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7

Pheromone Directed Behavior in Ants

Robert K. Vander Meer and Leeanne E. Alonso

Introduction

All ants are eusocial, which means there are overlapping generations in which adult workers (normally sterile) assist their mother in rearing sisters and brothers, and there are reproductive and non-reproductive castes (division of labor). There are about 11,000 known ant species that represent a large percentage of the earth's animal biomass. Ants occupy virtually every ecological niche on earth and are among the leading predators and scavengers of insects and small mammals. Concomitant with such variety comes tremendous diversity in colony structure and social organization. A large component of ant social organization is mediated by pheromonal communication.

The term pheromone was originally proposed by Karlson and Luscher (1959) and is defined as a substance secreted by an organism outside its body that causes a specific reaction in a receiving organism of the same species. Pheromones are classified into two broad categories: releaser types that result in an immediate behavioral response and primer types, where the initial perception results in the initiation of a complex physiological response. This chapter deals with releaser pheromones (see Vargo, this book, for ant primer pheromones).

Pheromone research has two basic elements. The first is observational, where a particular behavior is studied and experimental evidence suggests that pheromones are involved. The second part is the chemistry of the pheromones. A bioassay developed from behavioral observations is used to guide the isolation of active compounds. There are many papers that investigate the chemistry of glandular products without associated behavior (Cavill and Houghton

1974; Meinwald et al. 1983; Blum et al. 1987; Billen et al. 1988; do Nascimento et al. 1993a). This research is important, providing information on inter- and intraspecific chemical diversity and variation, and occasionally yielding novel chemistry. Similarly, there are many observational papers that report the probable existence of pheromones, but have not addressed the pheromone chemistry (Breed et al. 1987; Yamauchi and Kawase 1992; Passera and Aron 1993; Hölldobler et al. 1994a). These papers, too, have great value. They define the complexity and diversity of ant behavior and set the stage for the ultimate interaction between biologists and chemists.

Papers on ant behavior or pheromones account for over 18% of the 20,000 references currently in the comprehensive ant bibliography, FORMIS (Porter 1995). The number of pheromone specific publications (3.4%) have increased dramatically, since the term was coined in 1959, but now have leveled off to about 30/year. This large body of literature cannot be dealt with in this chapter, so we selected focus topics, and limit our discussion of other areas.

Types of Pheromone Interactions

Many pheromone induced behaviors associated with ants effectively maintain colony social structure, cohesiveness, and productivity. Worker/worker interactions focus on recruitment, colony immigration and alarm. Worker/queen associations involve worker attraction to queen produced pheromones and associated queen grooming, feeding, and protection. The queen can also influence the competitive functionality of sexuals, potential sexuals or other queens in the colony directly or through the workers (see primer pheromone Chapter by Vargo). Brood produced pheromones are thought to be produced because of the preferential treatment of brood by workers. Lastly, there are many potential pheromone mediated behaviors between male and female sexuals associated with mating activities. Morgan and Billen (this Book) deal in depth with the many exocrine glands available to the ant for the biosynthesis and distribution of pheromones.

Mating Flights and Male/Female Sexual Interactions

There are numerous points during mating flights and the interaction of male and female sexuals that have a high probability of being mediated by pheromones or more generally semiochemicals. These include (1) initiation of mating flight activity; (2) interaction of workers and alates during mating flight activity; (3) the actual flight of male and female alates (often synchronized); (4) cohesion of a male lek, if formed; (5) female location of the male lek; (6) and/or male location of females; (7) female mate selection (if this occurs); (8) inseminated female alate's choice of landing site; (9) newly mated queen's choice of nuptual chamber site; and (10) there are other possibilities that can match the many mating strategies of ants. As illustrated below, there is little actually known about the chemistry and behavior of these processes, perhaps because observations (and therefore bioassay development) are difficult, e.g. the fire ant, *Solenopsis invicta*, mates 300 meters in the air. However, we anticipate excellent future progress in this very important area of pheromone communication.

Sex Pheromones

The attraction of males to females (usually) for mating is especially well studied and understood in lepidopteran species; however, in ants there are only a few reports dealing with this phenomenon. Like most ant species,*Xenomyrmex floridanus*, male and female sexuals leave the nest on nuptual flights. The details of these flights are a puzzle. However, males are strongly attracted to the poison gland secretion of female sexuals (Hölldobler 1971a) and the secretion elicits male copulatory activity. Worker poison glands also attract males. It is unknown how this secretion and the behaviors noted are used in mating flights. Sexuals of the ant social parasite, *Formicoxenus nitidulus*, mate within the nest and are more amenable to observation (Buschinger 1976). As in the previous study, female poison gland products attract and release copulatory behavior in males. Here the alate female raises her gaster, and releases a droplet of venom through her extended sting. Males (wingless) are attracted to female alates over a short distance and attempt to copulate. The poison sac contents of other ant social parasite females, *Harpagoxenus canadensis*, *H. sublaeviv*, and *H. americanus*, act similarly to call and stimulate male copulation (Buschinger and Alloway 1979). The preceding examples appear to be ready and waiting for the isolation and identification of the sex pheromone components. Wingless female sexuals, ergatoids, of the primitive ant, *Rhytidoponera metalica*, gather at their nest entrance prior to male mating flights. They arch their gaster exposing the tergal gland. Compounds released from this gland attract males flying from nearby nests. Workers and reproductives have this gland, thus either the behaviors released are context specific or the chemistry produced by each caste is different (Hölldobler and Haskins 1977).

The sex pheromone of *Formica lugubris* has been isolated and identified (Walter et al. 1993). The chemistry is not novel, but the

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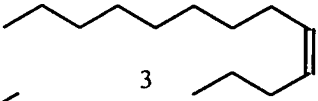

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chemistry/behavior is exciting. Male and female alates take nuptial flights and mate in open places on the forest floor. The females call males by releasing the following products from their Dufour's gland, undecane (**1**); tridecane (**2**); and Z-4-tridecene (**3**) (100:5.32:4.25, respectively). All are significantly attractive, although the attractant power of undecane by itself is not statistically different from the three compounds together. Undecane and the other two compounds are also found in the Dufour's glands of workers. Again, the context under which exocrine gland products are released affects the behavior elicited.

Mating Flight Activities

Heightened worker excitement and aggression at the onset of mating flights has been observed in several ant species. Male mandibular gland products of *Acromyrmex* and *Atta* species elicit worker excitement during nuptual flights (Fowler, 1982). This chemistry may initiate mating flight activity, protect sexuals during the flight, and through heightened worker aggressive behavior toward landing newly mated queens, prevent colony foundation near established colonies. Obin and Vander Meer (1994) induced *S. invicta* flights in the laboratory and showed that chemical cues from both male and female alates, but not from workers, attracted workers, induced alarm-recruitment behaviors in the workers, and promoted alate retrieval by workers. They proposed that volatile substances produced by the alates were responsible for eliciting the worker reactions. Alonso and Vander Meer (In press) determined that the glandular source of these excitant pheromones were the mandibular glands. The chemistry of this secretion is under investigation.

The role of "alarm" pheromones in mating flight activity is supported by related findings that the chemical concentration and/or composition of alarm pheromones often differ between workers, female alates, and males (e.g. Law et al. 1965, Brand et al. 1973, Lloyd et al. 1975). In particular, Pasteels et al. (1980) showed that heads of *Tetramorium caespitum* male and female alates contain 4-methyl-3-hexanone, a compound not found in workers. The ketone attracts workers and a role in mating flight activities was suggested. Alarm pheromones identified from the large mandibular glands of *Atta sexdens rubropilosa* (Blum et al. 1968) vary in concentration, but not composition, between female and male alates (do Nascimento et al. 1993b). Workers and alates differ in the concentration of alarm pheromones from the mandibular glands of *Camponotus abdominalis* (Blum *et al*. 1988), but not *C. schaefferi* (Duffield and Blum 1975). See also Alarm Pheromones in this Chapter.

Queen / Worker Interactions

Queens of most species are surrounded by workers, probably for protection and tending (Hölldobler and Bartz 1985). This process does not necessarily require an attractant pheromone, since workers could randomly contact the queen and be stimulated to aggregate around her. Unfortunately, many studies have used bioassays that cannot distinguish between aggregation and attraction.

Researchers investigating queen/worker interactions have come up with an extensive array of behaviors and descriptors, e.g. attraction, aggregation, arrestant, worker retrieval, recognition, and queen tending. Stumper (1956) showed that workers from *Lasius alienus* and *Pheidole pallidula* were "attracted" to their respective queens. A solvent extract of queens was also attractive to workers of the same species. Pheromone specificity was demonstrated by the application of *Pheidole* queen extract onto cadavers of *Lasius* queens. *Pheidole* workers adopted the *Lasius* queens for about one day. This was the first demonstration, by chemical extraction, of queen produced pheromones acting on workers. The bioassay placed workers and the treated surrogate queen in a common arena, then worker behaviors were observed. This kind of bioassay can detect attraction and/or aggregation, but it is difficult to distinguish one from the other.

Similarly, the "attraction" of workers to queens of several species of army ants was investigated (Watkins and Cole 1966). Queens were left in specific locations on filter paper, removed, and then workers were introduced. Again this type of bioassay confounds attraction and aggregation responses. Workers from all species tested showed some cross-specificity. It was interesting that workers generally preferred their own queen over a conspecific queen from another colony. Similar intra-colony queen preferences were observed for the fire ant, *Solenopsis invicta* (Jouvenaz et al. 1974). Polygyne species become more complicated, for example, *Myrmica rubra*, (Evesham 1984) workers are faced with multiple queens producing an attractant pheromone. The attractant pheromone is not different for each queen, therefore, workers are attracted to all queens in a colony. Other recognition factors come into play that allow workers to identify and interact differently with the first queen they encounter. Evesham (1984) states that workers may be attracted to and visit many queens, but are "loyal" to one.

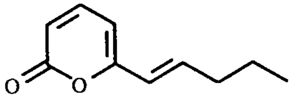
Fowler and Roberts (1982) appropriately described an "entourage" pheromone from the carpenter ant, *Camponotus pennsylvanicus*. This pheromone induces workers to cluster around their queen. In their assay they exposed blotter paper to queens and observed workers forming aggregations where the queens had been previously. No chemical isolation was attempted.

Oecophylla longinoda and *O. Smaragdina* queens are usually covered by a retinue of major workers. The queen produces a variety of releaser and primer pheromones from its head and abdominal intersegmental glands (Hölldobler and Wilson 1983). The pheromones are said to be "attractive" (aggregation?), induce worker regurgitation, and they induce workers to present trophic eggs to the queen (laid by major workers). See Vargo, this book, for more on ant primer pheromones.

