

**Chemical Communication
in the Social Insects**

Edward O. Wilson

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Insect societies are organized principally
by complex systems of chemical signals.

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In his famous lyric work, *The Life of the Bee*, published in 1901, Maurice Maeterlinck imagined the existence of an intangible social force that directs the activity of the colony. "Where is this 'spirit of the hive' . . ." he asked, "where does it reside? . . . It disposes pitilessly of the wealth and the happiness, the liberty and life, of all this winged people; and yet with discretion, as though governed itself by some great duty." Perhaps entomologists never accepted this *élan social*, yet until quite recently their attempts to explain the organization of insect societies in mechanistic terms have gone slowly. The reason is that much of the "spirit of the hive" is actually invisible—a complex of chemical signals whose identities we have only now begun to reveal by the combination of chemical analyses and detailed studies of exocrine glands. Today this subject invites closer attention, because, in the first place, as I will argue shortly, most communication in social insects appears to be chemical, while, in the second place, pheromone systems have evidently reached their highest evolutionary development in these insects.

A chemical signal used in communication among members of the same species is called a *pheromone*, a term coined in 1959 as a substitute for the older, self-contradictory *ectohormone* (1). Pheromones may be classified as olfactory or oral according to the site of their reception. Also, their various actions can be distinguished as releaser effects, comprising the classical stimulus-response mediated wholly by the nervous system (the stimulus

being thus by definition a chemical "releaser" in ethological terminology), or primer effects, in which endocrine and reproductive systems are altered physiologically (2). In the latter case, the body is in a sense "primed" for new biological activity, and it responds afterward with an altered behavioral repertory when presented with appropriate stimuli.

The individual social insect, in comparison with the individual solitary insect, displays behavioral patterns that are neither exceptionally ingenious nor exceptionally complex. The remarkable qualities of social life are mass phenomena that emerge from the meshing of these simple individual patterns by means of communication. If communication itself is first treated as a discrete phenomenon, the entire subject becomes much more readily analyzed. To date we have found it convenient to recognize about nine categories of responses, as follows: alarm, simple attraction, recruitment, grooming (including assistance at moulting), exchange of oral and anal liquid (the "trophallaxis" of the older literature), exchange of solid food particles, facilitation, recognition (of both nest mates and members of various castes), and caste determination either by inhibition or by stimulation (3). Each of these kinds of responses has been shown to require chemical signals to some degree in at least some species of social insects. Most of them appear to be evoked largely or entirely by such signals. The importance of tactile and auditory stimuli in phenomena such as the waggle dance and queen piping in honey bees need not be minimized. Yet a growing amount of evidence (for a partial summary see Figs. 1-3 and Table 1) now

suggests that pheromones have the central role in the organization of insect societies.

The Alarm Substances

A case in point is the alarm response. It was natural for earlier students of behavior, who relied on simple visual observation, to conclude that alarm spreads through colonies on waves of sound and agitated movement. Sounds transmitted through the substratum can initiate alarm, but it is now apparent that the response is communicated among individuals in large part, and in some species entirely, by the discharge of certain volatile glandular secretions. Alarm, which is the normal response to intruders within the nest premises, typically consists of swift oriented movement. Some castes, or entire colonies or species, are passive, retreating into the interior of the nest or, in extremity, abandoning the nest altogether. Workers of many other species are aggressive, literally throwing their lives away in the famed altruistic manner of social insects. The responses characteristic of a given caste can be produced by presentation of the contents of certain glands, in the absence of other stimuli; happily, this provides a swift and uncomplicated bioassay. This finding, together with the simple structure of the pheromone molecules, has made the chemical identification of many of the alarm substances a straightforward task.

In the literature, *alarm* is often used synonymously with *recruitment*, and in some cases the two phenomena are indeed the same. Stuart (4, 5) showed that in *Zootermopsis nevadensis* (Hagen), a lower termite species, odor trails generated from the sternal gland are laid to breaks in the nest wall; recruited workers assist in repelling invaders and repairing the breaks. In the higher termites, which forage outside the nests, the trails are employed to recruit workers to new food sources. Stuart theorized that, in termite evolution, alarm recruitment was gradually extended to foraging recruitment, as the nests themselves no longer sufficed for food. In some ant species—for example, *Pogonomyrmex badius* (Latreille) and *Iridomyrmex pruinosus* (Roger)—alarm secretions act as attractants at low concentrations, as releasers of alarm and attack

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behavior at high concentrations. In the fire ant *Solenopsis saevissima* (Fr. Smith), on the other hand, an unidentified cephalic substance causes unorientated alarm behavior at both low and high concentrations; in other words, it is an alarm pheromone but not an attractant (6).

The number of alarm substances that have been identified is greater than the number of all other identified pheromones. This is partly due to the fact that many alarm substances are volatile, produce conspicuous odors, and are stored in easily accessible glandular reservoirs. It is also due in

part to the typically small size and structural simplicity of the molecules. Besides the substances listed in Table 1, with which behavioral tests have been performed, various elementary aldehydes and ketones which may be performing an alarm function have been identified from other ant species. These include methylheptenone and propyl isobutyl ketone in *Tapinoma nigerrima* (Nylander)—compounds which are exciters of alarm behavior in the related *T. sessile* (Say) (7); methylheptenone in Australian species of *Iridomyrmex* and *Dolichoderus* (8); methylhexanone in *Acanthoclinea clarki*

Wheeler (8); 2-hexenal in *Crematogaster africana* Mayr. (9); and limonene in *Myrmecaria natalensis* (Fr. Smith) (10).

