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SEMIOCHEMICALS AND THE RED IMPORTED FIRE ANT (*SOLENOPSIS INVICTA* BUREN) (HYMENOPTERA: FORMICIDAE)

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Research on fire ant behavior has increased dramatically in the past few years and is reflected by an interest in deciphering the chemical messages used for individual and colony communication. Social insects provide a wealth of opportunity in this area as exemplified by the general behavioral responses in Table 1. All of these responses involve chemical communication.

TABLE 1. GENERAL CATEGORIES OF BEHAVIORAL RESPONSES IN SOCIAL INSECTS (MODIFIED FROM WILSON 1971).

Alarm
Attraction
Recruitment to a new food source or nest site
Trail following
Grooming, including assistance at molting
Trophallaxis, exchange of liquid food
Exchange of solid food particles
Group effect, social facilitation or inhibition
Recognition of nestmates or castes
Caste determination, either by inhibition or by stimulation
Control of competing reproductives

Chemicals that mediate interactions between organisms are called semiochemicals, and when the individuals involved are of the same species the behavior-modifying chemicals are called pheromones. Chemical interactions between organisms of different species are broadly classified as allelochemics. Two commonly observed pheromone responses are alarm and trailing. These and other pheromones that elicit immediate responses are designated releaser pheromones. When the response is delayed, such as in caste determination or inhibition of oogenesis, the chemicals responsible are called primer pheromones. The list of general behavioral responses indicates that we can expect fire ant colony organization to be complex and to rely on pheromone communication for many essential functions.

A survey of fire ant pheromone literature shows scattered publications over more than 2 decades, starting in the same year that the term pheromone was coined by Karlson and Luscher (1959). The vast majority of papers described behavior mediated by particular pheromone systems; however, recent improvements in chemical technology are bringing the chemistry of pheromones into sharper focus. This review covers the documented areas of trail, queen and brood pheromones, as well as behavioral and chemical aspects of species and colony odor. There are several excellent recent reviews of social insect pheromones that the reader is encouraged to read for an overview of the fields (Parry and Morgan 1979, Hölldobler 1978, Blum 1977).

Trail Pheromone

The trail pheromone was the first fire ant pheromone system to be investigated. Wilson (1959) tested the trailing response of the red imported fire ant *Solenopsis invicta* Buren to numerous extracts of potential glandular sources of the pheromone and ultimately discovered that Dufour's gland secretion functions as both a releaser and orientator of trail following. Dufour's gland (Fig. 1E) is composed of a single layer of cuboidal cells lining a thin intima ca. 1-1.5 mm long. The Dufour's gland and poison sac open into the poison bulb at the base of the sting (Fig. 1F) where the contents of either can be emitted from the sting tip. The structure of the base of the sting bulb makes it possible for the Dufour's secretion to be released either by itself or in concert with poison sac contents (Callahan et al. 1959). Although there is no evidence indicating that venom is released with Dufour's gland secretion, the mechanism is available to vary the concentration of released trail pheromone complex.

When a foraging worker discovers a food source it examines the material with its antennae, and if the object is small enough, the worker will pick it up or drag it back to the nest. If the food object is too large, the forager will, after inspection, lay a trail back to the home nest. The chemical trail passes from the Dufour's gland through the sting to the ground. The actual trail consists of a series of streaks made by periodic extension and withdrawal of the sting away from the surface substrate (Wilson 1962b). Hantgartner (1969) has suggested that in the case of *Solenopsis geminata* F. the foraging ant controls the continuity and intensity of its trail depending on the immediate physiological state of the colony. The Dufour's secretion of *S. invicta* acts as an attractant that draws