Iridomyrmex humilis queens produce a worker "attractant" (Keller and Passera 1989). Their assay consisted of an arena with nestmate and non-nestmate queens confined by wire mesh, such that workers could contact the queen but the queen could not get out. Aggregation versus attraction is again an issue. Interestingly, the source of the queen's action on workers was determined to be the thorax, either from epidermal gland cells or from thoracic glands (Cariouetienne et al. 1992). Later, these researchers recognized that they could not distinguish between attraction and aggregation effects and defined "queen power" as the combined result of these two behaviors (Cariouetienne and Passera 1993). They determined that "queen power" was related to the egg-laying process and not insemination and dealation. More on this later.

The Chemistry of Queen/Worker Interactions

Although the bioassays in the above studies should be adequate to commence the isolation and identification of the pheromones, the chemistry involved in the interactions is mostly unknown. *Solenopsis invicta* is an outstanding exception. As already mentioned Jouvenaz et al. (1974) first noted that *S. invicta* workers aggregated at spots where their queens had been placed. Bioassays were developed to measure the behavioral effects (Glancey 1980, Lofgren et al. 1983), which were useful in determining the pheromone source (Vander Meer et al. 1980). The bioassays were not behavior specific. A surrogate queen bioassay could not differentiate between attraction or aggregation. An "olfactometer" bioassay allowed worker contact with a cotton tipped swab through which volatiles from test samples were being passed, but since the cotton tipped swab could trap these volatiles aggregation was again a possibility. However, these assays were used to determine that the elicited behaviors were derived from compounds produced from the queen's poison sac (Vander Meer et al. 1980). The pyrone, (E)-6-(1-pentenyl)-2H-pyran-2-one (4), invictolide (5), and dihydroactinidiolide (6) were subsequently isolated and identified from whole queen extracts (Rocca et al. 1983a, Rocca et al. 1983b). A "disrupted colony" field bioassay was developed where a colony was dug into, and the soil, workers, and brood were placed in an observation tray. Surrogate queen (rubber septum) test treatments were placed in the tray and attraction, clustering, movement of brood around the surrogate queen, development of a "queen trail", and movement of the surrogate queen back into the nest were observed. Components 4 and 5 were clearly required for the behavioral response; however, the role of component 6 remains unclear (Glancey et al. 1984).



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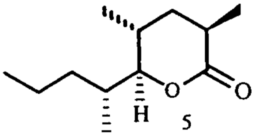

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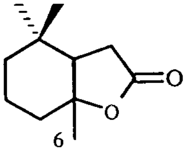

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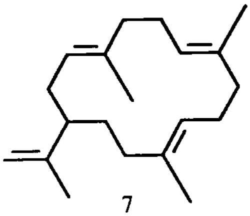
The other example comes from the pharaoh's ant, *Monomorium pharaonis*. Fertile queens produce (E,E,E)-1-isopropenyl-4,8,12-trimethylcyclotetradeca-3,7,11-triene (neocembrene) (Edwards and Chambers 1984). This compound is queen specific, produced in the Dufour's gland, and must be released through the sting. Neocembrene is attractive to Pharaoh's ant workers and *may* serve as a "queen recognition" pheromone.



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Fire ant queens deposit poison sac contents on their eggs as they are laid (Vander Meer and Morel, 1995). This marks the eggs with the queen/worker pheromone and antimicrobial alkaloids. The deposition process involves extension of the sting, movement of the egg to the base of the sting, where the sting is then drawn across the egg. Release of pheromone is related to the queen's egg-laying rate, thus the workers have a mechanism for assessing their queen's fecundity based on the amount of queen pheromone released. A relationship between the queen's fecundity and the magnitude of dealation inhibition has been demonstrated (Fletcher and Blum 1983). Fire ant queens treated with the insect growth regulator, fenoxycarb, do not lay eggs (Glancey and Banks 1988), nor do they inhibit dealation or attract workers (Obin et al. 1988). However, queen attractant was present in the poison sacs of fenoxycarb treated queens, but they were not releasing the pheromone because the egg laying process was stopped.

This egg laying behavior was also observed in *Monomorium pharaonis* (Vander Meer and Morel, 1995). Pharaoh's ant queens produce a worker attractant (see above) that is released through the sting (Edwards and Chambers 1984). Worker ant assessment of their queen's fecundity results in caste regulation by the workers. If the queen lays many eggs only workers are produced, but if the queen's egg production is low or the queen dies, sexuals are produced (Edwards 1987). Thus, the egg-laying process may be involved in queen / worker communication. *Iridomyrmex humilis* queens exhibit a significant increase in "queen power" when egg-laying commences (Cariouetienne and Passera 1993). A *Myrmica rubra* queen's "aggregative (queen recognition) power" was correlated with the sum of the diameters of eggs occupying the terminal zone of each ovariole, thus probably related to the egg production rate. There are many other examples (see Keller and Nonacs 1993; Hölldobler and Bartz 1985; Fletcher and Ross 1985) of a worker's ability to determine its queen's reproductive capability.

Alarm Pheromones

Alarm pheromones constitute a major evolutionary development for eusocial species that permits the collective resources of the colony to be rapidly exploited in response to stresses or perturbations to the colony (Blum 1985). Therefore, the function of alarm signals is not to ward off intruders or benefit the emitter, but to alert other members of the colony. Goetsch (1957) astutely pointed out that alarm signals themselves have no descriptive content, but merely transmit a state of excitement. What the alarmed ants do after receiving the alarm signal depends on other stimuli. It may be difficult to dissociate the other stimuli, thus alarm is often associated with attraction, recruitment, and defense (Hölldobler and Wilson 1990). These behaviors may be elicited by the alarm pheromones themselves, or may result from other chemicals released at the same time (Blum 1969). Gabba and Pavan (1970) suggest that alarm behavior is the initial stage of a complex of coordinated defensive acts. However, we believe that recognition of an object (animate or inanimate) as a non-nestmate represents the initiating process (see Vander Meer and Morel, this book).

Behavioral Responses to Alarm

Wilson and Regnier (1971) divided alarm behavior into two basic behavioral categories: "panic alarm," characterized by rapid non-directional movement and excited bursts of running, and "aggressive alarm," in which workers not only run excitedly but also move toward the source of the alarm substance, assume a defensive posture, and often attack.

In general, alarm behaviors differ between species (Hölldobler and Wilson 1990). In addition, it is often difficult to characterize alarm behaviors of even a single species because reactions vary with a multitude of factors (Parry and Morgan 1979). Alarm behaviors in some species consist only of attraction to the pheromone source or simply of raised heads and outstretched antennae (Table 7.1). Other species react with increased speed and orientation, frenzied erratic movement, or with aggressive behaviors such as spread mandibles, biting, stinging, and spraying of poison gland products (Table 7.1).

Reactions to alarm pheromones depend on pheromone concentration, the length of time workers are exposed to the alarm substance, as well as context (Gabba and Pavan 1970). Wilson (1958a) distinguished different behaviors released in *Pogonomyrmex badius* workers by low and high concentrations of its alarm pheromone. At low concentrations (10^{10} molecules/cm^3), ants moved toward the source of the pheromone while at higher concentrations ($>10^{11}$ molecules/cm^3) the ants reacted in an aggressive frenzy. Wilson and Bossert (1963) proposed a model of alarm pheromone diffusion in which receiving ants need to contact the inner, active space of the chemicals released to give a full reaction. If ants contact the chemicals at the periphery of the chemical plume, where the pheromone is less concentrated, their reaction may be lessened. This has been observed for several ant species, particularly for species in which several chemicals are involved in eliciting the alarm reaction. Each chemical has a different dispersion rate from the source (Regnier and Wilson 1968, Bradshaw et al. 1979a).

TABLE 7.1 Observed Alarm Behaviors of Workers and Related References

Alertness: Wave Antennae/ Raise Head
Wilson 1958a; Duffield et al. 1977; Blum et al. 1988.
Colony Disperses/ Runs From Nest
Leuthold and Schlunegger 1973; Janssen et al. 1995.
Attraction To Source Of Pheromone
Wilson 1962; Cammaerts et al. 1978, 1981, 1985; Cammaerts and Mori 1987; Kugler 1979; Blum 1985; Blum et al. 1988; Hölldobler et al. 1990.
Increased Speed Of Movement
Wilson 1958a; Cammaerts et al. 1978, 1981, 1983, 1985; Cammaerts and Mori 1987; Kugler 1979; Blum et al. 1988; Scheffrahn et al. 1984; Hölldobler et al. 1990.
Frenzied Running/Nondirectional Running/Increased Sinuosity
Goetsch 1957; Wilson 1958a; Bergstrom and Lofqvist 1970; Leuthold and Schlunegger 1973; Duffield et al. 1977; Scheffrahn et al. 1984; Tomalski et al. 1987.
Arrested Motion
Olubajo et al. 1980
Aggressive Posture (Mandible Gaping, Defensive Stance)
Wilson 1958a; Blum et al. 1988; Tomalski et al. 1987; Kugler 1979.
Aggression: Bite, Sting, Or Attack Alien Object
Duffield and Blum 1973; Leuthold and Schlunegger 1973; Kugler 1979; Blum 1985; Tomalski et al. 1987; Blum et al. 1988; Hölldobler et al. 1990.
Mark Intruder With Chemical
Blum 1985

The Context of Alarm

The context in which alarm is released adds another dimension to the definition of alarm behavior. Disturbance to the colony results in alarm, whether the disturbance is mechanical, chemical, or from an enemy or predator. The response of workers varies greatly in relation to the severity of the disturbance, the concentration of the chemicals released, as well as with the nature of the ant species. Alarm can also be released by ants that are in trouble, e.g. ants trapped under soil after a cave-in, to call for help from nestmates.

The age of the ant colony, the state of activity or inactivity of the workers, and many other factors can also affect the type and intensity of the alarm reaction (Gabba and Pavan 1970). This proves a problem for defining alarm with any precision. Instead of a tight definition, as can be used in recruitment reactions, a range of behaviors are generally included in the definition of "alarm behavior" (Table 7.1). For example, near the nest individuals usually are attracted to the odor source and display aggressive behaviors (Shorey 1973). Further away from the nest, the same species may behave differently, perhaps fleeing from the disturbance instead of confronting it (Shorey 1973).

Another problem defining alarm based behavior is that similar behaviors may be observed in contexts that do not involve danger or disturbance. For example, alarm behaviors documented in association with mating flights (See Mating Flight Activity section, this Chapter).

Alarm and Aggression

The release of alarm pheromones from mandibular and poison glands, both associated with defensive structures (mandibles and sting) led to the hypothesis that alarm pheromones may have evolved from defensive compounds (Wilson and Regnier 1971, Hölldobler and Wilson 1990). Species with large, densely concentrated colonies may not be able to disperse readily when disturbed. These species appear to have evolved to meet danger head on and attack the source of disturbance (Regnier and Wilson 1968). Ant species with small, mobile colonies often disperse (Regnier and Wilson 1968) or freeze (Olubajo et al 1980) in response to disturbance or danger. Execution of these behaviors is facilitated by the ability of ants and other social insects to alert nestmates through alarm pheromones and then recruit others to the source, something that solitary animals cannot do.

