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Trail Pheromones in Pest Control

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1. Introduction

Insects are considered pests if they threaten a resource that is valued by humans, such as human health. The protection of a resource from a pest is usually achieved by poisoning the pest with a toxic pesticide, but protection can also be achieved by manipulating a behavior of the pest. Manipulation is defined as the use of stimuli that either stimulate or inhibit a behavior, thereby changing its expression. This definition excludes some areas in which changes in pest behavior are advantageous to pest management, notably those resulting from the sublethal effects of toxic chemicals or substances that induce a gross change in physiology (Gould, 1991) and those that merely consider the pest's behavior, such as planting a crop out of synchronization with the pestilential behavior. Intuitively, one might expect that the manipulation of a pestilential behavior (e.g., feeding on the resource) or a behavior closely related to the pestilential behavior (e.g., finding the resource) is more likely to be useful for pest management than the manipulation of behaviors unrelated to the resource (e.g., mating). The attract-annihilate method is by far the most widely used behavioral manipulation for pest management. The strategy of this method is simple: attract the pests to a site where as many of the pests as possible can be removed from the environment (Lanier, 1990).

The principle of using a pest's own communication system as a weapon against it is not new, nor is it restricted to the control of fruit pests. A similar idea is at the heart of a number of initiatives to control a range of stock pests and to control a range of insects that present a risk to human health, either directly or as a result of the agents of disease that they transport. Once chemists learned that communication among a variety of organisms depends on chemical substances termed pheromones, they isolated, identified and synthesized hundreds of pheromones for such practical applications as pest control. Pheromones are a class of semiochemicals that insects and other animals release to communicate with other individuals of the same species. The key to all of these behavioral chemicals is that they leave the body of the first organism, pass through the air (or water) and reach the second organism, where they are detected by the receiver.

In insects, these pheromones are detected by the antennae on the head. The signals can be effective in attracting faraway mates and, in some cases, can be persistent, remaining in

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place and active for days. Long-lasting pheromones allow the marking of territorial boundaries or food sources. Other signals are notably short-lived and are intended to provide an immediate message, such as a short-term warning of danger or a brief period of reproductive readiness.

Pheromones can be of many different chemical types, which serve different functions. As such, pheromones can range from small hydrophobic molecules to water-soluble peptides. Pheromones regulate many types of insect behavior. Sex pheromones are produced by one sex (usually the female) to attract the other sex for mating. Mass attacks by certain bark beetles are coordinated by aggregation pheromones that attract other beetles to the same tree. Alarm pheromones are produced by honey bees and aphids to help in colony defense. Trail pheromones are produced by ants to help other worker ants find food sources.

Despite the discovery and characterization of ant trail pheromones over the past few decades (El-Sayed, 2010), surprisingly few investigations of these compounds have been undertaken for pest management. Research on the potential for using odorants in this way has targeted the control of leaf cutting ants and the red imported fire ant (Vander Meer, 1996), but the current paradigm remains largely confined to improving the performance of toxic baits (Rust et al., 2004). New application technologies that deliver pheromones against invasive pest ants could help reduce our reliance on the use of insecticides for ant pest control in sensitive ecosystems or where insecticides are undesirable. Trail pheromone disruption that affects recruitment is an example of a novel tactic for ant pest management. A synthetic trail pheromone has been applied in combination with insecticidal bait (hereafter 'bait') in an attempt to develop a novel strategy for controlling invasive ants in a small treatment area.

Trail pheromones are species-specific chemical compounds that affect insect behavior and bioactivity. These pheromones are active (e.g., attractive) in extremely low doses (one millionth of an ounce) and are used to bait traps or confuse a mating population of insects. Pheromones can play an important role in integrated pest management for structural, landscape, agricultural, or forest pest problems. In this chapter, we introduce certain principal aspects of trail pheromones, including source, optimum dose, longevity, and specificity. We also discuss synthetic trail pheromones and the possibility of applying them in pest control.