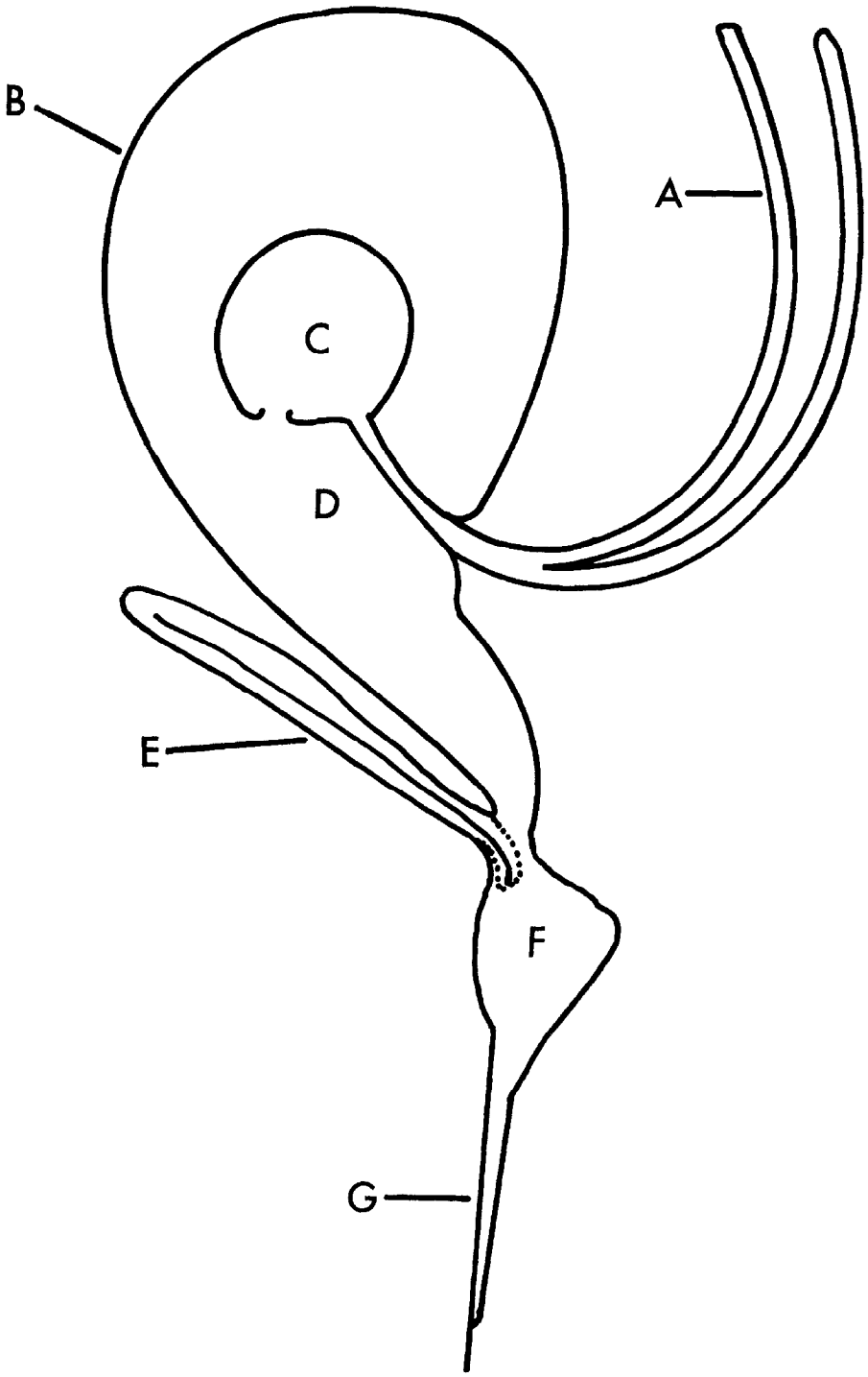


Fig. 1. The sting apparatus and Dufour's gland. A. free filaments, B. poison sac, C. poison gland, D. venom reservoir, E. Dufour's gland, F. bulb of sting, G. sting.

workers over short distances to the trail and subsequently to the food source. In the laboratory an extract of Dufour's gland rapidly recruited large numbers of workers from a nest in the direction of the extract (Wilson 1962a). The quality of the food is communicated by the strength of the chemical trail, which is predicated on the number of returning workers that reinforce the trail with their own Dufour's secretion. The better the food the greater the trail reinforcement and hence greater recruitment. The concentration of workers at a food site is limited by the number of workers able to physically gather around the food source and gain positive stimulation. Those workers that can not reach the food return to the nest without reinforcing the trail, consequently the number of workers at the food site stabilizes, and is a function of the surface area and quality of the food. After the food source has been consumed the trail is no longer reinforced and dissipates via evaporation (Wilson 1962a) or decomposition.

Behaviors mediated by the Dufour's gland secretion are complex. According to Wilson (1962c) it is the primary releaser of hunting behavior and directional movement in general. It is involved in mass foraging, alarm recruitment and under laboratory conditions, colony emigration (Wilson 1962c). Although the Dufour's gland secretion is undoubtedly the major releaser of these behaviors in the field, Stratton and Coleman (1973) showed in laboratory studies with *S. invicta* that distal-visual and kinesthetic cues are also important in the aquisition and retention of food location and that learning was possible.

Several investigators (Wilson 1962a, Barlin et al. 1976, and Jouvenaz et al. 1978) have addressed the question of trail pheromone specificity. Table 2 summarizes their combined results, which with minor exceptions, are in agreement. The main conclusions are that the 2 imported species, *S. invicta* and *Solenopsis richteri* Forel respond exclusively to each others Dufour's gland extract and the 2 indigenous species, *S. geminata* and *Solenopsis xyloni* (McCook) also exclusively respond to each others Dufour's gland extract. Wilson (1962a) also noted that the Dufour's gland secretion of *Monacis bispinosa* (Oliver) elicited a full response from *S. invicta*, however, the thief ant *Solenopsis molesta* (Say), and members of other myrmicine genera do not share *S. invicta*'s trail pheromone. The *M. bispinosa* result may have simply been coincidence since it is known to emit its trail pheromone from the ventral scent gland and not the Dufour's gland

TABLE 2. SPECIES SPECIFICITY OF *Solenopsis* SPP. TRAIL PHEROMONES.

Source of trail pheromone extract	Numbers refer to references and a positive response from test species			
	S. invicta	*S. richteri*	*S. geminata*	*S. xyloni*
S. invicta	1,2,3	*,2,3,	3	
S. richteri	*,2,3,	*,2,3,	*	*
S. geminata		*	1,2,3,	2,3,
S. xyloni	1	*,2	1,2,3	1,2,3,

[1]Wilson (1962), Dufour's gland extracts.
[2]Barlin et al. (1976) Dufour's gland extracts.
[3]Jouvenaz et al. (1978) Purified whole ant extracts.
*Reference 1 did not test *S. richteri*.

(Wilson and Paven 1961). This was verified by the observation that *M. bispinosa* did not respond to *S. invicta* Dufour's gland extract.

Barlin et al. (1976) compared the response of the 4 *Solenopsis* species in a trial following bioassay using natural trails, purified gas chromatographic fractions of Dufour's gland extract, and Dufour's gland extract itself. The results for the natural trails were similar to those obtained with Dufour's gland extract, except *S. richteri* would not follow *S. invicta* or *S. xyloni's* trail. This may be due to additional masking agents or species specific components added to the natural trail that are not found in Dufour's gland itself. The species specificity studies carried out with gas chromatographic fractions of Dufour's gland extracts showed conclusively that *S. invicta* and *S. richteri* do have species specific major trail pheromone components, which also differ from the major pheromone component apparently shared by *S. geminata* and *S. xyloni.* This does not preclude blends of components in Dufour's gland, minor and major that may be necessary to elicit a full behavioral response and serendipitously contribute to the observed non-specificity of some of the trail bioassay results (Barlin et al. 1976).

The inquisition of the chemical nature of the trail pheromones of *Solenopsis* species began with Wilson's (1959) paper indicating that bioassay active trail pheromone components could be isolated from the steam distillate of whole *S. invicta* workers. The steam distillate could be purified by gas chromatography; however, under these conditions both the crude and purified material rapidly lost activity (Walsh et al. 1965). Barlin et al. (1976) significantly contributed to the chemical understanding of fire ant trail pheromones with gas chromatography studies of the 4 species in Table 2. Preliminary characterization of the main trail pheromone component of *S. richteri* showed it to have a molecular weight of 218 and empirical formula of $C_{16}H_{26}$. Based on comparative gas chromatography retention indices and the assumption that the chemical nature of *Solenopsis* species trail pheromones were similar they suggested empirical formulas of $C_{15}H_{24}$ for *S. invicta,* and $C_{17}H_{28}$ for both *S. geminata* and *S. xyloni* major trail pheromone components.