In most cases aggression is triggered by an interaction of the pheromone stimulus with other appropriate stimuli coming from the intruding enemy (Shorey 1973). However, some authors report that the alarm pheromone alone can cause aggressive behavior (Moser et al. 1968, Regnier and Wilson 1968, Fales et al. 1972). When ants exhibit an aggressive alarm reaction they usually move towards the source of a disturbance where they attack alien objects (Wilson and Regnier 1971). Most bioassays that have shown aggressive reactions to alarm pheromones were conducted with test substances applied to alien material that could be contacted by the workers (e.g. Tomalski et al. 1987, Kugler 1979, Hölldobler et al. 1990). Bioassays that prohibited contact between the ants and a physical object usually resulted in rapid panic alarm or attraction to the source, but no defensive posture or attacking (e.g. Wilson 1958a, Duffield et al. 1977, but see Blum et al. 1968). This suggests that in addition to the alarm pheromone, physical contact may be required for aggressive behavior to occur. To explain why aggressive behavior is not directed toward nestmates, Tricot et al.

(1972) proposed that the alarm pheromones of *Myrmica rubra* may be comprised of inhibitory and stimulative components that direct the aggressiveness of alarmed workers toward the cause of the disturbance instead of toward the worker emitting the alarm pheromone.

Bioassays Used to Detect "Alarm"

A wide range of behavioral bioassays have been used in the laboratory to show alarm behaviors in different ant species and to determine the source and chemical compounds responsible for eliciting alarm reactions. The bioassays are usually conducted on ant colonies housed in the laboratory with tests occurring in a foraging arena attached to the colony's nest tray. Few assays are conducted on colonies in their natural setting (but see Adams 1994 and Janssen et al. 1995). Development of a quick, quantifiable, and reproducible bioassay is essential for pheromone isolation and identification. There have been few studies that start with investigation of natural alarm behaviors, and then identify the chemical releaser. However, there have been several studies that first identify a chemical compound from an ant gland and then try to determine what behaviors the compound(s) elicits. The two approaches are not the same.

Most assays test substances presented to ants on a substrate such as a small filter paper disc that the ants are allowed to contact (Morgan et al. 1978; Cammaerts et al. 1978, 1981, 1983, 1985, 1988; Bradshaw et al. 1975, 1979a, 1979b; Kugler 1979; Blum et al. 1981; Scheffrahn et al 1984; Tomalski et al. 1987; Blum et al. 1988; Scheffrahn and Rust 1989; Hölldobler et al. 1990). In another type of assay, test materials are presented on a substrate that is held or pinned above the ants so that the ants do not come in direct contact with the substrate or test material (Wilson 1958a, Leuthold and Schlunegger 1973, Duffield et al. 1977, Duffield et al. 1980, Olubajo et al. 1980, Pasteels et al. 1989). Other bioassays involve holding a crushed body part directly over a group or trail of workers (Duffield et al. 1980) or applying a test solution onto paper that covers the floor of the foraging arena of an ant colony (Adams 1994). Blum et al. (1968) used a bioassay set-up in which air was drawn at a constant rate over the test material before it reaches ants enclosed in a small arena. Janssen et al. (1995) presented test chemicals on wooden applicator sticks that were inserted into the soil at nest openings of a laboratory contained colony. Alonso and Vander Meer (et al.) used a syringe to draw air from vials containing test samples. They then applied this air to small groups of workers.

Most alarm pheromone studies have not quantified the alarm response. In fact, many studies do not report how they analyzed the alarm reaction but simply state that alarm behavior was observed (Bergstrom and Lofqvist 1970; Duffield et al. 1977, 1980; Blum et al. 1968; Blum et al. 1981; Blum et al. 1988; Pasteels et al. 1989). However, assays have been developed to quantify the alarm reaction of workers. The work of Cammaerts and colleagues on ants in the genera *Myrmica* and *Manica*, may be the most precise. They measured the increase in linear and angular speed of workers exposed to alarm substances and measured the orientation of worker movement by calculating the angles between the workers' course and a direct line to the stimulus (Cammaerts et al. 1978, 1981, 1983, 1985, 1988; Morgan et al. 1978; Cammaerts and Mori 1987). Other methods of quantifying alarm have included counting the number of ants that aggregate at test substance vs. the number at the control (Tomalski et al. 1987, Scheffrahn and Rust 1989, Hölldobler et al. 1990, Adams 1994), time that workers stay at the substance (Tomalski et al. 1987), number of workers that move in response to the test substance (Olubajo et al. 1980, Salzemann et al. 1992), time to and duration of movement (Wilson 1958a), number of ants that are attracted or repelled by the substance or that attack the substance (Bradshaw et al. 1975, 1979a, 1979b; Kugler 1979), the number of ants leaving their nest (Janssen et al. 1995), or evaluation of responses on an alarm scale (from no reaction to full alarm reaction; Leuthold and Schlunegger 1973, Alonso and Vander Meer (In press).

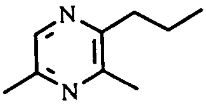
Glandular Sources of Alarm Pheromones

The glandular sources of alarm pheromones have been identified from seven of the 11 extant subfamilies of ants, with some similarity between subfamilies in the sources and chemistry of the alarm pheromones. Ant species in the Dolichoderinae release alarm substances only from their pygidial glands (=supra-anal or anal glands?) (Parry and Morgan 1979). Alarm substances have so far been found only from the mandibular glands of ants in the Ecitoninae (Brown 1960, Torgerson and Akre 1970) and Pseudomyrmecinae (Blum 1969). In contrast, alarm substances are released from the mandibular gland, Dufour's gland, and poison gland in ant species of the Formicinae and Myrmecinae (Parry and Morgan 1979). Ants in the Myrmeciinae release alarm compounds from their mandibular glands, Dufour's glands, and rectal glands (Blum 1969, Parry and Morgan 1979). In these subfamilies, full alarm behavior sometimes is released only by a combination of chemicals from multiple glandular sources (Blum 1969).

Chemistry and Concentration of Alarm Pheromones

As predicted by Bossert and Wilson (1963), chemicals that elicit alarm reactions typically are in the C5-C10 range and have a molecular weight of 100-200. These chemicals volatilize rapidly and most have a boiling point between 151-263°C (Blum 1969). Hölldobler and Wilson (1990; Table 7.4) provide an excellent tabular review of ant alarm pheromones. Alarm signals usually require an immediate and quick response to a perceived danger, which should not last long. Thus, alarm pheromones are likely released as a quick puff, with a short fade time (Bossert and Wilson 1963). Wilson and Bossert (1963) hypothesized that alarm pheromones have an "active space" in which the concentration of the volatile compounds are at or above the threshold to release alarm behaviors. As pheromone diffuses through space the concentration diminishes, finally falling below the response threshold (Regnier and Wilson 1968). They also developed models that could predict the threshold concentration of alarm substances in the air. Using these models they estimated that alarm pheromones in the ant *Acanthomyops claviger* had a threshold concentration of 10^{10}-10^{12} molecules/cm^3 and that of *Pogonomyrmex badius* to be about 10^{13} molecules/cm^3. Using a different method, Moser et al. (1968) estimated the detection threshold of *Atta texana* to be approximately 10^6 molecules/cm^3 and the alarm threshold to be 10^8 molecules/cm^3.

Alarm pheromones represent a wide range of chemical structures including terpenoids, alcohols, aldehydes, ketones, esters, nitrogen heterocycles, and even sulfur containing compounds. Examples are shown below (see also Figure 1.19, Chapter 1, this book). Pyrazine nitrogen heterocycles and sulfur compounds have been found in the Ponerinae, e.g. 2-6-dimethyl-3-propylpyrazine (**8**) from *Odontomachus brunneus* (Wheeler and Blum 1973) and dimethyl disulfide (**9**) from *Paltothyreus tarsatus* (Casnati et al. 1967). Cyclic ketones have been found in Dolichoderinae, e.g. 2-methyl cyclopentanone (**10**) from *Azteca* spp. (Wheeler et al. 1975). Like the previous types of compounds, terpenoids appear to be more specific to subfamily, in this case, Formicinae. Geraniol (**11**) is found in *Cataglyphis* spp. (Hefetz 1985) and *Oecophylla longinoda* (Bradshaw et al. 1975). Other classes of compounds may be found in several subfamilies. For example, aldehydes (hexanal, **12**; *Oecophylla longinoda*; Bradshaw et al. 1975), aliphatic ketones (3-decanone, **13**; *Manica bradleyi*; Fales et al. 1972, and 6-methyl-5-hepten-2-one, **14**; *Conomyrma pyramica*; McGurk et al. 1968; *Tapinoma melanocephalum*; Tomalski et al. 1987; and others). Esters (e.g. methyl anthranilate, **15**; *Aphaenogaster fulva* and *Xenomyrmex floridanus*; Duffield et al. 1980), and alcohols (e.g. 4-



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$H_3CS-SCH_3$

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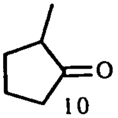

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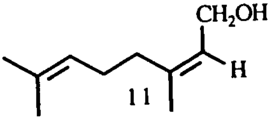

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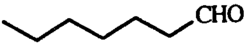

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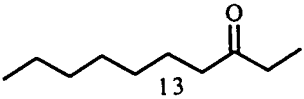

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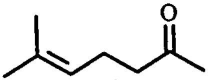

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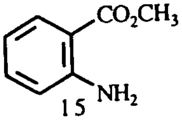

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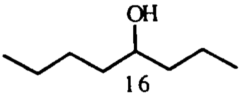

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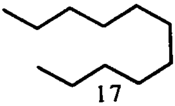

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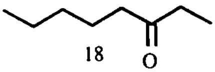
heptanol, **16**; *Zacryptocerus varians*; Olubajo et al. 1980), each occur in several different subfamilies. Formic acid is the only carboxylic acid that induces an alarm response and is found in several species, including *Polyrhachis* and *Cataglyphis* spp. (Hefetz and Orion 1982). The hydrocarbon n-undecane (17) is also found in several species, e.g. *Cataglyphis* spp. (Hefetz and Orion 1982).

Specificity of Alarm Pheromones

Alarm pheromones are generally considered to be the least species-specific of all pheromone classes (Blum 1969, Parry and Morgan 1979). Many of the same alarm compounds are found in a number of ant species, even multiple subfamilies (Hölldobler and Wilson 1990; Table 7.4) and a compound can often cause an alarm reaction in species other than the one in which it was found. As many researchers have pointed out, it would seem to be a defensive advantage to an ant colony to be able to detect the alarm pheromone of other ant species, as well its own (Blum 1969, Wilson 1971, Parry and Morgan 1979). However, the advantage would only be realized in species that were sympatric and competed for territory and resources. On the other hand, an equally justified case can be made for species-specific alarm pheromones. In fact, it has been shown that some ant species react with full alarm only to their natural alarm pheromone and not to closely related chemical compounds (Blum 1969, Parry and Morgan 1979). When *Iridomyrmex pruinosis* was exposed to its natural alarm substance as well as other compounds with similar physical properties, full alarm behavior was released by the natural substance, a lesser response was observed to related substances and no response to unrelated compounds.

