 1967. *Comportements trophallactiques chez les guêpes sociales*. Paris: Service du Film de Recherche Scientifique, Film no.B 2053.
- Montagner, H., and Pain, J., 1971. Étude préliminaire des communications entre ouvrières d'abeilles au cours de la trophallaxie. *Ins. Soc.*, 18:177-92.
- Morse, R. A., 1972. Honeybee alarm pheromone: another function. *Ann. Entomol. Soc. Amer.*, 65:1430.
- Morse, R. A.; Gary, N. E.; and Johanson, T. S.; 1962. Mating of virgin queen honey bees (*Apis mellifera*) following mandibular gland extirpation. *Nature* (London), 194:605.
- Morse, R. A.; Shearer, D. A.; Boch, R.; and Benton, A. W.; 1967. Observations on alarm substances in the genus *Apis*. *J. Apicult. Res.*, 6:113-18.
- Moser, J. C., 1964. Inquiline roach responds to trail-marking substance of leaf-cutting ants. *Science*, 143:1048-49.
- Moser, J. C., and Blum, M. S., 1963. Trail marking substance of the Texas leaf-cutting ant: source and potency. *Science*, 140:1228.
- Moser, J. C., and Silverstein, R. M., 1967. Volatility of trail marking substance of the town ant. *Nature* (London), 215:206-207.
- Naumann, M. G., 1970. The nesting behavior of *Protopolybia punnula* in Panama (Hymenoptera, Vespidae). Ph.D. diss. University of Kansas, Lawrence.
- Nunez, J. A., 1967. Sammelbienen markieren versiegt Futterquellen durch Duft. *Naturwissenschaften*, 54:322-23.
- Pain, J., 1961. Sur la pheromone des reines d'abeilles et ses affects physiologique. *Ann. Abeille*, 4:73-152.
- Pain, J., 1973. Pheromones and hymenoptera. *Bee World*, 54:11-24.
- Pain, J., and Ruttner, F., 1963. Les extraits de glandes mandibulaires des reines d'abeilles attirent les mâles lors du vol nuptial. *C. R. Acad. Sci. (Paris)*, 256:512-15.
- Pardi, L., 1940. Ricerche sui Polistini, I: poliginia vera ed apparente in *Polistes gallicus* (L.). *Processi Verb. Soc. Tosc. Sci. Nat. (Pisa)*, 49:3-9.

- Pardi, L., 1948. Dominance order in *Polistes* wasps. *Physiol. Zool.*, 21:1-13.
- Pardi, L., and Calvacanti, M., 1951. Esperienze su meccanismo della monoginia funzionale in *Polistes gallicus* (L.) (Hymenopt. Vesp.). *Boll. Zool.*, 18:247-52.
- Pavan, M., and Ronchetti, G., 1955. Studi sulla morfologia esterna e anatomia interna dell'operaia di *Iridomyrmex humilis* Mayr e ricerche chimiche e biologiche sulla iridomirmecina. *Atti Soc. Ital. Sci. Nat. (Milan)*, 94:379-477.
- Petersen, M., and Buschinger, A., 1971. Das Begattungsverhalten der Pharaoameise *Monomorium pharaonis*. *Z. angew. Entomol.*, 68:168-75.
- Plateaux, L., 1960. Adoptions expérimentales de larves entre des fourmis de genres différents: *Leptothorax nylanderii* Förster et *Solenopsis fugax* Latreille. *Ins. Soc.*, 7:163-70.
- Regnier, F. E.; Nieh, M.; and Hölldobler, B.; 1973. The volatile Dufour's gland components of the harvester ants *Pogonomyrmex rugosus* and *P. barbatus*. *J. Insect Physiol.*, 19:981-92.
- Regnier, F. E., and Wilson, E. O., 1968. The alarm defence system of the ant *Acanthomyops claviger*. *J. Insect Physiol.*, 14:955-70.
- Regnier, F. E., and Wilson, E. O., 1969. The alarm defence system of the ant *Lasius alienus*. *J. Insect Physiol.*, 15:893-98.