A major breakthrough in trail pheromone chemistry occurred when Vander Meer et al. (1981) isolated and identified several trail pheromone components from *S. invicta* (Fig. 2). The structures of 2 components, *Z,E* and *E,E*-α-farnesene (I and II), were confirmed by synthesis and 2 homofarnesenes were assigned the structures *Z,Z* and *Z,E*-3,4,7,11-tetramethyl-1,3,6,10-dodecatetraene (III and IV) based on spectral data. Later Williams et al. (1981 a,b) reported the presence of an allofarnesene (*Z,Z,* *Z*-3,7,11-trimethyl-2,4,6,10-dodecatetraene) (VI) in the Dufour's gland of *S. invicta.* In trailing bioassays components I-IV all showed good activity in comparison with related α- and β-farnesenes (Table 3). In fact, component I by itself was capable of reproducing the trailing activity produced by Dufour's gland extract. Components II-IV were 10-100 times less active, and V, heptadecane (reported initially by Barlin et al. 1976, to be a component of *S. invicta's* Dufour's gland), was inactive. Component VI was reported to show bioassay activity to 5 fg/cm (Williams et al. 1981b), which is considerably lower than the value found by Vandeer Meer (unpublished results, Table 3) for Dufour's gland extract. An answer to these apparent discrepancies must await further investigation. In any

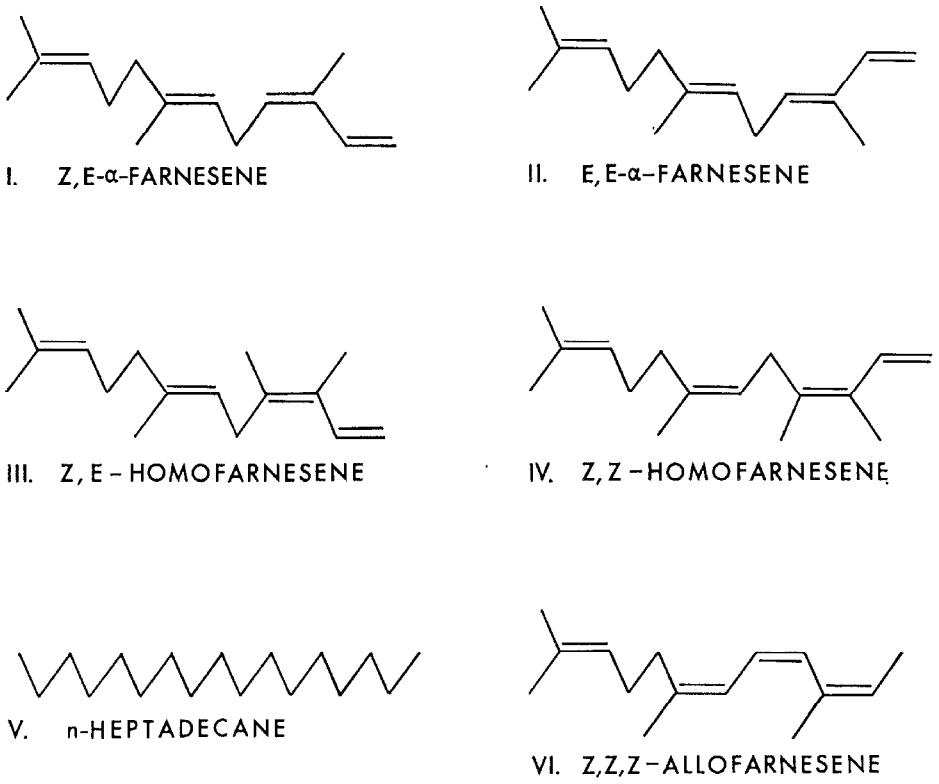


Fig. 2. *Solenopsis invicta* trail pheromone components identified from Dufour's gland.

event, from a behavioral and energetics point of view, one wonders what role components II-IV play. A definitive answer to this question may soon be forthcoming. Preliminary results using a trail bioassay (Jouvenaz et al. 1978) and a spot bioassay designed to measure the recruitment aspect of

TABLE 3. CONCENTRATION OF *S. invicta* TRAIL PHEROMONE COMPONENTS AND RELATED COMPOUNDS REQUIRED TO GIVE A POSITIVE TRAIL BIOASSAY.

Compound	picograms/cm
I[1]	0.4
II[2]	23
III[2]	40
IV[2]	40
V[2]	—
Z,Z-α-farnesene[2]	3,500
E,Z-α-farnesene[2]	37,000
E-β-farnesene[2]	73,000
Z-β-farnesene[2]	29,000
Dufour's gland extract[2]	0.4 (Based on the amount of I in the mixture)

[1]Vander Meer et al. (1981).
[2]Vander Meer, unpublished data.

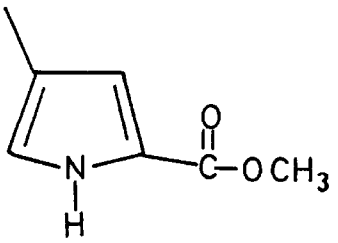
the overall behavior associated with mass foraging have shown that component I will by itself release maximum trail following activity, but has no effect on recruitment of workers. The combination of components I-IV better duplicated the recruitment response of Dufour's gland extract when heptadecane was added to the mixture. By itself heptadecane was inactive in both the trail and spot bioassay. It would appear then that the 2 measured behaviors (trail following and recruitment) are mediated by different components produced in the same gland (Vander Meer unpublished results). A careful examination of mass foraging and other behaviors associated with Dufour's gland in conjunction with the individual pheromone components and their combinations may reveal similar chemical and glandular parsimony.

α-Farnesenes have been reported in the Dufour's gland of several ant species (Bergstrom and Lofquist 1968, Cavill et al. 1976), Morgan and Wadhams 1972, and Morgan et al. 1979), although no behavioral function has been attributed to them. The Dufour's glands of *Myrmica scabrinodis* Nylander (Morgan et al. 1979) and *M. rubra* (Morgan and Wadhams 1972) contain a different homofarnesene, 7-ethyl-3,11-dimethyl-1,3,6,10-dodecatetraene, also of no known function. *Trans*-β-farnesene, a close relative of the α-farnesenes does have behavioral activity as an alarm pheromone of the green peach aphid (Edwards et al. 1973), and an α-farnesene is a natural attractant for codling moth larvae (Sutherland and Hutchins 1972).

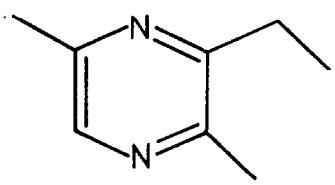
There have been only a few trail pheromones isolated and identified from other ant species (Fig. 3). The nitrogen containing trail pheromone of *Atta texana* (Buckley), methyl 4-methyl-pyrrole-2-carboxylate (VII), and *Atta sexdens rubropilosa* Forel, 3-ethyl-2,5,-dimethyl pyrazine (VIII), were isolated from the ant's venom (Tumlinson et al. 1971, Cross et al. 1979). Other alkaloid trail pheromones, monomorine I (IX) and monomorine III (X), were isolated from the venom of *Monomorium pharaonis* (L.) (Ritter et al. 1973 and 1977a); however, a more effective trail following pheromone, faranal (XI), was subsequently isolated from the Dufour's gland (Ritter et al. 1977b). The straight chain fatty acids C_6-C_{12} (XII) were isolated from the hindgut of *Lasius fuliginosus* (Latrielle) and shown to be trail pheromones of this species (Huwyler et al. 1973). Higher molecular weight fatty acids were found to be trail pheromone components of *Pristomyrmex pungens* Mayr (Hayashi and Komae 1977). It is evident that there is a great deal of diversity in the source of trail pheromones (also known to be produced in Pavan's gland and tibial glands, Parry and Morgan 1979), which probably contribute to their structural diversity. Fire ant trail pheromones (I-VI) represent yet another chemical type.