Cammaerts et al. (1978, 1981, 1983, 1985) isolated chemicals from the mandibular glands of *Myrmica* species that function as alarm pheromones. They found that the mandibular glands of six *Myrmica* species contained 3-octanone (**18**) and 3-octanol (**19**), but in different proportions between species (Crewe and Blum 1970). Furthermore, the alarm response of each species depended on different ratios and mixtures of the two chemicals. 3-Decanol (**20**) was required in *M. lobicronis* (Cammaerts et al. 1983) and *M. scabrinodis* (Morgan et al. 1978) to produce a full alarm reaction that included orientation toward the source. The six *Myrmica* species were differentiated based on their mandibular gland chemistry and alarm responses. In *M. rubra, M. ruginodis, M. lobicornnis,* and *M. sulcinodis*, 3-octanone (**18**) attracted and increased speed in workers, with 3-octanol (**19**) acting as a synergist (Cammaerts et al. 1978, 1981). In contrast, 3-octanol (**19**) caused attraction and increased movement in *M. scabrinodis* and *M. sabuleti* (Cammaerts et al. 1978, 1981, 1983). Chemicals from multiple glands in one species were found to contain alarm compounds, with chemicals from the mandibular gland, Dufour's gland, and venom gland necessary to cause a full alarm reaction in *Myrmica rubra* (Tricot et al. 1972, Cammaerts-Tricot 1974). Earlier, the ant, *Myrmica rubida*, was identified by its mandibular gland chemistry to differ significantly from other *Myrmica* species and was subsequently placed in the genus *Manica* (Maschwitz 1966). Further studies are needed to determine the relative frequency of specific versus general alarm pheromones in ants.



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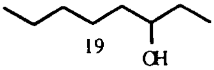

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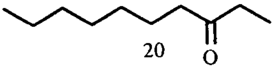

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We anticipate that future research in ant alarm pheromones will focus on a critical definition of the behavior to be measured, e.g. distinguish between attraction, repellency, aggressive alarm, and passive alarm. Emphasis will be on developing close links between behavior and chemistry -- with a behavioral assay guiding the chemical isolation. Also, it will be interesting to see whether or not the instances where alarm pheromones lack specificity, impart advantages or disadvantages to the ants in real world situations.

Brood Pheromones

By definition a brood pheromone is a chemical or mixture of chemicals released by immature stages that elicits a behavioral response in conspecific adults. There are several reported behavioral responses associated with brood pheromones: (1) Brood recognition -- worker ants recognize the various immature stages (Le Masne 1953). This implies that each immature stage is recognized by workers through differences in its surface chemistry (pheromones); (2) Attraction -- brood release a volatile pheromone that attracts adults (Glancey and Dickens 1988); (3) Aggregation -- Worker ants cluster around a brood pheromone that has a settling affect on the workers (Watkins and Cole 1966); and (4) Brood-tending -- a general term for feeding, grooming, and when a nest is disturbed, brood retrieval.

Brood pheromone literature prior to 1988 was critically reviewed by Vander Meer and Morel (1988; see also Morel and Vander Meer 1988). They identified several problems in demonstrating the existence of brood pheromones, such as bioassay inadequacy due to confounding food responses and aggregation with brood retrieval and attraction, respectively. Other problems revolved around the reliability of controls, lack of quantitation, and/or inappropriate chemical techniques. The interspecific adoption of brood is widely reported (Jaisson 1971). This creates a basic problem, since by definition a pheromone is a substance that causes a specific behavioral or physiological reaction in a receiving organism of the same species (Nordlund and Lewis 1976). Brood from one species may receive similar differential treatment from workers of several species. Are there alternative non-pheromonal explanations?

Vander Meer and Morel (1988) offer an explanation for the differential treatment of brood that does not involve pheromones. The hypothesis is based on (1) reports that the basic immature stages (egg, larvae, pupae) are often morphologically distinguishable (Robinson and Cherrett 1974; Brian 1975; Petralia and Vinson 1979); (2) unlike workers, brood are immobile and lack the ability for agonistic display, thus it is predicted that con- or hetero-specific worker aggression toward brood should be significantly less then toward other workers; (3) the cuticular chemistry comprising nestmate recognition cues, changes continuously; (4) the developmental stages can offer a reward to workers through regurgitation or secretions. Thus, the lack of brood/worker aggression allows newly introduced interspecific brood time to acquire their new colony's recognition profile. Associative learning based on the above characters (morphological, behavioral and chemical) and a reward, provide the basis of the non-pheromone differential treatment of brood by workers. For details see Vander Meer and Morel 1988).

What Is New in Brood Pheromones

Carlin (1988) states in his review of brood discrimination in ants that there are strong generalized brood stimuli, these stimuli are similar enough to facilitate acceptance across kin, colony and species categories; and there is sufficient variation in brood stimuli so that non-exclusive discrimination of kin, nestmates and species can occur.

The purpose of the Vander Meer and Morel (1988) review was to stimulate interest and research on brood pheromones; however, the past seven years have not brought us closer to the identification of a brood pheromone. *Rhytidoponera confusa* workers could not distinguish between their own larvae and conspecific or allospecific larvae (Crosland 1988). Similarly, slave-making ant, *Formica sanguinea,* workers cared for homo- and heterospecific (slave *Formica cunicularia*) cocoons without preference, regardless of the early social experience of *F. sanguinea* (Mori et al. 1992).

The pre-imaginal experience of workers in *Camponotus floridanus* influenced nestmate brood recognition for only a short time, after which, no preference in conspecific brood was observed (Carlin and Schwartz 1989). Similarly, teneral *Ectatomma tuberculatum* worker experience has a temporary effect on their brood discrimination (Fénéron and Jaisson 1995). This illustrates the transient nature of pre-imaginal and early adult experience. Brood tending *Ectatomma tuberculatum* workers (2-10 weeks old) preferentially tend nestmate rather than non-nestmate brood, however, older workers (>10 weeks) showed no preference (Fénéron and Jaisson 1992; 1995).

Workers from queenright *Monomorium pharaonis* colonies accept conspecific worker larvae, but cannibalize nestmate and introduced conspecific sexual larvae (Edwards and Abraham 1991). If the queens are absent, sexual brood are allowed to develop and conspecific sex brood are accepted. Worker larvae are covered with bifurcated hairs, whereas sexual larvae are hairless. The author suggests that this morphological difference may allow workers to differentiate between sexual and worker larvae.

The bottom line is we are still awaiting definitive experimental evidence for brood pheromones or alternative explanations.

Recruitment Pheromones

Ants have evolved a wide variety of mechanisms for recruitment and orientation using pheromones. One of the least complicated is tandem running, exemplified by *Leptothorax* spp. (Möglich et al. 1974). After finding a food source and returning to its nest a scout worker raises its gaster and releases poison sac contents through its extended sting. As soon as an attracted worker contacts the scout "tandem running" begins. The recruited worker closely follows and maintains contact with the scout by touching the gaster and hind legs. In this case the poison gland is the source of the pheromone; however, in *Pachycondyla obscuricornis* (Traniello and Hölldobler 1984) tandem running is mediated by pheromones released by the pygidial gland. In these examples, orientation pheromones are not needed. Going up the complexity ladder is *Camponotus socius*, whose scouts lay a chemical trail from the hindgut, then they perform a mechanical waggle that can induce tens of other workers to follow the initiating scout back to the food source (Hölldobler 1971b). In other species, e.g. *Formica fusca*, scouts lay an orientation trail back to their nest and use a mechanical waggle to excite and induce nestmates to follow that trail unaided by the originating scout (Möglich and Hölldobler 1975). Analogous to the latter system is that of *Solenopsis invicta*, except that pheromones released by the Dufour's gland are responsible for orientation (Vander Meer et al. 1981), attraction (Vander Meer et al. 1988), and orientation induction (Vander Meer et al. 1990). The recruitment system of the weaver ant, *Oecophylla longinoda* (Hölldobler and Wilson 1978), is extremely complicated and uses at least five different systems. There is long range recruitment to intruders, invoked by rectal gland odor trails and by antennation and jerking physical cues; short range recruitment to territorial intruders where the pheromones are produced by the sternal gland; recruitment to new terrain elicited by pheromones produced from the rectal gland and the tactile stimulus of antennation; recruitment to new food sources, that is mediated by trail pheromones produced by the rectal gland and modulated by tactile stimuli; and finally emigration to new sites (Hölldobler and Wilson 1978).

Glandular Sources

Recruitment pheromones are diverse in orgin, although almost all are derived from abdominal exocrine glands. The glands thus far identified as sources of recruitment pheromones are the (1) poison, (2) Dufour's, (3) cloacal, (4) hindgut, (5) pygidial, (6) rectal, (7) sternal, and (8) tibial glands (see Chapter 1, this book for illustrations, and Hölldobler and Wilson [1990] for specific citations). In most species the recruitment pheromones are from a single glandular source; however, multiple glands may be involved. For example, *Megaponera foetens* uses products from the pygidial gland to recruit workers, and poison gland secretions for a long lasting orientation effect (Hölldobler et al. 1994b). The variety of sources leads to a complex variety of structures.

The Chemistry of Recruitment Pheromones

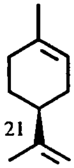
There has been significant activity in the isolation and identification of recruitment pheromones in the last five to six years. Thus, this section will only deal with recruitment pheromones reported since Hölldobler and Wilson (1990) and the reader is referred to the latter reference and to Chapter 1, this book, for additional information.

Scout ants of *Myrmicaria eumenoides* release a recruitment pheromone from their poison gland via the sting (Kaib and Dittebrand 1990). In this species when the scout worker finds prey or an enemy, it recruits other workers to the site of encounter with an attractant pheromone. The major volatile compound from the poison sac was determined to be (+)-limonene (**21**). This compound by itself induced the alarm recruitment observed with the whole gland extract. There is also an alkaloid dominant fraction of lower volatility that may serve to regulate the release rate of the volatile limonene. This species applies venom to prey or enemy, instead of injecting the venom. So for prey suppression or defense the limonene helps the venom components penetrate the cuticle of prey or enemy.