- Regnier, F. E., and Wilson, E. O., 1971. Chemical communication and "propaganda" in slave maker ants. *Science*, 172:267-69.
- Renner, M., 1960. Das Duftorgan der Honigbiene und die physiologische Bedeutung ihres Lockstoffes. *Z. vergl. Physiol.*, 43:411-68.
- Renner, M., and Baumann, M., 1964. Über Komplexe von subepidermalen Drüsenzellen (Duftdrüsen?) der Bienenkönigin. *Naturwissenschaften*, 51:68-69.
- Ribbands, C. R., 1953. *The Behaviour and Social Life of Honeybees*. London: Bee Research Association, Ltd. 352pp.
- Ribbands, C. R., 1954. Communication between honeybees, I: the response of crop-attached bees to the scent of their crop. *Proc. Roy. Entomol. Soc. (London)*, ser. A, 29:10-12.
- Ribbands, C. R., 1955a. Communication between honeybees, II: the recruitment of trained bees, and their response to improvement of the crop. *Proc. Roy. Entomol. Soc. (London)*, ser. A, 30:1-3.
- Ribbands, C. R., 1955b. The scent perception of the honeybee. *Proc. Roy. Soc.*, ser. B, 143:367-79.
- Riley, R. G.; Silverstein, R. M.; and Moser, J. C.; 1974a. Biological responses of *Atta texana* to its alarm pheromone and the enantiomer of the pheromone. *Science*, 183:760-62.
- Riley, R. G.; Silverstein, R. M.; and Moser, J. C.; 1974b. Isolation, identification, synthesis and biological activity of volatile compounds from heads of *Atta* ants. *J. Insect Physiol.*, 20:1629-37.
- Röseler, P. F., 1967. Untersuchungen über das Auftreten der 3 Formen im Hummelstaat. *Zool. Jb. (Physiol.)*, 74:178-97.
- Röseler, P. F., 1970. Unterschiede in der Kastendetermination zwischen den Hummelarten *Bombus hypnorum* and *Bombus terrestris*. *Z. Naturforsch.*, 25:543-48.
- Roubaud, E., 1911. The nature history of the solitary wasps of the genus *Synagris*. *Rept. Smith. Inst.*, 1910, pp.507-25.
- Ruttner, F., and Kaissling, K. E., 1968. Über die interspezifische Wirkung des Sexuallockstoffes von *Apis mellifica* and *Apis cerana*. *Z. vergl. Physiol.*, 59:362-70.
- Ruttner, F., and Ruttner, H., 1965. Untersuchungen über die Flugaktivität und das Paarungsverhalten der Drohnen, 2: Beobachtungen an Drohnensammelplätzen. *Z. Bienenforsch.*, 8:1-18.
- Ruttner, F., and Ruttner, H., 1968. Untersuchungen über die Flugaktivität und das Paarungsverhalten der Drohnen, 4: Zur Fernorientierung und Ortstetigkeit der Drohnen auf ihren Paarungsflügen. *Z. Bienenforsch.*, 9:259-65.
- Ruttner, H., and Ruttner, F., 1972. Untersuchungen über die Flugaktivität und das Paarungsverhalten der Drohnen, 5: Drohnensammelplätze und Paarungsstanz. *Apidologie*, 3:203-32.
- Sakagami, S. F., 1960. Preliminary report on the specific difference of behaviour and other ecological characters between European and Japanese honeybees. *Acta Hymenopterol.*, 1:171-98.
- Schandinischky, L., and Ishay, J., 1968. On the nature of the sounds produced within the nest of the oriental hornet *Vespa orientalis* F. *J. Acoust. Soc. Amer.*, 44:1290-1301.
- Schneirla, T. C., 1971. *Army ants: A Study in Social Organization*, H. T. Topoff, ed. San Francisco: W. H. Freeman.
- Schremmer, F., 1972. Beobachtungen zum Paarungsverhalten der Männchen von *Bombus confusus* Schenck. *Z. Morph. Tiere*, 72:263-94.