Queen Pheromone

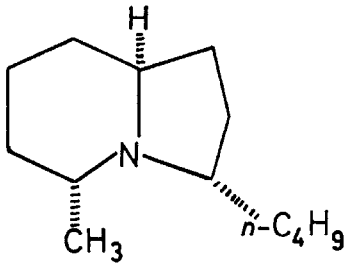
The term queen pheromone is a general term that encompasses many different queen-related behavioral responses. The first specific fire ant queen pheromone investigated was reported to be an attractant produced by colony queens (Jouvenaz et al. 1974). It was observed that workers of *S. invicta* and *S. geminata* aggregated around areas of a test paper on which their respective queens had been confined. Interestingly, the workers responded more to areas occupied by their mother queen than by con-



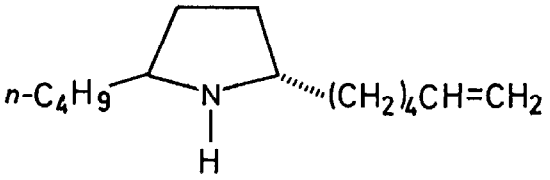
VII.



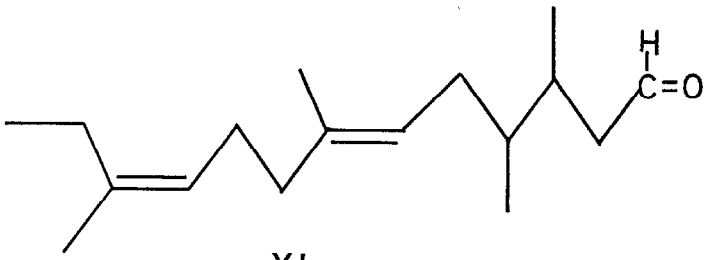
VIII.



IX.



X.



XI.

$$C_6H_{12}O_2 \longrightarrow C_{12}H_{24}O_2$$

XII.

Fig. 3. Trail pheromone components isolated from other ant species: VII *Atta texana;* VIII *Atta sexdens rubropilosa;* IX-XI *Monomorium pharaonis;* XII *Lasius fuliginosus.*

specific queens, which is suggestive of a species specific pheromone enmeshed in colony specific odors. Although similar tests with female alates and workers were ambiguous, it was clear that a strong worker response was unique to the pheromone produced by the queen. One-sided species specificity was observed, since *S. invicta* workers strongly reacted to a spot previously occupied by an *S. geminata* queen as well as their own queen, but *S. geminata* workers only responded to a spot once occupied by their own species queen. Although Jouvenaz et al. (1974) refer to the

secretions as "queen-tending pheromones" they acknowledge that they may be merely attractants. Actually the authors did not experimentally establish that volatile attractants were involved, since similar results would have been obtained if the secretions acted as worker arrestants. Jouvenaz et al. (1974), showed that workers still responded to spots previously occupied by *S. invicta* queens even after 72 h, which is indicative of non-volatile components.

Glancey (1980) postulated the production of a queen recognition pheromone by *S. invicta* queens based on comparative bioassay results for extracts of mated queens and castes. The bioassay was quantified by counting the number of ants clustered around a piece of applicator stick that had been treated with an extract. This bioassay represents a variation of the bioassay used by Jouvenaz et al. (1974). Although the results did demonstrate the unique response of worker fire ants to queens or extracts of queens there was still ambiguity as to what was really being measured. Other more specific bioassays were developed. Vander Meer et al. (1980) defined 2 behavioral responses, worker attraction and queen recognition, which were measured by separate bioassays. Worker attraction was measured in an olfactometer that clearly demonstrated that the queen secretes volatile compounds that attract workers. Queen recognition was defined by the behavior of workers when placed in a test chamber containing brood and a queen. The usual worker response was aggregation, antennation and grooming of the queen, and the deposition of brood near the queen. All of these responses could be mimicked by applying a whole queen extract to a surrogate queen. Lofgren et al. (1982) found that queen extracts induced attraction at concentrations as low as 0.01 queen equivalents and that live queens stopped releasing the pheromone if they were isolated from the colony for more than 30 min.

Using the olfactometer and surrogate queen bioassays Vander Meer, et al. (1980) discovered that the attractants and queen recognition pheromones were stored in the poison sac, dispensed by the sting apparatus and most likely biosynthesized in the poison gland. Behaviorally and from a chemical isolation point of view, this result has broad implications. The queen can dispense the pheromone through the sting apparatus (Fig. 1) at whatever time and concentration a particular situation requires. This ability must increase the potential for pheromonal parsimony, part of which has already been observed as worker attraction and queen recognition. Blum (1977) has suggested that pheromonal parsimony is a key element in the evolution of sociality in arthropods, and many examples already exist in the literature (Blum and Brand 1972, Gabba and Pavan 1970). These data also rationalize the apparent dichotomy of observed behavior and glandular development, since fire ant queens do not sting yet have a well developed venom apparatus. In counterpoint, queens do not lay trails and therefore their Dufour's gland is atrophied in comparison with that of workers. To add even more to the pheromonal parsimony, Vander Meer (unpublished results) has determined that the queen's sting apparatus is involved in the egg laying mechanism and that the queen attractant-recognition pheromones are applied to the eggs. The advantage for the eggs are the initial worker attraction and attention given to them immediately after oviposition and perhaps the bactericidal activity of the venom components (Jouvenaz et al. 1972) gives them a greater chance for survival.

The remarkable multifunctional role of worker and queen venom is summarized in Fig. 4.

The major components of fire ant venom have been thoroughly characterized as *cis* and *trans*-2-methyl-6-alkyl or alkenyl substituted piperidines (MacConnell et al. 1971). In female alates and even more pronounced in queens, *cis*-2-methyl-6-undecyl piperidine predominates (Brand et al. 1973, Vander Meer unpublished results). Vander Meer et al. (1980) showed that these alkaloids and other nitrogenous components of a queen's venom were not responsible for the observed attraction, and that the queen pheromone attractant must consist of minor non-alkaloid components of the venom. In a preliminary study on the isolation and identification of the above defined queen pheromones, Tumlinson (1980) was able to retain activity from benzene extracts of whole queens after concentration by distillation and after 1-2 days at room temperature, indicating that the pheromone components are stable. The accumulation of material for chemical analysis was facilitated by the observation of Glancey et al. (1981), that mechanically dealated virgin females of *S. invicta* produce a pheromone that attracts workers in the same way as described for mated queens.