Bossert and I (2) predicted, on the basis of a priori considerations of potential molecular diversity in the pheromones and of olfactory efficiency in insect chemoreceptors, that most alarm substances would prove to have between five and ten carbon members and to have molecular weights between 100 and 200. The very limited species specificity known to prevail in substances with molecules in this size range could be attained by the available diversity in molecular structure. We also concluded that in order for a substance to have a short fading time—a necessary property for an efficient alarm system—an intermediate response-threshold concentration, neither very high nor very low, is needed. Insect chemoreceptors appear to have been so constructed in the course of evolution as to respond with increasing efficiency to molecules of increasing size in a homologous series. They are capable of being very efficiently adjusted to volatile odorants with molecular weights in the 100-to-200 range. The properties of alarm communication have been investigated quantitatively in *Pogonomyrmex badius*. By directly measuring the effects of alarm substances from whole crushed heads, we obtained estimates for the " Q/K ratio"—the ratio of (i) pheromone molecules released to (ii) response-threshold concentrations (in molecules per cubic centimeter)—ranging between 939 and 1800. The threshold concentration was

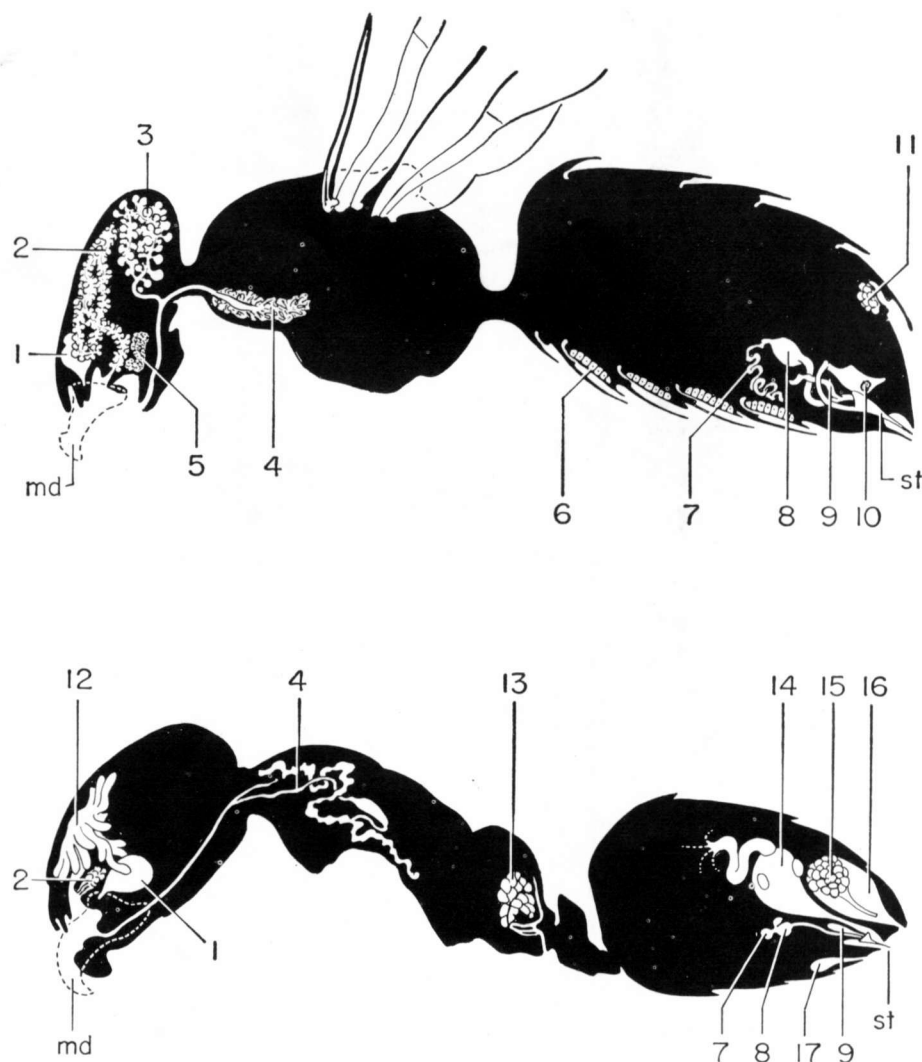


Fig. 1. Exocrine gland systems of (top) the honey bee worker (*Apis mellifera*) and (bottom) worker of the ant species *Iridomyrmex humilis*. Glands of the two species are labeled with the same number if they are considered homologous; where different names have been used in the literature, name used for ants is given in parentheses in the following key; several minor glands of unknown function are omitted. (1) Mandibular gland; (2) hypopharyngeal (= maxillary) gland; (3) head labial gland; (4) thorax labial gland; (5) postgenal gland; (6) wax glands; (7) poison gland; (8) vesicle of poison gland; (9) Dufour's gland; (10) Koschevnikov's gland; (11) Nasonoff's gland; (12) postpharyngeal gland; (13) metapleural gland; (14) hindgut (glandular nature uncertain); (15) anal gland; (16) reservoir of anal gland; (17) Pavan's gland. [Diagram of the honey bee system, modified from Ribbands (53), after R. E. Snodgrass, with Koschevnikov's gland added; diagram of the ant system, modified from Pavan and Ronchetti (54); homologies of cephalic glands, according to Otto (37)]