- Shearer, D. A., and Boch, R., 1965. 2-Heptanone in the mandibular gland secretion of the honeybee. *Nature* (London), 206:530.
- Simpson, J., 1966. Repellency of the mandibular

- gland scent of worker honeybees. *Nature* (London), 209:531-32.
- Simpson, J., and Cherryl, S. M., 1969. Queen confinement, queen piping and swarming in *Apis mellifera* colonies. *Anim. Behav.*, 17:271-78.
- Spradbery, J. P., 1973. *Wasps*. Seattle: University of Washington Press. 408pp.
- Stein, G., 1963. Über den Sexuallockstoff von Hummel Männchen. *Naturwissenschaften*, 50:305.
- Stejskal, M., 1962. Duft als "Sprache" der tropischen Bienen. *Sudwestdeut. Imker*, 49:271.
- Stumper, R., 1956. Sur les sécrétions des fourmis femelles. *C. R. Acad. Sci. (Paris)*, 242:2487-89.
- Sudd, J. H., 1957a. Communication and recruitment in Pharaoh's ant, *Monomorium pharaonis* (L.). *Anim. Behav.*, 5:104-109.
- Sudd, J. H., 1957b. A response of worker ants to dead ants of their own species. *Nature* (London), 179:431-32.
- Sudd, J. H., 1962. The source and possible function of the odour of the African stink-ant, *Paltothyreus tarsatus* F. (Hym. Formicidae). *Entomol. Mon. Mag.*, 98:62.
- Szlep, R., and Jacobi, T., 1967. The mechanism of recruitment to mass foraging in colonies of *Monomorium venustum* Smith, *M. subopacum* ssp. *phoenicium* Em., *Tapinoma israelis* For. and *T. simothi* v. *phoenicium* Em. *Ins. Soc.*, 14:25-40.
- Szlep-Fessel, R., 1970. The regulatory mechanism in mass foraging and recruitment of soldiers in *Pheidole*. *Ins. Soc.*, 17:233-44.
- Torgerson, R. L., and Akre, R. D., 1970. The persistence of army ant chemical trails and their significance in the ecitonine-ecitophile association (Formicidae: Ecitonini). *Melandria*, 5:1-28.
- Tumlinson, J. H.; Moser, J. C.; Silverstein, R. M.; Brownlee, R. G.; and Ruth, J. M.; 1972. A volatile trail pheromone of the leaf-cutting ant, *Atta texana*. *J. Insect Physiol.*, 18:809-14.
- Tumlinson, J. H.; Silverstein, R. M.; Moser, J. C.; Brownlee, R. G.; and Ruth, J. M.; 1971. Identification of the trail pheromone of a leaf-cutting ant, *Atta texana*. *Nature* (London), 234:348-49.
- Velthuis, H. H. W., 1970a. Queen substances from the abdomen of the honeybee queen. *Z. vergl. Physiol.*, 70:210-22.
- Velthuis, H. H. W., 1970b. Ovarian development in *Apis mellifera* worker bees. *Entomol. Exptl Appl.*, 13:377-94.
- Velthuis, H. H. W., 1972. Observations on the transmission of queen substances in the honey bee colony by the attendants of the queen. *Behaviour*, 41:105-29.
- Voogd, S., 1955. Inhibition of ovary development in worker bees by extraction fluid of the queen. *Experimentia*, 11:181-82.
- Wallis, D. J., 1961. Food-sharing behavior in the ants *Formica sanguinea* and *Formica fusca*. *Behaviour*, 17:17-47.
- Walsh, J. P., and Tschinkel, W. R., 1974. Brood recognition by contact pheromone in the red imported fire ant, *Solenopsis invicta*. *Anim. Behav.*, 22:695-704.
- Wasmann, E., 1910. Die Doppelwirtigkeit der *Atemeles*. *Deut. eng. Nat.*, 1:1-11.
- Wasmann, E., 1915. Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles*, mit kritischen Bemerkungen über das echte Gastverhältnis. *Z. wiss. Zool.*, 114:233-402.