No ant queen pheromone components have as yet been isolated and identified, although the literature has many behavioral examples of ant queen pheromones possessing many different functional roles. Table 4 lists the species and reported functions of several queen pheromones. Along with queen recognition and sex attraction the major themes are worker attraction and control of caste or sexual development. The latter area, as related to *S. invicta*, has recently been investigated by Fletcher and Blum (1981a,b). Virgin *S. invicta* alate queens are produced primarily

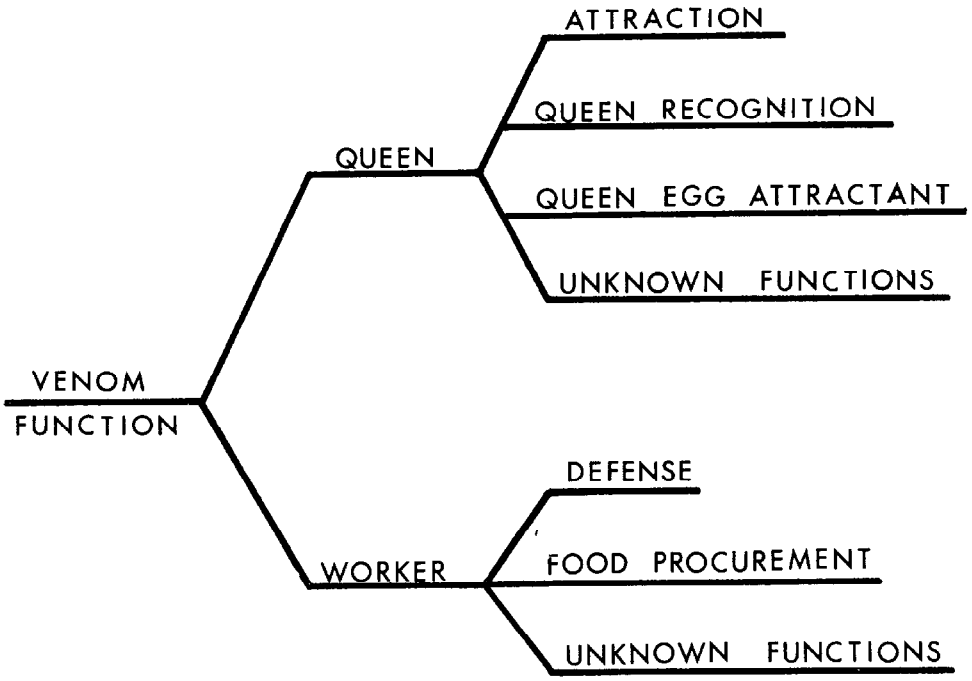


Fig. 4.. Diagrammatic representation of the multifunctional role of the imported fire ant queen and worker venom.

TABLE 4. FUNCTIONS OF SEVERAL ANT QUEEN PHEROMONES OTHER THAN *Solenopsis* SPECIES.

Ant species[a]	Function of Queen Pheromone
Lasius alienous Foerster (1)	Attractant
Pheidole palludula Nylander (1)	Attractant
Neivamyrmex, several species (2,3)	Attractant, colony cohesion
Myrmica rubra L. (4)	Queen recognition and caste control
Plagiolepis pygmaea Latr. (5)	Inhibition of oogenesis and queen larvae differentiation
Odontomachus haematodes L. (6)	Control of caste development and egg laying in workers
Monomorium pharaonis L. (7)	Control of sexual development
Tetraponera anthracina Santschi (8)	Inhibition of queen development
Xenomyrmex floridanus Emory alates (9)	Male attractant

[a]References: 1. Stumper (1956), 2. Schneirla (1957), 3. Watkins and Cole (1956), 4. Brian (1973), 5. Passera (1980), 6. Colombel (1978), 7. Berndt & Nitschman (1979), 8. Terron (1977), 9. Holldobler (1971).

during the warm months of the year, and they remain in the parent mound until environmental conditions are correct for a mating flight. Newly-mated queens shed their wings, which triggers numerous physiological changes from wing muscle histolysis and oogenesis to the production of the attractant-queen recognition pheromone (Vander Meer et al. 1981, Glancey et al. 1981). These same physiological changes could occur in virgin alate females within an established colony simply through dealation. Fletcher and Blum (1981a) found that in the presence of a queen the workers and alates receive, via trophallaxis or physical contact, a non-volatile primer pheromone that inhibits the dealation process. Although it was originally reported that workers were directly involved in the dealation process, more recent evidence indicates that the inhibitory pheromone acts exclusively on the female alates (D. Fletcher, personal communication). In orphaned colonies dealation of sexually mature female alates began within 24 h, and a few days later workers started to kill some of the dealates until only a few remained. Dealation then stopped, indicating that the dealates present were now capable of producing the inhibitory primer pheromone. The execution of dealates suggested that workers tolerated only certain levels of queen derived pheromones and an excess prompted workers to eliminate the source until tolerable levels were once again reached (Fletcher and Blum 1981a).

An inhibitory-primer-pheromone bioassay was developed based on workers tending mother queen corpses or body parts (Fletcher and Blum 1981b). Using this technique they determined that isolated queen abdomens inhibited dealation for a longer period of time (8 days) than isolated heads or thoraces (2.6 days). However, in related work Williams et al. (1981) reported that *S. invicta* workers tend dead queens and, in particular, queen abdomens for many weeks. The tending of queen gasters was identical to worker behavior when tending a live queen and could be reproduced on a surrogate queen treated with an extract of queen poison sac. The venom gland is the source of the attractant-queen recognition pheromones (Vander Meer et al. 1980), and the poison sac and sting apparatus provide an excellent

controlled release mechanism for venom in dead queens or their abdomens. It follows that workers will tend abdomens longer than heads or thoraces. The results of Fletcher and Blum (1981b) may simply be indicative of the duration of tending activity (mediated by the queen attractant-recognition pheromone) and may not demonstrate the probable site of inhibitory pheromone production or storage. Since the primer pheromone requires queen-worker contact, which is a behavior induced by the attractant-queen recognition pheromone, I feel that these behaviorally different pheromones are in fact intimately linked. This does not mean that they are necessarily one and the same, but without worker attraction to the queen and subsequent tending, the workers would not imbibe the inhibitory primer pheromone for passage to other colony targets. The results of the dealation process in queenless colonies are the ultimate production of the queen attractant-recognition pheromones (Glancey et al. 1981), the inhibitory pheromone (Fletcher and Blum 1981a), oogenesis and the production of male sexuals. Eventually the colony would die through natural attrition of the remaining workers; however, the colony gene pool would survive if the males successfully mated with alate virgin females.