2. Pheromones

Pheromones were originally defined as 'substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction, for instance, a definite behavior [releaser pheromone] or developmental process [primer pheromone]. The word pheromone comes from the Greek *pherein*, meaning to carry or transfer, and *hormon*, meaning to excite or stimulate. The action of pheromones between individuals is contrasted with the action of hormones as internal signals within an individual organism.

Pheromones are often divided by function, such as sex pheromones, aggregation pheromones and trail pheromones.

The main methods for utilizing an understanding of pheromones to control pests are monitoring, mating disruption, 'lure and kill' or mass trapping, and other manipulations

of pest behavior. Some of these techniques have been applied to control other animal pests, including vertebrate herbivores, such as deer. A major strength of pheromones is their effectiveness as part of integrated pest management (IPM) schemes because of their compatibility with biological control agents and other beneficial invertebrates, such as bees and spiders. Pheromones fit neatly into the *virtuous* spiral, for example, in greenhouse IPM, where the use of one biological control agent, such as a predatory spider mite, encourages (or requires) moving away from conventional pesticides for other pests (Lenteren & Woets 1988).

2.1 Sex pheromones

Sex pheromones have been identified for a large number of insect pests, particularly Lepidoptera. These chemicals have a number of useful attributes for the attract-annihilate method, including specificity, eliciting long-distance responses and longevity in the field. However, because most sex pheromones are produced by females and elicit responses from males, they have been used primarily in the mating disruption method, or for monitoring, rather than for the attract-annihilate method. The removal of adult males, unless at a very high proportion of the population, is unlikely to have a large impact on the size of subsequent generations compared with the removal of females (Lanier, 1990). Sex pheromones have also been used as attractants to facilitate contact with and the dispersal of pathogens in pest populations (Pell et al., 1993). Pheromones have been identified for many insect pests. The website 'Pherolist', for example, cites more than 670 genera from nearly 50 families of Lepidoptera in which female sex pheromones have been identified (Arn et al., 1995).

2.2 Aggregation pheromones

Aggregation pheromones lead to the formation of animal groups near the pheromone source, either by attracting animals from a distance or by stopping ('arresting') passing conspecifics (Wyatt, 2003). In contrast to sex pheromones (which attract only the opposite sex), aggregation pheromones, by definition, attract both sexes (and/or, possibly, larvae).. The pheromones' ability to attract females makes them well suited for the attract-annihilate method (Lanier, 1990). Aggregation pheromones have been used successfully for controlling various Coleoptera, including the cotton boll weevil *Anthonomus grandis* in the United States (Hardee, 1982) and bark beetles in North America and Europe (Lanier, 1990). Innocenzi et al. (2001) characterized a male-produced aggregation pheromone of *An. rubi* as a 1:4:1 blend of grandlure I, grandlure II and lavandulol (note: 'grandlure' is the name given to four components in the aggregation pheromone lure of the cotton boll weevil, *An. grandis* Boh.). A blend of the synthetic compounds was shown to attract both male and female beetles.

2.3 Alarm pheromones

Alarm pheromones have been identified most frequently from social insects (Hymenoptera and termites) and aphids, which usually occur in aggregations. In many cases, these pheromones consist of several components. The function of this type of pheromone is to raise an alert in conspecifics, to raise a defense response, and/or to initiate avoidance (Rechcigl & Rechcigl, 1998). Weston et al. (1997) showed a dose response of attraction and

repellence for several pure volatiles from the venom of the common wasp *Vespula vulgaris* and the German wasp *V. germanica*. The compounds are usually highly volatile (low molecular weight) compounds, such as hexanal, 1-hexanol, sesquiterpenes (e.g., (E)- β -farnesene for aphids), spiroacetals, or ketones (Francke et al., 1979). The alarm pheromones of aphids have been used commercially to increase the effectiveness of conventional pesticides or biological control agents, such as the fungal pathogen *Verticillium lecanii* (Howse et al., 1998). Synthetic alarm pheromones and the increased activity of the aphids in response to their alarm pheromones increases mortality because they come in contact more often with insecticide or fungal spores (Pickett et al., 1992).