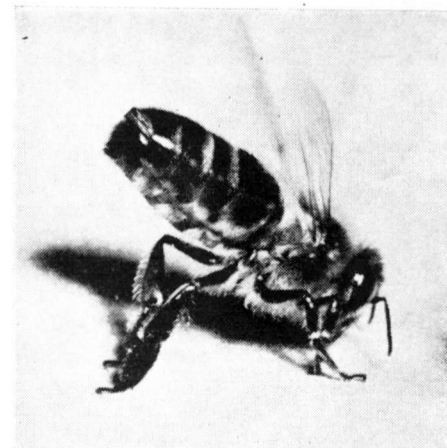


Fig. 2. Honey bee worker discharging attractant pheromones from its Nasonoff's gland. This signaling typically occurs when workers discover a new food source or when they rejoin their nest mates after a period of isolation. [After Renner (39)]

then indirectly estimated to be about 5×10^{13} molecules per cubic centimeter. The Q/K ratio for these alarm substances falls far below the ratios calculated for the sex attractants of moths and is well above those for the trail substance of fire ants (11). In agreement with these parameters, the entire contents of the paired mandibular glands of *P. badius* provides a brief signal when discharged in air. A small "active space" (that is, space within which the concentration is at or above the response threshold) is generated, attaining a maximum radius of only about 6 centimeters. After approximately 35 seconds, further diffusion reduces the active space to nearly zero, and the signal vanishes. The *Pogonomyrmex* colony is thus able to localize its alarm communication sharply in time and space.

The rule that alarm substances have small, relatively simple molecules has continued to hold since we first formulated it in 1962. At that time there seemed to be one conspicuous exception. Dendrolasin, a furan with a molecular weight of 218, found in the mandibular glands of *Lasius fuliginosus*, was said by its discoverer M. Pavan to cause an alarm response in *L. fuliginosus* workers (12). However, later quantitative assays by Maschwitz (13) show that, in this species, the alarm substances are concentrated in Dufour's gland, while the mandibular glands are relatively inactive. Synthetic dendrolasin has not to my knowledge been assayed quantitatively, and large doses may well cause the alarm effect reported by Pavan.

Although cataloging of the alarm substances has only begun, three of them—citral, 2-heptanone, and methylheptenone—have already been found in more than one species of social hymenopteran. This discovery is not surprising in view of the simplicity of the molecular structure. The range of candidate substances must have been further narrowed by requirements of diffusivity and by probable limitations in the biosynthetic capacity of the insects themselves.

At least some of the pheromones serve also as defensive secretions. Roth and Eisner (14) report that citronellal facilitates the penetration of formic acid into the cuticle of enemy arthropods. Maschwitz (13) claims that formic acid itself, long known to be a primary defensive secretion in formi-

cine ants, serves as a secondary alarm pheromone in *Formica polyctena* Foerster. Pinenes manufactured in the cephalic glands of nasute soldiers of the termite genus *Nasutitermes* probably serve both in defense and in the

communication of alarm (15). It seems appropriate that the two functions, which are required simultaneously in times of danger, should be served by the same substances. The question remains, Which function was served first