Brood Pheromone

The grooming, licking and antennation of brood by worker ants and the general ability of workers to segregate brood by age and caste (Wilson 1971) provide strong circumstantial evidence for the existence of brood recognition pheromones. These phenomena have been observed with *S. invicta,* whose workers also assist molting larvae and help remove the meconium (O'Neal and Markin 1973). *S. invicta* workers feed liquid food to all instars and place solid proteinaceous material of a specific size range on the anteroventral region of 4th instar larvae (Petralia and Vinson 1978). The feeding distinction made by workers between instars is either due to the change in 4th instar morphology (Petralia and Vinson 1979) or possibly changes in chemical cues.

Glancey et al. (1970) demonstrated that an *S. invicta* brood pheromone could be extracted from immature forms with hexane. The brood pheromone bioassay was based on the observation that if brood was scattered outside a nest cell, *S. invicta* workers rapidly picked them up and placed them on a brood pile inside the cell. Grits, clay granules, or pieces of paper treated with hexane extracts of brood and scattered outside a nest cell were picked up and placed with brood in the nest. Untreated control particles were not picked up, and grits treated with vegetable oil were fed upon and the few particles moved into the nest were not placed on the brood pile. The most difficult and essential part of a brood pheromone bioassay is the ability to differentiate between a feeding response and a pheromone response. Extracts of worker larvae and sexual larvae gave positive responses, whereas, extracts of worker and sexual pupae gave no response. This result can be rationalized in that pupae no longer require the attention of workers, at least not until the time of eclosion. Glancey et al. (1970) suggested that the action of *S. invicta* workers toward the treated particles demonstrated that a pheromone was associated with brood recognition and tending.

The work of Glancey et al. (1970) was expanded by Walsh and Tschinkel (1974) who modified the bioassay to include a nest cell with a well defined

brood chamber. Once *S. invicta* workers had a sample inside the nest cell, air was blown into the entrance to cause an alarm reaction that caused workers to quickly deposit brood into the brood chamber. A positive worker response to sexual prepupae was unaffected by worker numbers, worker size, or whether the queen or brood were present in the nest cells. Auditory brood communication was ruled out by positive tests with freshly killed sexual prepupae, which after 21 h started to lose significant activity. The chemical signal appeared to be spread evenly over the surface of sexual prepupae and sexual pupae, however, after adult eclosion all retrieval activity was lost. The positive result with sexual pupae was in contrast to that observed by Glancey et al. (1970).

Walsh and Tschinkel (1974) also showed by olfactometer studies that chemical communication between brood and workers is not through long range chemical interactions, but must be short range or contact pheromones. Hexane rinsed brood of all castes were inactive in the bioassay. However, reapplication of this extract or diethyl ether, methanol or benzene extracts on rinsed prepupae or blotter paper surrogates at concentrations up to 6 prepupae equivalents failed to produce any activity. Intact sexual prepupae were exposed to vapors of several chemical reagents that react with specific chemical functional groups. Only bromine significantly reduced the workers response, which would normally suggest the presence of double bonds in the active compounds. However, insignificant reduction of worker response with other double bond attacking reagents (iodine, aqueous hydrogen bromide, and ethanolic ozone) indicate that other factors may be involved, perhaps sample repellency. A lot of interesting information was obtained from this work, however, the failure to recover activity from extracts when applied to surrogate brood was disappointing.

Bigley and Vinson (1975) utilized a brood pheromone bioassay similar to that of Glancey et al. (1970). A positive brood tending response was indicated when workers palpitated and antennated filter paper discs treated with brood extract. Placement of the discs in the colony and the time they were retained in the colony were monitored. Appropriate controls and soybean oil treated discs were also tested. Initially, *S. invicta* workers tended discs treated with chloroform: methanol (2:1) extracts of sexual prepupae, then quickly moved them into the colony and maintained them there for at least 24 h. Soybean oil controls generally elicited only a feeding response.

Using the above bioassay, Bigley and Vinson (1975) followed the chemical separation of the positive activity found in whole sexual prepupae extracts. Activity was shown by thin layer chromatography (TLC) to be localized in the triglyceride region of the chromatogram. Of 9 spots, the triglyceride spot was the largest. Saponification of the active fraction destroyed its activity. The fatty acids from the saponification reaction were isolated by standard procedures and identified solely by TLC as oleic acid. From that it was an easy step to conclude that the *S. invicta* brood pheromone was triolein. Although I do not doubt that triolein is a component of the mixture of triglycerides produced by *S. invicta* sexual prepupae, I do not feel confident in a structural assignment based solely on TLC R_f values. There are accepted methods for determining the composition of triglycerides, none of which are based entirely on TLC (Christie 1973). It also seems highly unlikely that an insect would produce only a single triglyceride composed of a single fatty acid as implied by Bigley and Vinson

(1975). Another problem is the lack of information regarding the number of sexual prepupae equivalents applied to the filter paper discs. Not knowing the concentration of natural material makes it impossible to compare the worker's responses to standards and extracts. In any event diolein and triolein elicited a better response from workers than the original sexual prepupae extract. Significantly, in view of Walsh and Tschinkel's (1974) observation that the brood tending pheromone resides primarily on the cuticle, Bigley and Vinson (1975) obtained only weak activity from hexane or chloroform sexual prepupae rinses and only a faint triglyceride spot on TLC. To obtain good activity and significant triglyceride TLC spots the samples had to be "soaked" or extracted in chloroform: methanol (2:1). The worker response is initiated by contact with only a small portion of the larva's total surface area and workers even respond to the prepupal skin alone (Walsh and Tschinkel 1974). It seems peculiar then that a total sexual prepupae extract was required to obtain positive results.