The trail pheromone of *Tetramorium meridionale* consists of four pyrazines: methylpyrazine (**22**), 2,5-dimethylpyrazine (**23**), trimethylpyrazine (**24**), and 3-ethyl-2,5-dimethylpyrazine (**25**) and indole (**26**). As in the previous example the source of this pheromone blend is the poison gland. The pyrazines (1-10 pg each per individual) and indole (ca 1 ng per individual) work together synergistically (Jackson et al. 1990). Indole (**26**) and trimethylpyrazine (**24**) each release some trail following behavior, but at a much weaker level then the mixture of pyrazines and indole.

In contrast to the above, the source of *Tapinoma simrothi*'s trail pheromone is the pygidial gland (Simon and Hefetz 1991). Interestingly, the pygidial gland also has been reported to be the source of alarm pheromones for this species (Hefetz and Lloyd 1983). Iridomyrmecin (**27**) and iridodials (**28**) were found to elicit both alarm and trail following behavior, depending on the concentration and whether the compounds were released from a point source or streaked as a trail. The higher concentration released alarm, while lower concentrations released trail following (Simon and Hefetz 1991). This is a good example of context (and concentration) dependent behaviors derived from the same glandular source and products.

After finding appropriate prey, *Leptogenys diminuta* scouts lay a chemical trail back to their nest using poison and pygidial gland secretions. The scout enters the nest and recruits many workers, then leads them to the prey along the trail (Wilson 1958b). The (3R,4S) 4-methyl-3-heptanol (**29**) isomer elicits trail following. The other three stereoisomers were not present in poison gland extracts, but neither did they interfere with the activity of the natural isomer when a synthetic mixture of all four possible isomers was presented to the ants (Attygale et al. 1988; Steghaus-Kovâc et al. 1992). The recruitment part of the system is associated with the pygidial gland, and *cis*-isogeraniol (**30**) was identified as the active agent (Attygale et al. 1988; 1991). Electrophysiology studies (Kern and Bestmann 1993) clearly showed the selective activity of trail pheromone component (**29**) and that only recruitment pheromone (**30**) was detected by the ant's antennae among several isomers presented to the ants. The electroantennagram results were much more definitive than the behavioral assays and is illustrative of how useful this technique can be in cutting through chemical complexity. This is a complex recruitment system, utilizing products from two exocrine glands.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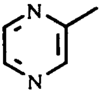

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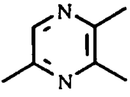

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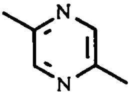

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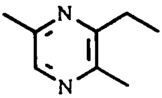

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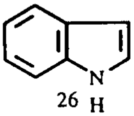

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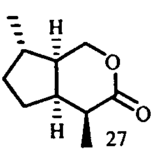

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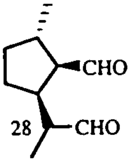

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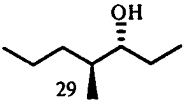

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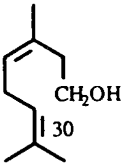

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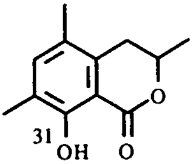

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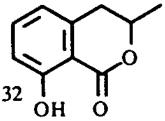

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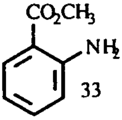

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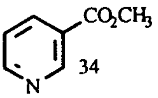

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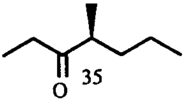

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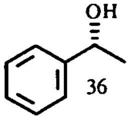

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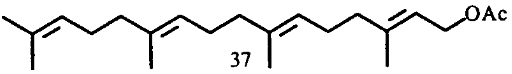

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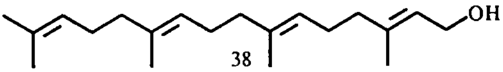

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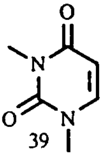

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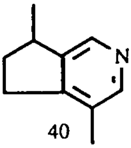

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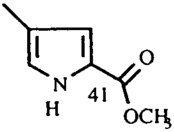

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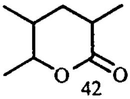
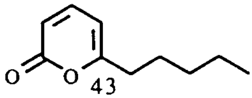


42



43

A new class of trail pheromone was reported from *Lasius niger* (Bestmann et al. 1992). The pheromone is produced in the rectal sac and was determined, at least in part, to be (R) 3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin (**31**). The related isocoumarin, mellein (**32**), was isolated from the rectal sacs of *Formica rufa*. This compound elicited trail following in *F. rufa* workers (Bestmann et al. 1992).

Army ants are blind, yet carry out sophisticated foraging raids, which have been assumed to be chemically mediated. Oldham et al. (1994) reported the first chemical dissection of this process using an *Aenictus* species. The source of the pheromone is the postpygidial gland, which contains at least two active components. Interestingly this system is analogous to the orientation, attraction, orientation primer situation in *Solenopsis invicta* (Vander Meer et al. 1981; 1988; 1990; Alvarez et al. 1987), where the sub-categories of recruitment are released by different pheromones from the Dufour's gland for *S. invicta*. For this *Aenictus* species, methyl anthranilate (**33**) released trail orientation behavior, but only if the workers ants had already been following a natural trail. Further chemical analysis and behavioral bioassays revealed that methyl nicotinate (**34**) acted in concert with component **33** to prime or induce workers to follow the trail. By itself (**34**) had no behavioral effect. This example and that of *S. invicta* illustrate the potential chemical and behavioral complexity of the recruitment process.

Hölldobler et al. (1995) investigated the recruitment pheromones from *Aphaenogaster albisetosus* and *A. cockerelli*. The pheromone is derived from the poison gland and is composed of (S) and (R)-4-methyl-3-heptanone (**35**, S structure shown) in a ratio of 8:2 for *A. albisetosus*. However, *A. cockerelli*'s trail pheromone is (R)-1-phenylethanol (**36**); however, (S)-4-methyl-3-heptanone (**35**) is also present. These results explain the asymmetric interspecific trail following results previously reported (Hölldobler et al. 1978). *A. cockerelli* only follows its own trail, since *A. albisetosus* does not produce compound **36**, whereas *A. cockerelli* follows the *A. albisetosus* trail due to the presence of compound **35**. It should be noted that these classes of compounds are not usually produced by poison glands. This is an interesting case where vibrational signals are used by scouts in the nest to prime or modulate the recruitment process (Markl and Hölldobler 1978).

Bestmann and co-workers (1995a) isolated all-*trans* geranylgeranyl acetate (**37**) and the corresponding alcohol (**38**) from the Dufour's glands of *Ectatomma ruidum*. Both compounds generated electroantennogram responses, but the acetate response was more pronounced. Similarly, orientation bioassays of the two compounds at physiological concentrations showed that the acetate performed significantly better than the alcohol. The acetate then, is considered the main trail pheromone component.

Two interesting compounds, N,N-dimethyluracil (**39**) and actinidine (**40**) were isolated from the poison and pygidial glands, respectively, of *Megaponera foetens* (Jannsen et al. 1995). A combination of electroantennogram and behavioral bioassays was used to monitor biological activity. Electroantennogram results showed compounds **39** and **40** to be significantly active; however, behavioral assays could only establish a trail following role for **39**. Actinidine (**40**) caused worker excitement, but did not elicit the recruitment observed with whole pygidial gland extracts. This is another complex recruitment system involving compounds from at least two glandular sources.

The first trail pheromone was isolated and identified by Tumlinson et al. (1971), as methyl 4-methylpyrrole-2-carboxylate (**41**) from *Atta texana*. Subsequently, this compound was identified as the trail pheromone of other leaf-cutting ant species, as was 3-ethyl-2,5-dimethylpyrazine (**25**) (Cross et al. 1979). Do Nascimento et al. (1994) added to our knowledge of this economically important group by identifying compound **41** as the sole trail pheromone component from *Acromyrmex subterraneus subterraneus*. No pyrazines could be detected and when pyrazines were assayed with compound **41**, no enhanced activity was observed.

Many carpenter ant species are well known pests and have been studied extensively (see below). It was only recently that the recruitment pheromone of a carpenter ant species was identified from hindgut extracts (Bestmann et al. 1995b). The carpenter ant, *Camponotus herculeanus,* was found to use 2,4-dimethyl-5-hexanolide (**42**) as a trail orientation pheromone component. This compound has three asymmetric centers and of the four possible diastereomer pairs, two were found in the natural material.

Of note are two recent papers that have reinvestigated early investigations of the trail pheromones of *Lasius fuliginosus* (Huwyler et al. 1975) and *Pristomyrmex pungens* (Hayashi and Komae 1977). Both initial papers report the trail pheromones as a series of short chain fatty acids. Quinet and Pasteels (1995) investigated the trail following behavior of a myrmecophilous staphyinid beetle, *Homeusa acuminata,* whose host is *Lasius fuliginosus*. The authors demonstrated that the beetles and ants follow artificial trails of hindgut extracts at 0.03 hindgut equivalents/cm. However, when experiments were conducted with the reported six straight chain fatty acids (Huwyler et al. 1975; C_6-C_{10} + C_{12}), neither the ants or the beetles responded to physiological levels. The ants only followed trails containing very high fatty acid concentrations, ca. 3 x 10^3 hindgut equivalents/cm

(Quinet and Pasteels 1995). Thus either the fatty acids are not acting as trail pheromone components or other unidentified compounds are acting synergistically in concert with the carboxylic acids.

In a second paper Hayashi and Komae (1977) isolate fatty acids from whole *Pristomyrmex pungens* worker extracts. The carboxylic acid fraction was active in a trail bioassay and contained typical fatty acids found in animal tissue ($C_{14:0}$, $C_{16:0}$, $C_{16:1}$, $C_{18:0}$, $C_{18:1}$, $C_{18:2}$, $C_{18:3}$, $C_{20:5}$, and $C_{20:5}$). Janssen et al. (1997) reinvestigated the trail pheromone of *P. pungens* and found that the source of the trail pheromone is the poison gland. They further isolated an active compound, 6-*n*-amyl-2-pyrone (**43**), by bioassay, electroantennograms, and chemical analyses. Thus, in this case it is clear that the fatty acids originally reported (Hayashi and Komae 1977) are not involved as trail pheromone components.

As evidenced by the chemical structures and the above references, over the past five years there has been a tremendous amount of activity in elucidating the chemistry and behavior of ant recruitment pheromones.

Conclusion

Early work in ant pheromones centered primarily on alarm and other defensive semiochemicals, due to their greater abundance. However, in the past decade, with better instrumentation and new techniques, we have seen excellent progress in other aspects of ant pheromone chemistry, especially the recruitment pheromones. Yet what has been accomplished is not even the tip of the ant pheromone iceberg. We anticipate progress to continue at an accelerated rate in the years to come and look forward to new and exciting chemical ecology stories from the fascinating world of the ant.

References Cited

Adams, E.S., 1994. Territory defense by the ant *Azteca trigona*: maintenance of an arboreal ant mosaic. *Oecologia, 97*: 202-208.