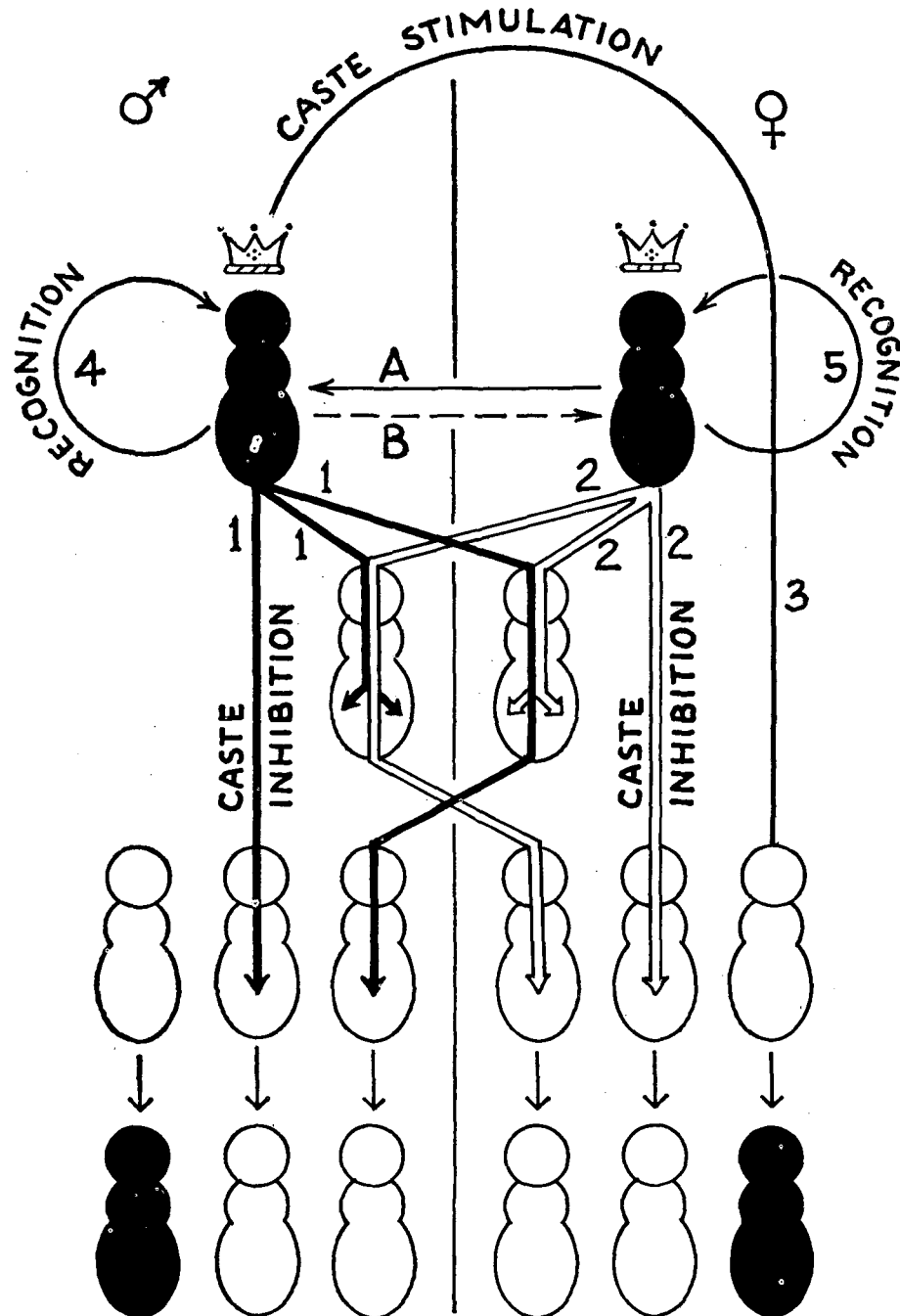


Fig. 3. The known pathways of pheromone action in the control of reproductive caste formation in the termite *Kaloterms flavicollis*. (Top row) Pair of figures representing the "royal" reproductives; (remaining rows) figures representing pseudergates. The king and queen produce substances (labeled 1 and 2, respectively) which inhibit development of pseudergates into their own royal castes. These inhibitory pheromones are passed directly from the reproductives to the pseudergates and are also circulated indirectly through the digestive tracts of the pseudergates. Another male substance (pheromone 3) stimulates the female pseudergates to transform to the reproductive caste, but the reverse relation does not hold. When supernumerary royal males are present, they recognize each other (through pheromone 4) and fight; similarly, supernumerary royal females recognize each other (through pheromone 5) and fight. Finally, royal males stimulate production of pheromone 2 in royal females, and royal females stimulate production of pheromone 1 in royal males; the nature of the stimuli, which are labeled A and B, is unknown. [After Lüscher (55)]

in the evolution of particular phyletic lines?

The Caste Pheromones

Building upon the early experimental work of A. L. Pickens in 1932 and E. M. Miller and S. F. Light in the 1940's, Martin Lüscher and his associates have developed a picture of remarkably complex and precise pheromonal caste control in the termites. Much of the information concerning specific inferred substances is given in Fig. 3. In *Kaloterme* *flavi-*

collis (Fabricius), the species of Lüscher's study, the key caste is the pseudergate, a large nymph-like stage that performs the tasks of the worker in other insect societies and is capable, when the inhibitory pheromones are removed, of transforming into a soldier or one of the two reproductive castes. It has become clear that the pheromones act by interfering with the endocrine system. In particular, the proportion of orphaned pseudergates that change into replacement reproductives shows a negative correlation with the volume of the corpora allata, while soldiers can be produced experi-

mentally from pseudergates by implantation of the corpora allata of reproductives (16). However, neither the responsible hormones of the corpora allata nor their exact modes of action have been elucidated. Also, to date, none of the caste-controlling pheromones have been chemically identified.

It is likely that patterns of caste control vary greatly within the termites as a whole. *Zootermopsis* and *Kaloterme*, in which pheromones have been demonstrated, are primitive genera. In the higher Termitidae, phylogenetically the most advanced group of all the termites, reproductives can

Table 1. Glandular source, chemical identity, and function of pheromones in the worker caste in the honey bee (*Apis mellifera*) and in several species of ants (Formicidae). The numbers in parentheses are literature citations. A question mark indicates that the social function of the gland, if any, is unknown; a zero indicates that the insect does not have the gland in question.