Early examples of worker-brood interactions described trophallactic exchange of liquids, with workers ingesting either proctodeal or stomodeal larval secretions (Stager 1923, LeMasne 1953, Torossian 1961). However, the first evidence of a brood pheromone came from Watkins and Cole (1966) who demonstrated that workers of the army ant, *Neivamyrmex apacithorax* (Emery), were attracted to secretions of their larvae and pupae. Brian (1975) did a study on larval recognition by *Myrmica rubra* workers similar to that of Walsh and Tschinkel (1974). There were several parallels in that *M. rubra* workers respond to larval skins and the chemical signal was of low volatility and widely distributed over the surface of the larva. Although the reactive substance was insoluble in hexane it was soluble in acetone, ether and chloroform. Application of these rinses to surrogate larvae were unsuccessful; however, when applied to previously rinsed brood a positive result was obtained. Robinson and Cherrett (1974) found that hexane washed pupae were less acceptable to *Atta cephalotes* (L.) workers than normal pupae indicating that the hexane dissolved a behaviorally active surface material. Surrogate brood experiments were considered a failure, since filter discs treated with various pupal extracts induced workers to pick up the discs but not to transport them back to the nest. Displaced brood of *Tapinoma erraticum* Latrielle were rapidly returned to their nest by workers, and a brood extract applied to *Solenopsis fugax* (Latrielle) brood induced *T. erraticum* workers to transport the foreign brood to their nest. However, only a small percentage of filter paper pieces treated with brood extract were taken by workers, which indicated that there were probably both physical and chemical factors involved (Meudec 1978).

Nestmate Recognition

There is ample evidence that species recognition and conspecific intercolony recognition in social insects has its basis in species and individual colony odors (Wilson 1971). We have already seen in previous sections how the specialized intracolony examples of fire ant queen recognition and brood recognition are mediated by chemical signals. Now we want to look at the broader picture of species and colony odors.

Colony odors appear to be comprised of innate odors characteristic of a

species and environmental odors absorbed onto the insects cuticle, which serve to distinguish colonies of the same species (Wilson 1971). Jutsum et al. (1979) found that individuals of *Acromyrmex octospinosus* (Reich) taken from widely separated nests were more hostile towards one another than to ants taken from local nests. In laboratory experiments *A. octospinosus* colonies fed on similar material were non-aggressive toward each other, but if fed different food materials they became aggressive. A colony split into 2 parts and fed on different materials responded with non-injurious aggression when recombined. Jutsum et al. (1979) concluded that both genetic and environmental factors contribute to colony odor, with environment being the more important.

Genetic differences within colonies of the same species may also be important in intracolony interactions as demonstrated by reports of colony specific pheromones. Workers of *Atta cephalotes* mark the area around their nests with components that are both colony specific and genus or species specific. The volatility of the territorial pheromones, necessitate that marking be a continuous process (Jaffé et al. 1979). Workers of *Lasius neoniger* (Emery) are able to differentiate their own rectal fluid derived trail pheromone from that of conspecifics. The trail pheromone of a related species, *L. fuliginosus*, was identified from rectal fluid as a series of fatty acids (Huwyler et al. 1973, Fig. 3 XII). It is not unreasonable that colony specificity in these species could be based on differences in blends of fatty acid pheromones. These differences could be due to genetic variations in queens, dietary differences between nests (environmental expression of colony odor) or a combination of both (Traniello 1980). In the same vein, harvester ants distinguish between their own conspecific nest materials (Hangartner et al. 1970) and detect differences in conspecific trails laid from the Dufour's gland (Regnier et al. 1973). Workers of *Oecophylla longinoda* (Latrielle) mark their territory with spots of rectal sac secretions and only successfully defend territory marked by their nestmates (Hölldobler and Wilson 1977).

Species specific factors were demonstrated in 4 sympatric species of *Pogonomyrmex* that often have mating flights on the same days. The species are isolated reproductively by a combination of distinct daily rhythms, mating site isolation, and by the ability of males to identify conspecific females through species specific cuticular components (Hölldobler 1976). Two species of *Myrmica* produce similar volatile components in their Dufour's gland that induce workers of both species to forage, but the less volatile part is different in the 2 species and is recognized as such by workers (Cammaerts et al. 1978).

In a study on the influence of nest material and colony odor on digging behavior in *S. invicta*, Hubbard (1974) determined that workers preferentially dug in nest materials from their own colony and not in unnested soil or nest material from other *S. invicta* colonies. Hubbard (1974) suggested that since the colony diets were identical, then the only difference between nested soil and unnested soil was the nesting of the ants. Therefore the ants themselves must transfer specific colony odors to the nest soil. It is possible for specific environmental odors to be absorbed onto an ant's cuticle and then subsequently transferred by contact to nest material. Another possibility is that the innate factors, which are considered species specific, have enough potential genetic variation to act by themselves as

colony markers or to synergize the environmental effects. Chemical components of the cuticle could easily and involuntarily be transferred to nest material during normal colony activities. This type of transfer was alluded to by Wilson (1976) in a study of *Pheidole dentata* Mayr defense against *S. geminata*. *P. dentata* major workers can distinguish trail laying minor workers that have just contacted fire ants, apparently by transfer of the *S. geminata* body odor. We have already discussed another example of fire ant conspecific preference in the Jouvenaz et al. (1974) report that *S. invicta* workers were more strongly attracted to squares previously occupied by the mother queen than those previously occupied by foreign *S. invicta* queens.

Although we have seen that territorial marking involves specific glandular secretions, it is appealing when considering species recognition of individuals to sheath the entire ant in a chemical construct that communicates its species identification to all those that come in contact with it. This follows the generalization that in all social insects recognition of a nestmate only involves a pause and sweep of the antennae over the other's body (Wilson 1971). Lok et al. (1975) found that hydrocarbons comprise 65-75% of the cuticular lipids from adult *S. invicta* and *S. richteri*. The hydrocarbon patterns were shown to be distinctly different for these 2 species and were composed of saturated, monomethyl and dimethyl branched hydrocarbons (Nelson et al. 1980, Thompson et al. 1981). Vander Meer (unpublished results) extended the study to *S. geminata* and *S. xyloni* and showed that their hydrocarbons consisted of distinct patterns of saturated and unsaturated paraffins. The 4 *Solenopsis* species studied could be readily identified by their hydrocarbon pattern. Cuticular hydrocarbons have been used as chemotaxonomic tools for other insect groups (Carlson and Service 1980, Carlson and Walsh 1981) and have been postulated to be semiochemical cues for caste and species recognition in termites (Howard et al. 1978, Blomquist et al. 1979).

Chemical studies in our laboratories with *S. invicta* indicate that the characteristic pattern of 5 major hydrocarbons is ubiquitous not only in adults but also in immatures. The pattern is found in the fat body, postpharyngeal gland, queen's ovarioles, eggs, and not surprisingly, in view of Hubbard's (1974) work, we have isolated the hydrocarbons even from nest soil (Vander Meer unpublished results). The hydrocarbons and their general pattern are unique to *S. invicta* and are not found in the surrounding environment. Workers of *S. richteri* treated with cuticular hydrocarbons of *S. invicta* have a much longer survival rate than normal *S. richteri* when placed with *S. invicta* workers, implying that the hydrocarbons convey a masking effect to the foreign ant (Glancey unpublished data).