Alonso, L. and R.K. Vander Meer, In press. Source of alate excitant pheromones in the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), *J. Insect Behavior.*

Alvarez, F. M., R.K. Vander Meer and C.S. Lofgren, 1987. Synthesis of homofarnesenes: Trail pheromone components of the fire ant, *Solenopsis invicta*. *Tetrahedron, 43:* 2897-2900.

Attygalle, A. B., O. Vostrowsky, H. J. Bestmann, S. Steghaus-Kovac and U. Maschwitz, 1988. (3R,4S)-4-Methyl-3-heptanol, the trail pheromone of the ant *Leptogenys dimminuta. Naturwissenschaften, 75*: 315-317.

Attygalle, A. B., S. Steghaus-Kovac, V. Ahmad, U. Maschwitz, O. Vostrowsky, and H. J. Bestmann, 1991. *cis*-Isogeraniol, a recruitment pheromone of the ant *Leptogenys dimminuta*. *Naturwissenschaften*. *78*: 90-2.

Bergstrom, G. and J. Lofqvist, 1970. Chemical basis for odour communication in four species of *Lasius* ants. *J. Insect. Physiol.* *16*: 2353-2375.

Bestmann, H. J., F. Kern, D. Schafer and M. C. Witschel, 1992. Pheromones 86. 3,4-dihydroisocoumarins, a new class of ant trail pheromones. *Angew. Chem. Int. Ed.* *31*: 795-796.

Bestmann, H.J., E. Janssen, F. Kern, B. Liepold and B. Hölldobler, 1995a. All *trans*-geranylgeranyl acetate and geranylgeraniol, recruitment pheromone components in the Dufour gland of the ponerine ant *Ectatomma ruidum*. *Naturwissenschaften*, *82*: 334-336.

Bestmann, H. J., U. Haak and F. Kern, 1995b. 2,4-Dimethyl-5-hexanolide, a trail pheromone component of the carpenter ant *Camponotus herculteanus*. *Naturwissenschaften* *82*: 142-144.

Billen, J.P. J., B.D. Jackson and E.D. Morgan, 1988. Secretion of the Dufour gland of the ant *Nothomyrmecia macrops* (Hymenoptera: Formicidae). *Experientia* *44*: 715-719.

Blum, M.S., 1969. Alarm pheromones. *Annu. Rev. Entomol.* *4*: 57-80.

Blum, M.S. , 1985. Alarm pheromones. In:, *Comprehensive Insect Physiology, Biochemistry, and Pharmacology* (Kerkut, G.A., and L.I. Gilbert, eds.) Vol. 9: Behaviour. Pergamon Press: New York. Pp. 193-224.

Blum, M.S., J.M. Brand and E. Amante, 1981. o-aminoacetophenone: identification in a primitive fungus-growing ant (*Mycocepurus goeldii*). *Experientia*, *37*: 816-817.

Blum, M.S., F. Padovani, H.R. Hermann, and P.B. Kannowski, 1968. Chemical releasers of social behavior, XI: Terpenes in the mandibular glands of *Lasius umbratus*. *Ann. Entomol. Soc. Am.*, *61*: 1354-1359.

Blum, M. S., L. Morel, and H. M. Fales, 1987. Chemistry of the mandibular gland secretion of the ant *Camponotus vagus*. *Comp Biochem Physiol B Comp Biochem* *86*: 251-252.

Blum, M. S., R.R. Snelling, R.M. Duffield, H.R. Hermann, and H.A. Lloyd, 1988. Mandibular gland chemistry of *Camponotus (Myrmothrix) abdominalis*: Chemistry and chemosystematic implications (Hymenoptera: Formicidae). In: *Advances in myrmecology*, (J. C. Trager, ed.) E. J. Brill, Leiden, pp. 481-490.

Bossert, W.H. and E.O. Wilson, 1963. The analysis of olfactory communication among animals. *J. Theor. Biol.* *5*: 443-469.

Bradshaw, J.W.S., R. Baker and P.E. Howse, 1975. Multicomponent alarm pheromones of the weaver ant. *Nature*, *258*: 230-231.

Bradshaw, J.W.S., R. Baker and P.E. Howse, 1979a. Multicomponent alarm pheromones in the mandibular glands of major workers of the African weaver ant, *Oecophylla longinoda*. *Physiol. Entomol.* *4*: 15-25.

Bradshaw, J.W.S., R. Baker, P.E. Howse, and M.D. Higgs, 1979b. Caste and colony variations in the chemical composition of the cephalic secretions of the African weaver ant, *Oecophylla longinoda*. *Physiol. Entomol.* *4*: 27-38.

Brand, J. M., R.M. Duffield, J.G. MacConnell, and M.S. Blum, 1973. Caste-specific compounds in male carpenter ants. *Science 179*: 388-389.

Breed, M.D., J.H. Fewell, A.J. Moore, and K.R. Williams. 1987. Graded recruitment in a ponerine ant. *Behav. Ecol. Sociobiol. 20*: 407-411.

Brian, M.V., 1975. Larval recognition by workers of the ant *Myrmica. Anim. Behav., 23*: 745-756.

Brown, W.L., 1960. The release of alarm and attack behavior in some New World army ants. *Psyche. 66*: 25-27.

Buschinger, A., 1976. Giftdrusensekret als Sexual-pheromon bei der Gastameise *Formicoxenus nitidulus* (Nyl.) (Hym., Form.). *Insectes Soc. 23*: 215-225.

Buschinger, A., and T.M. Alloway, 1979. Sexual behaviour in the slave-making ant, *Harpagoxenus canadensis* M. R. Smith, and sexual pheromone experiments with *Harpagoxenus canadensis, Harpagoxenus americanus* (Emery), and *Harpagoxenus sublaevis* (Nylander) (Hymenoptera; Formicidae). *Z. Tierpsychol. 49*: 113-119.

Cammaerts-Tricot, M.C., 1974. Recrutement d'ouvrieres, chez *Myrmica rubra,* par les pheromones de l'appareil a venin. *Behaviour, 50*: 111-122.

Cammaerts, M-C. and K. Mori, 1987. Behavioural activity of pure chiral 3-octanol for the ants *Myrmica scabrinodis* Nyl. and *Myrmica rubra* L. *Physiol. Entomol. 12*: 381-385.

Cammaerts, M.C., M.R. Inwood, E.D. Morgan, K. Parry and R.C. Tyler, 1978. Comparative study of the pheromones emitted by workers of the ants *Myrmica rubra* and *Myrmica scabrinodis. J. Insect Physiol. 24*: 207-214.

Cammaerts, M.C., R.P. Evershed and E.D. Morgan, 1981. Comparative study of the mandibular gland secretion of four species of *Myrmica* ants. *J. Insect Physiol. 72*: 225-231.

Cammaerts, M.C., R.P. Evershed and E.D. Morgan, 1983. The volatile components of the mandibular gland secretion of workers of the ants *Myrmica lobicornis* and *Myrmica sulcinodis. J. Insect Physiol. 29*: 659-664.

Cammaerts, M.C., A.B. Attygalle, R.P. Evershed, and E.D. Morgan, 1985. The pheromonal activity of chiral 3-octanol for *Myrmica* ants. *Physiol. Entomol. 10*: 33-36.

Cammaerts, M.C., A.B. Attygalle, O. Vostrowsky and H.J. Bestmann, 1988. Ethological studies of the mandibular gland secretion of the ant *Manica rubida* (Formicidae: Myrmicinae). *J. Insect Physiol. 34*: 347-350.

Cariouetienne, A., S. Aron and L. Passera, 1992. Queen attractivity in the Argentine ant *Iridomyrmex humilis* (Mayr.). *Behav. Process. 27*: 179-186.

Cariouetienne, A. and L. Passera, 1993. Queen power in relation to age and mating status in the argentine ant *Iridomyrmex humilis* (Mayr). *Insectes Sociaux 40*: 87-94.

Carlin, N.F. 1988. Species, kin and other forms of recognition in the brood discrimination behavior of ants. In:, *Advances in myrmecology*, 551 p. (J. C. Trager, Ed.) E.J. Brill, New York, pp. 267-295.

Carlin, N.F. And P.H. Schwartz, 1989. Pre-imaginal experience and nestmate brood recognition in the carpenter ant, *Camponotus floridanus*. *Anim. Behav. 38*: 89-95.

Casnati, G., A. Ricca and M. Pavan, 1967. Sulla secrezione difensiva delle glandole mandibolari di *Paltothyreus tarsatus* (Fabr.) (Hymenoptera: Formicidae). *Chimica e l'Industria (Milano) 49*: 57-58.

Cavill, G.W.K. and E. Houghton, 1974. Volatile constituents of the Argentine ant, *Iridomyrmex humilis*. *J. Insect Physiol. 20*: 2049-2059.

Crewe, R. M. And M.S. Blum, 1970. Alarm pheromones in the genus *Myrmica* (Hymenoptera: Formicidae). their composition and species specificity. *Z. Vgl. Physiol., 70*: 363-373.

Crosland, M. W. J., 1988. Inability to discriminate between related and unrelated larvae in the ant *Rhytidoponera confusa* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am., 81*: 844-850.

Cross, J.H., R.C. Byler, U. Ravid, R.M. Silverstein, S.W. Robinson, P.M. Baker, J. Sabino de Oliveira,A.R. Jutsum, and M.J. Cherrett, 1979. The major component of the trail pheromone of the leaf-cutting ant, *Atta sexdens rubropilosa* Forel. 3-ethyl-2,5-dimethylpyrazine. *J. Chem. Ecol.5*: 187-203.

do Nascimento, R.R. , B.D. Jackson, E.D. Morgan, W.H. Clark and P.E. Blom, 1993a. Chemical secretions of two sympatric harvester ants, *Pogonomyrmex salinus* and *Messor lobognathus*. *J. Chem Ecol.19*: 1993-2005.

do Nascimento, R.R., E.D. Morgan, J. Billen, E. Schoeters, T.M.C. Della Lucia and J.M.S. Bento, 1993b. Variation with caste of the mandibular gland secretion in the leaf-cutting ant *Atta sexdens rubropilosa*. *J. Chem. Ecol. 19*: 907-918.

do Nascimento, R.R., Morgan, D.D.O. Moreira and T.M.C. Della Lucia, 1994. Trail pheromone of the leaf-cutting ant Acromyrmex subterraneus subterraneus (Forel). *J. Chem. Ecol. 20*: 1719-1724.

Duffield, R.M. and M.S. Blum, 1973. 4-Methyl-3-Heptanone: Identification and function in *Neoponera villosa* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Amer. 66*: 1357.

Duffield, R.M. and M.S. Blum, 1975. Identification, role, and systematic significance of 3-octanone in the carpenter ant, *Camponotus schaefferi* Whr. *Comp. Biochem. Physiol. 51B*: 281-282.

Duffield, R.M., J.M. Brand and M.S. Blum, 1977. 6-methyl-5-hepten-2-one in *Formica* species: identification and function as an alarm pheromone (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am. 70*: 309-310.