2.4 Host marking pheromones

Spacing or host marking (epidictic) pheromones are used to reduce competition between individuals and are known from a number of insect orders. One of the best studied is from the apple maggot *Rhagoletis pomonella* (Tephritidae), where females ovipositing in fruit mark the surface to deter other females. This behavior has also been studied in the related cherry fruit fly (*R. cerasi*). Egg laying is a key stage determining subsequent population density; therefore, it is perhaps unsurprising that there is considerable evidence of such pheromones affecting gravid females of herbivores. There is also exploitation of prey host marking and sex pheromones by parasitoids, which use the signal persistence of these intraspecific cues to find their hosts. Mating-deterrent pheromones are also known from a number of insects, including tsetse flies, houseflies, and other Diptera. These pheromones are released by unreceptive females to deter males from continuing mating attempts (Rechcigl & Rechcigl, 1998).

2.5 Trail pheromones

Chemical trail communication allows group foragers to exploit conspicuous food sources efficiently, and it is the most prevalent form of recruitment behavior. Trail communication is commonly based on a multicomponent system, in which the secretions of different glands (or a blend of pheromones produced by the same gland) may contribute to the structure of the trail and regulate different behaviors in the process of recruitment (Hölldobler & Wilson 1990; Jackson et al. 2006).

Trail pheromones are used by animals as navigational aids in directing other members of the colony to a distant location, varying in length from hundreds of meters in bees to meters in terrestrial insects. The reasons for orienting members of the colony to a distant point may vary. In most cases, trails are laid by foraging workers as they return from a food source. These trails are then used by other foragers (Wilson & Pavan, 1959). In other cases, however, trails may be laid to recruit workers for slave raids, colony emigration, or the repair of a breach in the nest wall (Wilson, 1963). Different types of trail marking are found in terrestrial insects and flying insects. The terrestrial insects appear to lay a continuous or nearly continuous trail between points. Wilson (1962) showed that the fire ant (*Solenopsis saevissima*) drags its stinger and lays a trail in a manner similar to a pen inking a line. If the food source is of good quality, other workers choose to reinforce this trail, and a highway several centimeters wide may be formed.

2.5.1 Trail pheromones in bees

To ensure a sufficient food supply for all colony members, the stingless bee *Trigona corvina* has evolved various mechanisms to recruit workers for foraging or even to communicate the location of particular food sites. In certain species, foragers deposit pheromone marks between food sources and their nest, and these marks are used by recruited workers to locate the food (Jarau et al., 2010).

Honeybees have one of the most complex pheromonal communication systems found in nature, possessing 15 known glands that produce an array of compounds (Free, 1987). The stingless bee *Trigona subterranean* deposits scent marks from the mandibular glands every few meters between the nest and food to form a trail that alerts nest mates to follow it. When a scout bee has discovered a food source, it usually makes several trips between its nest and food before it lays down a trail pheromone. Scent marks are deposited on leaves, branches, pebbles and even clumps of earth.

The Dufour secretions of bee workers are similar to those of a healthy queen. The secretions of workers in queen right colonies are long-chain alkenes with odd numbers of carbon atoms, but the secretions of egg-laying queens and egg-laying workers of queenless colonies also include long chain esters (Soroker & Hefetz, 2002). Jarau et al. (2004) recorded that in *T. recursa*, the trail pheromone is produced in the labial glands and not in the mandibular glands. Hexyl decanoate was the first component of a trail pheromone identified, and it proved to be behaviorally active in stingless bees (Jarau et al., 2006).