Further evidence alluding to the role of cuticular hydrocarbons in species and colony recognition came from a study of the integration mechanism of the myrmecophilus beetle, *Myrmecophodius excavaticollis* (Blanchard). The beetle has been found living congenially with 4 *Solenopsis* species. It was experimentally determined that the beetle acquired the species specific cuticular hydrocarbons from its initial host, *S. richteri*. After removal from the ant host it lost host hydrocarbons leaving a pattern innate to the beetle. On transfer to *S. invicta* colonies, the surviving beetles acquired the species hydrocarbons associated with its new host. The mechaism of hydrocarbon transfer is unknown, however, the acquisition of host

hydrocarbons is associated with the beetles acceptance into fire ant colonies (Vander Meer and Wojcik 1982).

Other chemical classes of compounds such as wax esters, triglycerides, sterols and fatty acids are also present on fire ant worker cuticle (Lok et al. 1975) and may contribute to a blend of species specific components. However, hydrocarbons have the most appeal because of their past record for having physiological activity as sex pheromones (Conner et al. 1980, Carlson et al. 1978), alarm pheromones (Lofquist 1976), and kairomonal cues for parasites (Vinson et al. 1974). It would appear that cuticular hydrocarbons are important in fire ant species recognition and may be considered an important part of innate colony odor. Overlaying this are environmental odors, which create intraspecific colony odor differences. We have found that *S. invicta* laboratory colonies reared under identical conditions are less aggressive toward each other than they are toward field colony individuals, which is indicative of environmental colony odor factors (Glancey, unpublished data). It is possible, however, that queen genetic differences could be expressed in progeny through quantitative variations of species specific hydrocarbon patterns, which could be distinguished by workers and at least partially account for colony odor.

Summary

The trail pheromone has received by far the most attention over the years, and this has resulted in many excellent behavioral studies. The recent structure elucidation of several trail pheromone components has opened up the possibility of fully understanding this chemically and behaviorally complex pheromone system. It is very interesting that both recruitment and trail following are released by different pheromone components produced in the Dufour's gland. A more detailed look at these behaviors versus trail chemistry may reveal even more intriguing relationships. The outlook is very bright for trail pheromone research.

Interest in queen pheromones, in all of their aspects, has experienced a resurgence of activity since the initial discovery of their existence in 1974. Of particular importance was the development of specific bioassays to measure attraction and queen recognition, and the discovery of the venom sac and gland as the source of these pheromones. The venom of queen and worker will surely come to be classic examples of glandular and pheromonal parsimony. The primer pheromone that inhibits the dealation of alates is a behaviorally unique system. Certainly one of the major goals in queen pheromone research is the identification and isolation of pheromone components. This is a very difficult problem considering the requirement for large numbers of queens and the potentially complex chemistry. With reliable bioassays and modern instrumentation these problems will eventually yield to solution.

There has been no published work on the brood pheromone since 1975, perhaps because that paper claimed to have identified the pheromone as a triglyceride. However, I do not see any bona fide evidence for that claim and consider the brood pheromone as a problem waiting to be solved. Our research group is reinvestigating the brood pheromone and as mentioned previously the most difficult and crucial part of this work is the development of a reliable bioassay that clearly distinguishes between a feeding

response and a pheromone response. The prognosis for the brood pheromone is cautiously interesting.

Nestmate recognition has been an area of rapid research growth in last few years and promises to continue in that vein. The commonality of hydrocarbons within a species is the most obvious aspect of nestmate recognition and may even be linked to brood, queen, and trail recognition. The role of learning in nestmate recognition has been studied in other ant species and may also be important in fire ants. The prospects for additional significant work in this area are excellent.

Throughout this paper the various pheromones have been discussed as isolated entities. I feel an obligation to at least bring them all together diagrammatically, since in social insect colonies they are interrelated. And indeed when we look at a simplified life-cycle diagram with the known pheromone interactions included (Fig. 5) we find that disruption of any of the interactions would incapacitate the colony as a whole. For instance if the trail pheromone was not present the food gathering capacity of the colony would be inadequate. Disruption of any of the queen produced pheromones would result in either lack of queen tending or continuous dealation and annihilation of female sexuals. Areas that have received little attention so far are also represented in Fig. 5; caste differentiation, pheromones associated with mound opening during mating flights, male aggregation pheromones, and sex pheromones are some of the areas that are virgin research territories. On top of the colony diagram is overlaid species specific colony odors plus odors derived from the surrounding complex environment. In a field of fire ant colonies this picture is repeated again and again. As *Solenopsis invicta* has proven so well, the system works.

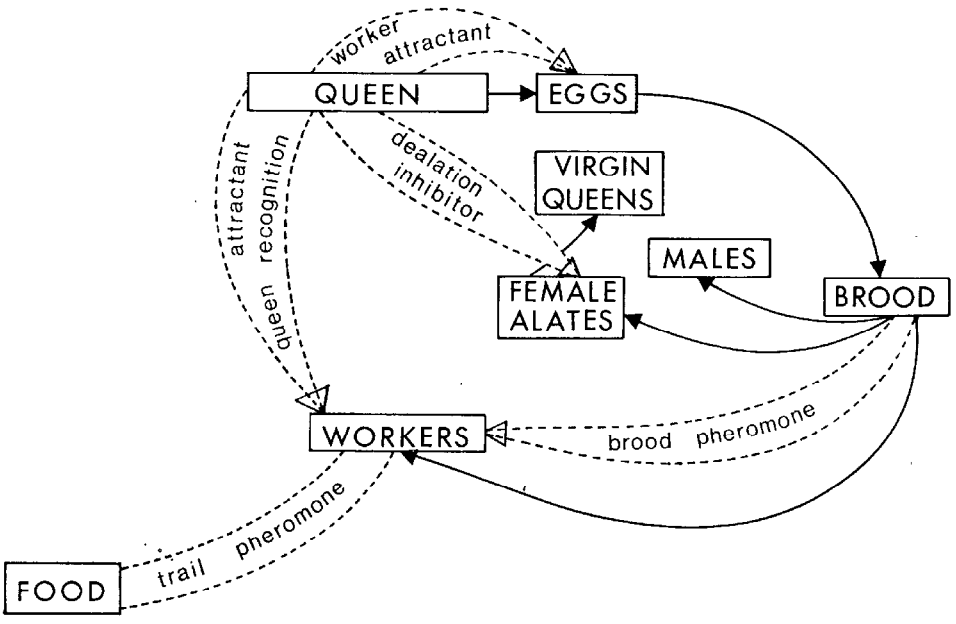


Fig. 5. Diagrammatic representation of the known imported fire ant pheromone systems superimposed on a simplified life-cycle diagram.

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