Duffield, R.M., J.W. Wheeler and M.S. Blum, 1980. Methyl anthranilate: identification and possible function in *Aphaenogaster fulva* and *Xenomyrmex floridanus*. *Florida Entomol. 63*: 203-206.

Edwards, J. P. 1987. Caste regulation in the pharaoh's ant *Monomorium pharaonis*: the influence of queens on the production of new sexual forms. *Physiol. Entomol. 12*: 31-39.

Edwards, J.P. and J. Chambers, 1984. Identification and source of a queen-specific chemical in the Pharaoh's ant, *Monomorium pharaonis* (L.). *J. Chem. Ecol. 10*: 1731-47.

Edwards, J.P. and L. Abraham, 1991. Caste regulation in the pharaoh's ant *Monomorium pharaonis*: recognition and cannibalism of sexual brood by workers. *Physiol. Entomol. 16*: 263-271.

Evesham, E.J.M. 1984. The attractiveness of workers towards individual queens of the polygynous ant *Myrmica rubra* L. *Biol. Behav. 9*: 144-156.

Fales, H.M., M.S. Blum, R.M. Crewe and J.M. Brand, 1972. Alarm pheromones in the genus *Manica* derived from the mandibular gland. *J. Insect Physiol. 18*: 1077-1088.

Fénéron, R. and P. Jaisson, 1992. Nestmate brood recognition among workers of different social status in *Ectatomma tuberculatum* Olivier (Formicidae, Ponerinae). *Behav. Process. 27*: 45-52.

Fénéron, R. and P. Jaisson, 1995. Ontogeny of nestmate brood recognition in a primitive ant, *Ectatomma tuberculatum* olivier (Ponerinae). *Anim. Behav. 50*: 9-14.

Fletcher, D.J.C. and M.S. Blum, 1983. The inhibitory pheromone of queen fire ants: effects of disinhibition on dealation and oviposition by virgin queens. *J. Comp. Physiol. A 153*: 467-475.

Fletcher, D.J.C. and K.G. Ross, 1985. Regulation of reproduction in eusocial Hymenoptera. *Annu. Rev. Entomol. 30*: 319-343.

Fowler, H.G. 1982. Male induction and function of workers' excitability during swarming in leaf-cutting ants (*Atta* and *Acromyrmex*) (Hymenoptera, Formicidae) pheromones. *Int J Invertebr Reprod, 4*: 333-335.

Fowler, H.G. and R.B. Roberts, 1982. Entourage pheromone in carpenter ant (*Camponotus pennsylvanicus*) (Hymenoptera: Formicidae) queens. *J. Kans. Entomol. Soc. 55*: 568-570.

Gabba, A. and M. Pavan, 1970. Researches on Trail and Alarm Substances in Ants (161-195). In *Advances in Chemoreception*. Vol. 1 *Communication by chemical signals*. (Johnston, J.W., Jr., Moulton, D.G. and Turk, A. Eds.) Appleton-Century Crofts, New York, 412 pp.

Glancey, B.M. 1980. Biological studies of the queen pheromone of the red imported fire ant. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage. 7*: 149-154.

Glancey, B.M. and W.A. Banks, 1988. Effect of the insect growth regulator Fenoxycarb on the ovaries of queens of the red imported fire ant (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am. 81*: 642-648.

Glancey, B.M., J. Rocca, C.S. Lofgren and J. Tumlinson, 1984. Field tests with synthetic components of the queen recognition pheromone of the red imported fire ant, *Solenopsis invicta*. *Sociobiology 9*: 19-30.

Glancey, B.M. and J.C. Dickens, 1988. Behavioral and electrophysiological studies with live larvae and larval rinses of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *J. Chem. Ecol. 14*: 463-473.

Goetsch, W., 1957. *The Ants* (Manheim, R., Trans.) University of Michigan Press, Ann Arbor

Hayashi, N. And H. Komae, 1977. The trail and alarm pheromones of the ant *Pristomymex pungens* Mayr. *Experientia. 33*: 424-425.

Hefetz, A. 1985. Mandibular gland secretions as alarm pheromones in two species of the desert ant *Cataglyphis*. *Z. Naturforschung ser. C 40*: 665-666.

Hefetz, A. and T. Orion, 1982. Pheromones of ants of Israel: I. The Alarm-Defense system of some larger formicinae. *Israel J. Entomol. 16*: 87-97.

Hefetz, A. and H.A. Lloyd, 1983. Identification of new components from anal glands of *Tapinoma simrothi Pheonicium*. *J. Chem. Ecol. 9*: 607-613.

Hölldobler, B. 1971a. Sex pheromone in the ant *Xenomyrmex floridanus*. *J. Insect Physiol. 17*: 1497-1499.

Hölldobler, B. 1971b. Recruitment behavior in *Camponotus socius* (Hym. Formicidae). *Z. Vergl. Physiologie. 75*: 123-142.

Hölldobler, B. and C.P. Haskins, 1977. Sexual calling behavior in primitive ants. *Science 195*: 793-794.

Hölldobler, B. And E.O. Wilson, 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol. 3*: 19-60.

Hölldobler, B. and E.O. Wilson, 1983. Queen control in colonies of weaver ants (Hymenoptera: Formicidae). *Ann. Entomol: Soc. America* 76: 235-238.

Hölldobler, B. and S.H. Bartz, 1985. Sociobiology of reproduction in ants. *Fortschr. Zool. 31*: 237-257.

Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Cambridge, Mass.: Belknap Press.

Hölldobler, B., R.C. Stanton and H. Markl, 1978. Recruitment and food retrieving behaviour in *Novomessor* (Hymenoptera: Formicidae). I. Chemical signals. *Behav. Ecol. Sociobiol.* 4:163-181.

Hölldobler, B., J.M. Palmer and M.W. Moffett, 1990. Chemical communication in the dacetine ant *Daceton armigerum* (Hymenoptera: Formicidae). *J. Chem. Ecol., 16*: 1207-1219.

Hölldobler, B., C. Peeters and M. Obermayer, 1994a. Exocrine glands and the attractiveness of the ergatoid queen in the ponerine ant *Megaponera foetens*. *Insect. Soc. 41*: 63-72.

Hölldobler, B., U. Braun, W. Gronenberg, W.H. Kirchner and C. Peeters, 1994b. Trail communication in the ant *Megaponera foetens* (Fabr.) (Formicidae, Ponerinae) *J. Insect Physiol.40*: 585-593.

Hölldobler, B., N.J. Oldham, E.D. Morgan and W.A. König, 1995. Recruitment pheromones in the ants *Aphaenogaster albisetosus* and *A. Cockerelli* (Hymenoptera: Formicidae). *J. Insect Physiol. 41*: 739-744.

Huwyler, S.K. Grob and M. Viscontini, 1975. The trail pheromone of the ant *Lasius fuliginosus*: identification of six components. *J. Insect Physiol. 21*: 299-304.

Jackson, B.D., S.J. Keegans, E.D. Morgan, M.C. Cammaerts and R. Cammaerts, 1990. Trail pheromone of the ant *Tetramorium meridionale*. *Naturwissenschaften 77*: 294-296.

Jaisson, P. 1971. Experiences sur l'agressivite chez les fourmis. *Acad Sci Paris C R Ser D, 273*: 2320-2323.

Janssen, E., H.J. Bestmann, B. Hölldobler and F. Kern, 1995. N,N-dimethyluracil and actinidine, two pheromones of the ponerine ant *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae). *J. Chem. Ecol. 21*: 1947-1955.

Janssen, E., B. Hölldobler, F. Kern, H.J. Bestmann and K. Tsuji, 1997. The trail pheromone of the myrmicine ant *Pristomyrmex pungens* (Hymenoptera: Formicidae). *J. Chem. Ecol.* 23: 1025-1034.

Jouvenaz, D.P., W.A. Banks and C.S. Lofgren, 1974. Fire ants: Attraction of workers to queen secretions. *Ann. Entomol. Soc. Am. 67*: 442-444.

Kaib, M. and H. Dittebrand, 1990. The poison gland of the ant *Myrmicaria eumenoides* and its role in recruitment communication. *Chemoecology 1*: 3-11.

Karlson, P. and M. Luscher, 1959. "Pheromones," a new term for a class of biologically active substances. *Nature (London) 183*: 155-176.

Keller, L. and L. Passera, 1989. Influence of the number of queens on nestmate recognition and attractiveness of queens to workers in the Argentine ant, *Iridomyrmex humilis* (Mayr). *Anim. Behav. 37*: 733-740.

Keller, L. and P. Nonacs. 1993, The role of queen pheromones in social insects: queen control or queen signal? *Anim. Behav.* 45: 787-794.

Kern, F. and H.J. Bestmann, 1993. Antennal elctrophysiological responsiveness of the ponerine ant *Leptogenus diminuta* to trail and recruitment pheromones and its structure analogs. *Naturwissenschaften 80*: 424-427.

Kugler, C. 1979. Alarm and defense: a function for the pygidial gland of the myrmicine ant, *Pheidole biconstricta* in coffee plantations in the foothills of the Sierra Nevada de Santa Marta in northern Colombia. *Ann. Entomol. Soc. Am., 72*: 532-536.

Law, J.H., E.O. Wilson and J.A. McCloskey, 1965. Biochemical polymorphism in ants. *Science. 149*: 544-546

Le Masne, G. 1953. Observations sur les relations entre le couvain et les adultes chez les fourmis. *Annales des Sciences Naturelles, ser. 1, 15*: 1-56.

Leuthold, R.H. And U. Schlunegger, 1973. The alarm behaviour from the mandibular gland secretion in the ant *Crematogaster scutellaris*. *Insectes Soc. 20*: 205-213.

Lloyd, H. A., M.S. Blum and R.M. Duffield, 1975. Chemistry of the male mandibular gland secretion of the ant, *Camponotus clarithorax*. *Insect Biochem. 5*: 489-494.

Lofgren, C.S., B.M. Glancey, A. Glover, J. Rocca and J. Tumlinson, 1983. Behavior of workers of *Solenopsis invicta* (Hymenoptera: Formicidae) to the queen recognition pheromone: Laboratory studies with an olfactometer and surrogate queens. *Ann. Entomol. Soc. Am. 76*: 44-50.

Markl, H. and B. Hölldobler, 1978. Recruitment and food retrieving behaviour in *Novomessor* (Hymenoptera: Formicidae). II. Vibrational signals. *Behav. Ecol. Sociobiol. 4*: 183-216.

Maschwitz, U. 1966. Alarm substances and alarm behavior in social insects. *Vitamins and Hormones, 24*: 267-290.

McGurk, D.J., J. Frost, G.R. Waller, E.J. Eisenbraun, K. Vick, W.A. Drew and J. Young, 1968. Iridodial isomer variation in dolichoderine ants. *J. Insect Physiol.14*: 841-845.