- Watkins, J. F., 1964. Laboratory experiments on the trail-following of army ants of the genus *Neivamyrmex* (Formicidae: Dorylinae). *J. Kansas Entomol. Soc.*, 37:22-28.
- Watkins, J. F., and Cole, T. W., 1966. The attraction of army ant workers to secretions of their queens. *Texas J. Sci.*, 18:254-65.
- Weaver, N.; Weaver, C. C.; and Law, J. H.; 1964. The attractiveness of citral to foraging honeybees. *Prog. Rept. Tex. Agric. Exptl. Stn.*, no. 2324, pp.1-7.
- Wells, P. H., and Wenner, A. M., 1973. Do honeybees have a language? *Nature* (London), 241:171-75.
- Wenner, A. M., 1962a. Sound production during the waggle dance of the honeybee. *Anim. Behav.*, 10:79-95.
- Wenner, A. M., 1962b. Communication with queen honeybees by substrate sound. *Science*, 138:446-48.
- Wenner, A. M., 1964. Sound communication in honeybees. *Sci. Amer.*, 210:117-23.
- Wenner, A. M., 1967. Honeybees: do they use the distance information contained in their dance maneuver? *Science*, 155:847-49.
- Wenner, A. M.; Wells, P. H.; and Johnson, D. L.; 1969. Honeybee recruitment to food sources: olfaction or language? *Science*, 164:84-86.
- Wenner, A. M.; Wells, P. H.; and Rohlf, F. J.; 1967. An analysis of the waggle dance and recruitment in honeybees. *Physiol. Zool.*, 40:317-44.
- Wheeler, W. M., 1911. Notes on the myrmecophilous beetles of the genus *Xenodusa*, with a description of the larva of *X. cava* LeConte. *N. Y. Ent. Soc.*, 19:164-69.
- Wheeler, W. M., 1918. A study of some ant larvae with a consideration of the origin and meaning of social

- habits among insects. *Proc. Amer. Phil. Soc.*, 57:293-343.
- Wilson, E. O., 1958. A chemical releaser of alarm and digging behavior in the ant *Pogonomyrmex badius* (Latreille). *Psyche* (Cambridge), 65:41-51.
- Wilson, E. O., 1959a. Source and possible nature of the odor trail of fire ants. *Science*, 129:643-44.
- Wilson, E. O., 1959b. Communication by tandem running in the ant genus *Cardiocondyla*. *Psyche* (Cambridge), 66:29-34.
- Wilson, E. O., 1962. Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith): 1. The organization of mass-foraging; 2. An information analysis of the odor trail; 3. The experimental induction of social response. *Anim. Behav.*, 10:134-64.
- Wilson, E. O., 1965. Trail sharing in ants. *Psyche* (Cambridge), 72:2-7.
- Wilson, E. O., 1971. *The Insect Societies*. Cambridge: Belknap Press of Harvard University Press. 548pp.
- Wilson, E. O., 1974. Aversive behavior and competition within colonies of the ant *Leptothorax curvispinosus*. *Ann. Entomol. Soc. Amer.*, 67:777-80.
- Wilson, E. O., and Bossert, W. H., 1963. Chemical communication among animals. *Rec. Prog. Hor. Res.*, 19:673-716.
- Wilson, E. O., and Eisner, T., 1957. Quantitative studies of liquid food transmission in ants. *Ins. Soc.*, 4:157-66.
- Wilson, E. O., and Pavan, M., 1959. Source and specificity of chemical releasers of social behavior in the dolichoderine ants. *Psyche* (Cambridge), 66:70-76.
- Woyke, J., 1971. Correlation between the age at which honeybee brood was grafted: characteristics of the resultant queens and results of inseminations. *J. Apicult. Res.*, 10:45-55.
- Wüst, M., 1973. Stomodeale und proctodeale Sekrete von Ameisenlarven und ihre biologische Bedeutung. *Proc. Seventh Int. Congr. IUSSI*, London, pp.412-18.