Species	Source									
	Mandibular glands	Hypopharyngeal glands	Labial glands	Nassanoff's gland	Hindgut	Dufour's gland	Poison gland	Glands of sting chamber	Pavan's gland	Anal gland
Apidae <i>Apis mellifera</i> L.	2-Heptanone: alarm (36)	Royal jelly: digestion (37)	Cleaning and dissolving (38)	Geraniol, citral, geranic acid, nerolic acid: attraction (39, 40)	?	?	?	Isoamyl acetate: alarm (41)	0	0
Formicidae: Ponerinae <i>Termitopone laevigata</i> (Fr. Smith)	?	?	?	0	Trail (42)	?	?	0	0	0
<i>Paraponera clavata</i> (Fabr.)	Alarm (43)	?	?	0	?	?	?	0	0	0
Formicidae: Dorylinae <i>Eciton</i> spp.	Alarm (43) ?		Nomadic behavior? (44)	0	Trail (45)	?	?	0	0	0
Formicidae: Myrmicinae <i>Solenopsis saevissima</i> (Fr. Smith)	Alarm (6)	?	?	0	?	Trail (6)	?	0	0	0
<i>Atta</i> spp.	Citral: alarm (46)	?	?	0	?	?	Trail (47)	0	0	0
<i>Tetramorium guineense</i> (Fabr.)	?	?	?	0	?	?	Trail (48)	0	0	0
Formicidae: Dolichoderinae <i>Iridomyrmex</i> spp.	?	?	?	0	?	?	?	0	Trail (7)	2-Heptanone: alarm (49)
<i>Tapinoma sessile</i> (Say)	?	?	?	0	?	?	?	0	Trail (7)	Methylheptenone: alarm (7)
Formicidae: Formicinae <i>Acanthomyops claviger</i> (Roger)	Citronellal, citral: alarm (50)	?	?	0	?	?	?	0	0	0
<i>Lasius fuliginosus</i> (Latreille)	β (4:8-dimethyl-nona-3,7-dienyl) furan ("dendrolasin"): alarm? (12)	?	?	0	Trail (51)	Alarm (13)	?	0	0	0
<i>Formica polyctena</i> (Foerster)	Alarm (13)	?	Larval and queen food (52)	0	?	Alarm (13)	Alarm (13)	0	0	0

be derived only from nymphs. A true worker caste exists which lacks the potential for caste alteration (17).

When the mother queen of a honey bee colony is removed, the workers respond in as short a time as 30 minutes by changing from a state of organized activity to one of disorganized restlessness. In a few more hours, they begin to alter one or more worker brood cells into emergency queen cells, within which a new nest queen is eventually produced. A few days later, some of the workers begin to experience increased ovarian development. These combined releaser and primer effects were known, as early as 1954, to be due to the removal of a pheromone present in the queen, called "queen substance" by C. G. Butler (18). Now it appears that at least two inhibitory pheromones are involved in these effects. Moreover, the special treatment accorded the queen is due to at least two additional attractive scents (19, 20).

One of the inhibitory pheromones present in the queen honey bee is *trans*-9-keto-2-decenoic acid. This substance was characterized in 1960 by Butler, Callow, and Johnston in England (21) and, at the same time, by Barbier and Lederer in France (22). It is produced entirely in the queen's mandibular glands. Its odor alone is sufficient to inhibit to some extent both queen-rearing behavior and ovary development in worker bees. It works in conjunction with a second inhibitory scent produced in a part of the body outside the mandibular glands. When experimentally injected into the body cavity of the worker, thus bypassing the external chemoreceptors, it continues to inhibit ovary development but not queen-rearing behavior (23). Lüscher and Walker (24) found that the corpora allata of workers increase in size for the first few days following removal of the queen, and they have hypothesized that the inhibitory pheromones act by suppressing secretion of the "gonadotropic" hormone. Whether the pheromones produce their effects by direct action on the corpora allata or indirectly through a more circuitous route in the central nervous system remains to be learned.

A paradox was raised by the early findings on inhibition by "queen substance": How can a normal colony produce new queens in the annual breeding season in the presence of the mother queen? The solution has

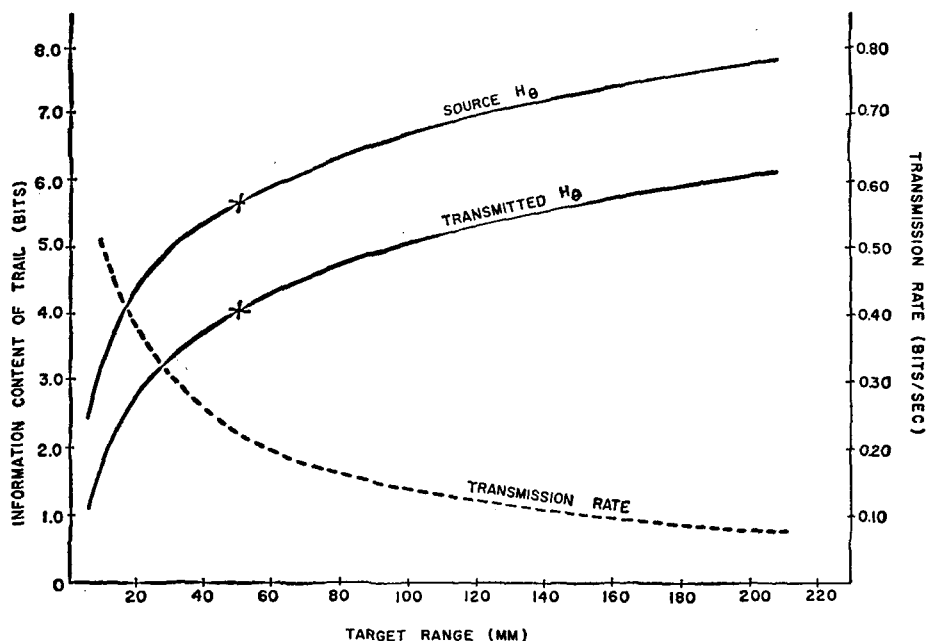


Fig. 4. Information content and transmission rate with reference to direction in the odor trail of the fire ant *Solenopsis saevissima*. (Source H_0) Curve represents the amount of information which would be transmitted if the trail were followed perfectly. (Transmitted H_0) Curve represents transmitted information, based on the actual performance of follower workers. Although the amount of information increases as the trails grow longer, the time required to lay and follow them increases disproportionately, with the result that the actual transmission rate drops off steadily. [After Wilson (6)]

been obtained by Butler (25). By appropriate experiments, he first excluded the hypothesis that the attractiveness of "queen substance" is greater for pre-swarm workers than for workers from nonswarming colonies. Then he determined that the amount of "queen substance" (as measured by the inhibiting power of whole-body extracts) in mother queens from colonies involved in normal reproduction, by means of swarming, is only about one-quarter that of mother queens from nonreproducing colonies.