Meinwald, J., D.F. Wiemer and B. Hölldobler, 1983. Pygidial gland secretions of the ponerine ant *Rhytidoponera metallica*. *Naturwissenschaften 70*: 46-47.

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

Möglich, M. U. Maschwitz and B. Hölldobler, 1974. Tandem calling: a new kind of signal in ant communication. *Science 86*: 1046-1047.

Morel, L. and R.K. Vander Meer, 1988. Do ant brood pheromones exist? *Ann. Entomol. Soc. Am. 81*: 705-710.

Morgan, E.D., M.R. Inwood and M.-C. Cammaerts, 1978. The mandibular gland secretion of the ant, Myrmica scabrinodis. *Physiol. Entomol. 3*: 107-114.

Mori, A., A. Zaccone and F. Le Moli, 1992. Experience-independent attraction to host-species ant cocoons in the slave-maker *Formica sanguinea* Latr. (Hymenoptera: Formicidae). *Ethol. Ecol. and Evol, Special Issue* 2: 85-89.

Moser, J.C., R.C. Brownlee, and R. Silverstein, 1968. Alarm pheromones of the ant Atta texana. *J. Insect Physiol. 14*: 529-535.

Nordlund, D.A. and W.J. Lewis, 1976. Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. *J. Chem. Ecol.* 2: 211-220.

Obin, M.S. and R.K. Vander Meer, 1994. Alate semiochemicals release worker behavior during fire ant nuptial flights. *J. Entomol. Sci., 29*: 143-151.

Obin, M.S., B.M. Glancey, W.A. Banks and R.K. Vander Meer, 1988. Queen pheromone production and its physiological correlates in fire ant queens (Hymenoptera: Formicidae) treated with fenoxycarb. *Ann. Entomol. Soc. Amer. 81*: 808-815.

Oldham, N.J., E.D. Morgan, B. Gobin and J. Billen, 1994. First identification of a trail pheromone of an army ant (*Aenictus* species). *Experientia 50*: 763-765.

Olubajo, O., R.M. Duffield and J.W. Wheeler, 1980. 4-Heptanone in the mandibular gland secretion of the Nearctic ant, *Zacryptocerus varians* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am. 73*: 93-94.

Parry, K. and E.D. Morgan, 1979. Pheromones of ants: a review. *Physiol. Entomol.* 4: 161-189.

Passera, L. and S. Aron, 1993. Factors controlling dealation and egg laying in virgin queens of the Argentine ant *Linepithema humile* (Mayr) (=*Iridomyrmex humilis). Psyche 100*: 51-63.

Pasteels, J.M., J.C. Verhaeghe, J.-C. Braekman, D. Daloze and B. Tursch, 1980. Caste-dependent pheromones in the head of the ant *Tetramorium caespitum*. *J. Chem. Ecol. 6*: 467-472.

Pasteels, J.M., D. Daloze and J.L. Boeve, 1989. Aldehydic contact poisons and alarm pheromone of the ant *Crematogaster scutellaris* (Hymenoptera: Myrmicinae): Enzyme-mediated production from acetate precursors. *J. Chem. Ecol. 15*: 1501-1511.

Petralia, R.S. and S.B. Vinson, 1979. Developmental morphology of larvae and eggs of the imported fire ant, *Solenopsis invicta*. *Ann. Entomol. Soc. Amer. 72*: 472-484.

Porter, S.D. 1995. *FORMIS: A Master Bibliography of Ant Literature*. Gainesville, FL. USA.

Quinet, Y. and J.M. Pasteels, 1995. Trail following and stowaway behaviour of the myrmecophilous staphylinid beetle *Homoeusa acuminata* during foraging trips of its host *Lasius fuliginosus* (Hymenoptera: Formicidae). *Insectes Sociaux 42*: 31-44.

Regnier, F.E. and E.O. Wilson, 1968. The alarm-defence system of the ant *Acanthomyops claviger*. *J. Insect Physiol. 14*: 955-970.

Robinson, S.W. and J.M. Cherrett, 1974. Laboratory investigations to evaluate the possible use of brood pheromones of the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae, Attini) as a component in an attractive bait. *Bull. Entomol. Res. 63*: 519-529.

Rocca, J.R., J.H. Tumlinson, B.M. Glancey and C.S. Lofgren, 1983a. The queen recognition pheromone of *Solenopsis invicta*, preparation of (E)-6-(1-pentenyl)-2H-pyran-2-one. *Tetrahedron Lett. 24*: 1889-1892.

Rocca, J.R., J.H. Tumlinson, B.M. Glancey and C.S. Lofgren, 1983b. Synthesis and Stereochemistry of Tetrahydro-3,5-dimethyl-6-(1-methylbutyl)-2H-pyran-2-one, a component of the queen recognition pheromone of *Solenopsis invicta*. *Tetrahedron Lett. 24*: 1893-1896.

Salzemann, A., P. Nagnan, F. Tellier and K. Jaffe, 1992. Leaf-cutting ant *Atta laevigata* (Formicidae: Attini) marks its territory with colony-specific dufour gland secretion. *J. Chem Ecol. 18*: 183-196.

Scheffrahn, R.H., L.K. Gaston, J.J. Sims and M.K. Rust, 1984. Defensive ecology of *Forelius foetidus* and its chemosystematic relationship to *Forelius* (*=Iridomyrmex*) *pruinosus* (Hymenoptera: Formicidae: Dolichoderinae). *Environ. Entomol., 13*: 1502-1506.

Scheffrahn, R.H. and M.K. Rust, 1989. Attraction by semiochemical mediators and major exocrine products of the myrmicine ant, *Crematogaster californica* Emery. *Southwest. Entomol., 14*: 49-55.

Shorey, H.H. 1973. Behavioral responses to insect pheromones. *Annu. Rev. Entomol. 18*: 349-380.

Simon, T. and A. Hefetz, 1991. Trail-following responses of *Tapinoma simrothi* (Formicidae: Dolichoderinae) to pygidial gland extracts. *Insect. Soc. 38*: 17-25.

Steghaus-Kovac, S., U. Maschwitz, A.B. Attygalle, R.T.S. Frighetto, N. Frighetto, O. Vostrowsky and H.J. Bestmann, 1992. Trail-following responses of *Leptogenys diminuta* to stereoisomers of 4-methyl-3-heptanol. *Experientia 48*: 690-694.

Stumper, R. 1956. Sur les sécrétions attractives des fourmis femelles. *Compt. Rend. Acad. Sci. Paris 242*: 2487-2489.

Tomalski, M.D., M.S. Blum, T.H. Jones, H.M. Fales, D.F. Howard and L. Passera, 1987. Chemistry and functions of exocrine secretions of the ants *Tapinoma melanocephalum* and *T. erraticum*. *J. Chem. Ecol., 13*: 253-263.

Torgerson, R.L. and R.D. Akre, 1970. The persistence of army ant chemical trails and their significance in the ecitonine-ectophile association (Formicidae: Ecitonini). *Melanderia. 5*: 1-28.

Traniello, J.F.A. and B. Hölldobler, 1984. Chemical communication during tandem running in *Pachycondyla obscuricornis* (Hymenoptera: Formicidae). *J. Chem. Ecol. 10*: 783-794.

Tricot, M.-C., J.M Pasteels, and B. Tursch, 1972. Phéromones stimulant et inhibant l' agressivité chez *Myrmica rubra. J. Insect Physiol. 18*: 499-509.

Tumlinson, J.H., R.M. Silverstein, J.C. Moser, R.G. Brownlee, and J.M. Ruth, 1971. Identification of the trail pheromone of a leaf-cutting ant, *Atta texana*. *Nature, 234*: 348-349.

Vander Meer, R.K. and L. Morel,1988. Brood pheromones in ants. In *(Advances in myrmecology,* J. C. Trager, Ed.) E.J. Brill, New York pp. 491-513.

Vander Meer, R.K. and L. Morel, 1995. Ant queens deposit pheromones and antimicrobial agents on eggs. *Naturwissenschaften. 82*: 93-95.

Vander Meer, R.K., B.M. Glancey, C.S. Lofgren, A. Glover, J.H. Tumlinson and J. Rocca, 1980. The poison sac of red imported fire ant queens: Source of a pheromone attractant. *Ann. Entomol. Soc. Amer. 73*: 609-612.

Vander Meer, R.K., F.D. Williams and C.S. Lofgren, 1981. Hydrocarbon components of the trail pheromone of the red imported fire ant, *Solenopsis invicta*. *Tetrahedron Lett.* 22: 1651-1654.

Vander Meer, R.K., F. Alvarez and C.S. Lofgren, 1988. Isolation of the trail recruitment pheromone of *Solenopsis invicta*. *J. Chem. Ecol. 14*: 825-838.

Vander Meer, R.K., C.S. Lofgren and F.M. Alvarez, 1990. The orientation inducer pheromone of the fire ant *Solenopsis invicta*.. *Physiol. Entomol. 15*: 483-488.

Walter, F., D.J.C. Fletcher, D. Chautems, D. Cherix, L. Keller, W. Francke, W. Fortelius, R. Rosengren and E.L. Vargo, 1993. Identification of the sex pheromone of an ant, *Formica lugubris* (Hymenoptera, Formicidae). *Naturwissenschaften 80*: 30-34.

Watkins, J.F., II. and T.W. Cole, 1966. The attraction of army ant workers to secretions of their queens. *Tex. J. Sci. 18*: 254-265.

Wheeler, J.W. and M.S. Blum, 1973. Alkylpyrazine Alarm Pheromones in Ponerine Ants. *Science 182:* 501-503.

Wheeler, J.M., S.L. Evans, M.S. Blum, and R.L.Torgerson, 1975. Cyclopentyl ketones: Identification and function on *Azteca* ants. *Science 187*: 254-255.

Wilson, E.O. 1958a. A chemical releaser of alarm and digging behavior in the ant *Pogonomyrmex badius* (Latreille). *Psyche, 65*: 41-51.

Wilson, E.O. 1958b. The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution, 12*: 24-31.

Wilson, E.O. 1962. Chemical Communication Among Workers of the Fire Ant *Solenopsis saevissima* (Fr. Smith). *Animal Behaviour 10*: 134-164.

Wilson, E.O. 1971. *The insect societies.*, Harvard University Press, Cambridge, MA.

Wilson, E.O. and W.H. Bossert, 1963. Chemical communication among animals. *Recent Prog. Hormone Res. 19*: 673-716.

Wilson, E.O. and F.E. Regnier, Jr., 1971. The evolution of the alarm-defense system in the formicine ants. *Am. Nat. 105*: 279-289.

Yamauchi, K. and N. Kawase, 1992. Pheromonal manipulation of workers by a fighting male to kill his rival males in the ant *Cardiocondyla wroughtonii*. *Naturwissenschaften 79*: 274-276.