2.5.2 Trail pheromones in termites

Foraging termites produce a variety of chemicals, known as pheromones that influence their behavior. While tunneling underground, foraging termites lay down a trail of pheromones, which they secrete from glands on their abdomen. When a food source is located, the odor trail is intensified to recruit other termites to the feeding site (Miller, 2002). However, the intensity of the recruitment effort (odor trail) is influenced by soil temperature, moisture and compaction, as well as the size and quality of the food source. Sillam-Dussès et al. (2007) studied the trail pheromone in the most basal extant termite, *Mastotermes darwiniensis* (Mastotermitidae), and two other basal termites, the Termopsidae *Porotermes adamsoni* (Porotermitinae) and *Stolotermes victoriensis* (Stolotermitinae). Although workers of *M. darwiniensis* do not walk in single file when exploring a new environment under experimental conditions and are unable to follow artificial trails in 'open field' experiments, they do secrete a trail-following pheromone from their sternal glands. The major component of the pheromone appears to be the same in the three basal species: the norsesquiterpene alcohol (*E*)-2, 6, 10-trimethyl-5, 9-undecadien-1-ol. The quantity of the pheromone was estimated as 20 pg / individual in *M. darwiniensis*, 700 pg / individual in *P. adamsoni*, and 4 pg / individual in *S. victoriensis*. The activity threshold was 1 ng/cm in *M. darwiniensis* and 10 pg / cm in *P. adamsoni*.

2.5.3 Trail pheromones in ants

Ants deploy a pheromone trail as they walk; this trail attracts other ants to walk the path that has the most pheromones. This reinforcement process results in the selection of the

shortest path: the first ants coming back to the nest are those that took the shortest path twice (to go from the nest to the source and to return to the nest); therefore, more pheromone is present on the shortest path than on longer paths immediately after these ants have returned, stimulating the nest mates to choose the shortest path (Jackson & Ratnieks, 2006). Nicolis (2003) suggested that the modulation of trail laying is determined not only by food quality but also by the intrinsic capacity of individuals to lay a certain quantity of pheromone. Furthermore, small colonies (or small groups of ants specialized in trail laying) are less capable of taking advantage of the trail recruitment than large colonies (or large groups of trail-laying foragers). The trail is deposited on the ground by dragging the tip of the abdomen along the ground or by touching the surface with the anal hairs or the tip of the lancet of the sting (Wilson, 1963). In *Crematogaster* species, the trail is deposited on the ground by placing the hind legs close together and drumming on the surface with the tips of the tarsi (Fletcher & Brand, 1968).

In *Componotus socius* (Hölldobler, 1971) and in *Formica fusca* L. (Möglich & Hölldobler, 1975), workers lay trail contents from the food sources to the nest, but the trail is followed by worker ants only if they are preceded by a "waggle" display of the recruiting ant. In *Aphaenogaster* (*Novomessor*) and *Messor*, stridulation enhances the effectiveness of recruitment pheromones (Hahn & Maschwitz, 1985). Some *Polyrhachis* species employing leader-independent trail communication do not follow artificial trails without being mechanically invited first (*P. arachne*, and *P. bicolor*) (Liefke et al., 2001). The accumulation of fire ants in electrical equipment is the result of a foraging worker finding and closing electrical contacts followed by releasing exocrine gland products that attract other workers to the site, who, in turn, are electrically stimulated (Vander Meer et al., 2002).