Similarly acting inhibitory pheromones have recently been located in the heads of queens of the ant genus *Myrmica* (26). It is thus proved that each of the most advanced groups of the social insects—the termites, the honey bees, and the ants—has evolved pheromonal control by the queen. In

groups with less distinct caste systems, the control devices are more crude and direct. In some wasps of the genus *Polistes* and some bumble bees of the genus *Bombus* the queen differs only slightly in appearance from other adult females of the colony. She dominates them by threat behavior and, in addition, appears to bear a distinctive odor recognized by her subordinates (27). In the quite primitively social *LasioGLOSSUM zephytum* (Smith), some degree of reproductive domination is achieved by females who remove eggs of rivals from brood cells and substitute their own (28). Evolution of reproductive control in social insects can be interpreted as having consisted of a transition from direct intervention among rival females utilizing recognition scents to indirect control by means of directed worker behavior and primer pheromones.

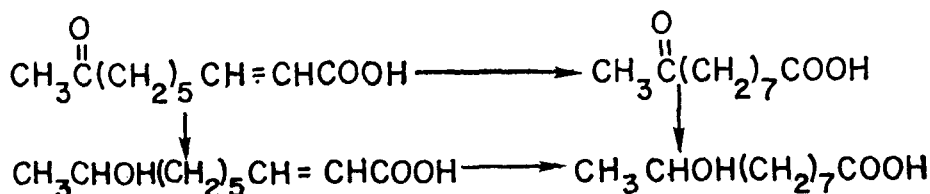


Fig. 5. *Trans*-9-keto-2-decenoic acid and its inactive derivatives produced within the body of the worker honey bee. [After Johnston *et al.* (29)]

The Increase of Information

An individual pheromone is capable of communicating far more information than the maximum single unit (the "bit") implicit in a simple on-or-off signal. The parameters of diffusion rate, emission rate, and response threshold have clearly been evolved in animal species to permit both localization of the source in space and an appropriate fading time (2). The actual information transmitted has been measured in the case of the odor trail of the fire ant (*Solenopsis saevissima*). When worker ants find a new food source or a superior nest site, they run homeward, laying a trail consisting of minute traces of Dufour's gland secretion. The secretion is a volatile attractant. As it diffuses in still air it forms a semi-ellipsoidal active space whose transverse maximum radius is only about 1 centimeter. During the lifetime of the active space—approximately 100 seconds when the trail is laid on a nonabsorbing surface—recruited workers run away from the nest while orienting themselves to remain inside the space. If they are able to keep this up long enough they arrive in the vicinity of the "target." By recording the points at which responding workers turn back to the nest or lose the trail, I was able to measure response errors with reference to the target from which the trail had been drawn. These statistics were then translated into information measures, with the results shown in Fig. 4. Although the amount of directional information increases with the length of the trail (due to the nearly constant diameter of the ellipsoidal active space throughout its length), the rate of information transmission drops off because of the disproportionately increasing period of time required to lay and follow the trail. Even so, both the total amount of information transmitted and the transmission rate are considerable; the amount of directional information, for example, is comparable to that transmitted by the waggle dance of the honey bee.

The fading time of a chemical signal can easily be adjusted, in the course of evolution, by altering the Q/K ratio, the emission rate, or both. In the case of ingested pheromones, it might conceivably also be shortened by enzymatic deactivation of the molecules. Just such a mecha-

nism in the case of *trans*-9-keto-2-decenoic acid has recently been discovered by Johnston, Law, and Weaver (29). These investigators traced the metabolism of a radioactive form of the pheromone fed to worker bees and found that within 72 hours over 95 percent of it had been converted into inactive substances, consisting principally of 9-ketodecanoic acid, 9-hydroxydecanoic acid, and 9-hydroxy-2-decenoic acid. The metabolic route shown in Fig. 5 was then postulated. Johnston *et al.* have further hypothesized the existence of a "pheromone cycle." The inactive molecules might be passed back to the queen as part of the regurgitated glandular queen food. The queen could then convert them into the active form by very simple enzymatic processes, resulting in a saving to the queen of a "relatively enormous amount of energy required for the complete synthesis of the fatty acid chain." The queen, it should be added, carries only a little more than 100 micrograms of the ketodecenoic acid on her at any given moment (20), and she must dispense on the order of 0.1 microgram of this substance per day per worker in the colony to suppress queen rearing.

So far I have emphasized adjustments of fading time and of the geometrical properties of the active space as two ways in which the information in a chemical communication system may be increased. A third device found in social insects is the employment of medleys of substances with more than one "meaning." A minimum of 32 substances have been detected in the heads of honey bee queens, including methyl 9-ketodecanoate, methyl 9-keto-2-decenoate, nonoic acid, decanoic acid, 2-decenoic acid, 9-ketodecanoic acid, 9-hydroxy-2-decenoic acid, 10-hydroxy-2-decenoic acid, 9-keto-2-decenoic acid, and others. Most or all are present in the mandibular gland secretion (30). The biological significance of most of these products is unknown. Some are undoubtedly precursors to pheromones, but at least two are known pheromones with quite contrasting effects: the 9-ketodecenoic acid is the inhibitory pheromone already mentioned, while the 9-hydroxydecanoic acid causes clustering and stabilization of worker swarms (31).

A fourth device found in social insects for increasing information in a chemical communication system is for

the same pheromone to convey different meanings in different contexts. *Trans*-9-keto-2-decenoic acid serves as a caste-inhibitory pheromone inside the honey bee nest and as the primary volatile sex attractant during the nuptial flight (32). The Dufour's gland secretion of the fire ant *Solenopsis saevissima* is an attractant that is effective on members of all castes during most of their adult life. Under different circumstances it serves variously to recruit workers to new food sources, to organize colony emigration, and—in conjunction with a cephalic secretion—to cause alarm behavior (6).

A fifth modification is for the insects to respond in different ways to different concentrations of a substance, and to different durations of exposure. Workers of *Pogonomyrmex badius* react to low concentrations of mandibular gland secretion by simple positive chemotaxis and to higher concentrations by typical aggressive alarm behavior. When exposed to high concentrations for more than a minute or two, many individuals switch from alarm to digging behavior (33). The digging is directed to the source of the substance and has the result of bringing aid to injured or trapped nest mates.

In a sixth modification, pheromones acquire additional or even different meanings when they are presented in combination. When released near fire ant workers, cephalic and Dufour's gland secretions cause unoriented alarm behavior and attraction, respectively; when expelled simultaneously by a highly excited worker, they cause oriented alarm behavior (6). Honey bee workers confined closely with queens for hours acquire scents from her which, evidently in combination with their own worker-recognition scent, cause them to be attacked by nest mates (34). Males of the ant *Lasius neoniger* Emery discharge most of their mandibular gland contents during the nuptial flight, almost certainly as an aerial courtship signal. The glands contain 2,6-dimethyl-5-hepten-1-ol, citronellol, geraniol, and a few other simple compounds. The two species of *Lasius* and the one species of the related genus *Acanthomyops* that have been studied thus far have many mandibular gland components in common, but, perhaps as an evolutionary solution to the problem of interspecific sexual isolation, the propor-

tions of the components in the three species differ radically (35).

A Large Gap in Pheromone Research

If the information given here seems limited—and it certainly should, in view of the enormous diversity of social insects—it must be considered even further narrowed by the existence of a gap in our knowledge, one that is largely unappreciated. The pheromones studied in detail to date have been mostly of two kinds: those that are ingested to influence caste and those that are transmitted in volatile form through the air to attract or alarm. For various technical reasons such substances have been relatively easy to extract and bioassay. There is a third category of substances that have proved far more refractory, comprising what might be termed the “surface pheromones.” These substances either are absorbed on the body surface or generate such shallow active spaces in air that they must be perceived by contact chemoreception. Indirect evidence is adequate to demonstrate their existence; in particular they are the colony odors, which include the species odors, the caste-recognition scents, the releasers of grooming behavior, and (in at least some social insects) the secretions that stimulate food exchange. Of fundamental importance to social organization, they are nevertheless extremely difficult to study because of the typically complex and delicate stimulus context in which they are found. When removed from the other surface odors or masked by alien substances that are added in conventional extraction techniques, they no longer produce behavioral effects. We do not now have suitable extraction tech-

niques or sufficient information on pheromone chemistry to make much progress in studying surface pheromones, but, hopefully, they are not beyond our reach.

References and Notes

1. P. Karlson and A. Butenandt, *Annu. Rev. Entomol.* **4**, 39 (1959); P. Karlson and M. Lüscher, *Nature* **183**, 55 (1959).
2. E. O. Wilson and W. H. Bossert, *Recent Progr. Hormone Res.* **19**, 673 (1963).
3. Current reviews of these subjects have been provided by M. Lindauer, *Physiology of Insecta*, M. Rockstein, Ed. (Academic Press, New York, 1965), vol. 2, p. 123, and E. O. Wilson, *Annu. Rev. Entomol.* **8**, 345 (1963).
4. A. M. Stuart, *Nature* **189**, 419 (1961); *Proc. Zool. Soc. London* **143**, 43 (1964).
5. The origin of the trail substance in the sternal gland was independently discovered in *Zootermopsis* by M. Lüscher and B. Müller [*Naturwissenschaften* **47**, 503 (1960)], and it has since been found in the sternal gland in *Reticulitermes flavipes* (Kollar) by R. B. Smythe and H. C. Coppel [*Bull. Amer. Entomol. Soc.* **10**, 168 (1964)].
6. E. O. Wilson, *Animal Behaviour* **10**, 134 (1962).
7. — and M. Pavan, *Psyche* **66**, 79 (1959) [*Iridomyrmex humilis* Mayr and *Tapinoma sessile* (Say)].
8. G. W. K. Cavill and H. Hinterberger, *Proc. Intern. Congr. Entomol.* **11th**, London (1960), vol. 3, p. 284.
9. C. W. L. Bevan, A. J. Birch, H. Caswell, *J. Chem. Soc.* **1961**, 488 (1961).
10. P. Grünanger, A. Quilico, M. Pavan, *Rend. Accad. Sci. Fis. Mat. (Soc. Naz. Sci.)* **28**, 293 (1960).
11. W. H. Bossert and E. O. Wilson, *J. Theoret. Biol.* **5**, 443 (1963).
12. M. Pavan, *Atti Accad. Naz. Ital. Entomol. Rend.* **8**, 228 (1961).
13. U. Maschwitz, *Z. Vergleich. Physiol.* **47**, 596 (1964).
14. L. M. Roth and T. Eisner, *Annu. Rev. Entomol.* **7**, 107 (1962).
15. B. P. Moore, *J. Insect Physiol.* **10**, 371 (1964); personal communication, April 1965.
16. M. Lüscher, *Proc. Intern. Congr. Zool.* **16th**, Washington, D.C. (1963), vol. 4, p. 244.
17. C. Noirot, *Insectes Sociaux* **3**, 145 (1956).
18. C. G. Butler, *Trans. Roy. Entomol. Soc. London* **105**, 11 (1954).
19. —, *J. Insect Physiol.* **7**, 258 (1961); — and J. Simpson, *Veda. Prirodni. Vyzkum. Ust. Zemed.* (1965), p. 33. In the last-named article, one of the scents is reported as originating in Koschevnikov's gland.
20. C. G. Butler and P. N. Patton, *Proc. Roy. Entomol. Soc. London* **A37**, 114 (1962).
21. C. G. Butler, R. K. Callow, N. C. Johnston, *Proc. Roy. Soc. London* **B155**, 417 (1961).
22. M. Barbir and E. Lederer, *Compt. Rend.* **250**, 4467 (1960).
23. C. G. Butler and E. M. Fairey, *J. Apicultural Res.* **2**, 14 (1963).
24. M. Lüscher and I. Walker, *Rev. Suisse Zool.* **70**, 304 (1963).
25. C. G. Butler, *Proc. Roy. Entomol. Soc. London* **A35**, 129 (1960).
26. M. V. Brian and J. Hibble, *J. Insect Physiol.* **9**, 25 (1963).
27. J. B. Free, *Brit. J. Animal Behaviour* **3**, 147 (1955).
28. S. W. T. Batra, *Insectes Sociaux* **11**, 159 (1964).
29. N. C. Johnston, J. H. Law, N. Weaver, *Biochemistry*, in press.
30. R. K. Callow, J. R. Chapman, P. N. Paton, *J. Apicultural Res.* **3**, 77 (1964).
31. C. G. Butler, R. K. Callow, J. R. Chapman, *Nature* **201**, 733 (1964).
32. N. E. Gary, *Science* **136**, 773 (1962); C. G. Butler and E. M. Fairey, *J. Apicultural Res.* **3**, 65 (1964).
33. E. O. Wilson, *Psyche* **65**, 41 (1958).
34. R. A. Morse and N. E. Gary, *Bee World* **42**, 197 (1961). The effect was first described by Z. Orósi-Pál in 1955.
35. J. H. Law, E. O. Wilson, J. A. McCloskey, *Science*, in press.
36. D. A. Shearer and R. Boch, *Nature*, in press.
37. D. Otto, *Zool. Anz.* **161**, 216 (1958).
38. J. Simpson, *J. Insect Physiol.* **4**, 107 (1960).
39. M. Renner, *Z. Vergleich. Physiol.* **43**, 411 (1960).
40. R. Boch and D. A. Shearer, *Nature* **194**, 704 (1962); —, *ibid.* **202**, 320 (1964); N. Weaver, E. C. Weaver, J. H. Law, *Progr. Rep. Texas Agr. Exp. Sta. PR-2324* (1964).
41. R. Boch, D. A. Shearer, B. C. Stone, *Nature* **195**, 1018 (1962); R. L. Ghent and N. E. Gary, *Psyche* **69**, 1 (1962).
42. M. S. Blum, personal communication, May 1965.
43. E. O. Wilson, *Annu. Rev. Entomol.* **8**, 345 (1963).
44. E. R. Lappano, *Insectes Sociaux* **5**, 31 (1958). Lappano related certain suggestive histological findings to the “Schniebla cycle” of the army ant *Eciton burchelli* but offered no direct evidence of the function of the labial glands.
45. M. S. Blum and C. A. Portocarrero, *Ann. Entomol. Soc. Amer.* **57**, 793 (1964).
46. A. Butenandt, B. Linzen, M. Lindauer, *Arch. Anat. Microscop. Morphol. Exp.* **48**, 13 (1959) [*Atta rubropilosa* Forel].
47. J. C. Moser and M. S. Blum, *Science* **140**, 1228 (1963) [*Atta texana* (Buckley)].
48. M. S. Blum and G. N. Ross, *J. Insect. Physiol.*, in press.
49. M. S. Blum, S. L. Warter, R. S. Monroe, J. C. Chidester, *ibid.* **9**, 881 (1963).
50. R. L. Ghent, thesis, Cornell University (1961).
51. J. D. Carthy, *Nature* **166**, 154 (1950); W. Hangartner and S. Bernstein, *Experientia* **20**, 396 (1964).
52. K. Gösswald and W. Kloft, *Zool. Beitr.* **5**, 519 (1960).
53. R. Ribbands, *The Behaviour and Social Life of Honeybees* (Bee Research Association, London, 1953), p. 57.
54. M. Pavan and G. Ronchetti, *Atti Soc. Ital. Sci. Natur. Museo Civico Storia Natur. Milano* **94**, 379 (1955).
55. M. Lüscher, *Symp. Roy. Entomol. Soc. London* **1**, 57 (1961).
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