In ants, the different recruitment mechanisms include tandem running in which the scout ant leads one nest mate to the resource; group recruitment, which recruits tens of nest mates; and mass communication, which uses pheromones to recruit large numbers of nest mates (Wyatt 2003). Jackson & Châline (2007) found that pheromone trails are self-organized processes, where colony-level behavior emerges from the activity of many individuals responding to local information. The Pharaoh's ant is an important model species for investigating pheromone trails. Pharaoh's ant foragers mark their path with trail pheromones using their stinger on both the outgoing and return leg of foraging trips. An examination of trail markings showed that 10.5% of returning fed ants simply made marks by dragging their engorged gaster, as stinger marks were absent. After discounting gaster-dragging hair marks, fed ants (42.5%) did not mark significantly more than unfed ants (36.0%). However, the trail-marking fed ants marked pheromone trails with a significantly greater intensity compared with trail-marking unfed ants if the food source was high quality (1.0 M sucrose). When the food quality was low (0.01 M sucrose) there was no significant difference in marking intensity between fed and unfed trail-marking ants. In Pharaoh's ants, individual trail marking occurs at a frequency of ~40% among fed and unfed foragers, but the frequency of individuals marking with high intensity (continuous marking) is significantly greater when a food source is high quality. This behavior contrasts with another model species, *Lasius niger*, where trail strength is modulated by an all-or-nothing individual response to food quality. The reason for this fundamental difference in mechanism is that the Pharaoh's ant is highly reliant on pheromone trails for environmental orientation; therefore, it must produce trails, whereas *L. niger* is proficient at visually based orientation.

Robinson et al. (2008) reported that Pharaoh's ants (*Monomorium pharaonis*) use at least three types of foraging trail pheromones: a long-lasting attractive pheromone and two short-lived pheromones, one attractive and one repellent. They measured the decay rates of the behavioral response of ant workers at a trail bifurcation to trail substrate marked with either repellent or attractive short-lived pheromones. The results show that the repellent pheromone effect lasts more than twice as long as the attractive pheromone effect (78 min versus 33 min). Although the effects of these two pheromones decay at approximately the same rate, the initial effect of the repellent pheromone on branch choice is almost twice that of the attractive pheromone (48% versus 25% above the control). These researchers hypothesize that the two pheromones have complementary but distinct roles, with the repellent pheromone specifically directing ants at bifurcations, while the attractive pheromone guides ants along the entire trail.

2.5.3.1 Source of trail pheromones

The sources of trail pheromones are the venom gland, Dufour's gland and the hind tibia in Myrmicinae; the pygidial gland in Ponerinae; Pavan's gland in Dolichoderinae; the postpygidial gland in Aenictinae; and the hindgut in Formicinae (Fig. 1) (Billen & Morgan, 1998). The Dufour glands of at least a portion of myrmicine, formicine, poneromorph, myrmeciine, pseudomyrmecine and dolichoderine ants contain a mixture of straight-chain hydrocarbons from approximately C9 to C27 (Morgan, 2008).

The Dufour gland contains the trail pheromone in a few species; in several others, it has been shown to have a homemarking effect (Cammaerts et al., 1981); and in *Pogonomyrmex* species, it provides longer-lasting trunk route markers (Hölldobler et al., 2004), and its secretion confuses or repels potential slaves of slave-making species. Dufour's gland is the source of trail pheromone in *Solenopsis* species (Robert, et al., 1989), in *Pheidole fallax* Mayr (Wilson 1963), in *M. destructor* (Ritter et al., 1980), in *Gnamptogenys menadensis* (subfamily Ponerinae) (Gobin et al., 1998), in the slave-making ant *Polyergus rufescens* (Visicchio et al., 2001), in *M. mayri* (Mashaly, 2010), in the samsum ant *Pachycondyla sennaarensis* (Mashaly et al., 2011) and in *Messor meridionalis* and *M. foreli* (Mashaly, 2011).

The poison gland is the source of the trail pheromone in genus *Atta*, such as *A. sexdens arthropilosa* Forel (Cross et al., 1979); in genus *Monomorium*, such as *M. niloticum* and *M. najrane* (Mashaly, 2010) and *M. lepineyi* and *M. bicolor* (Mashaly et al., 2010); and in genus *Tetramorium*, such as *T. simillimum* (Ali & Mashaly, 1997a). Cammaerts et al. (1994) found, in *T. aculeatum*, that the trail pheromone contained a complex mixture of substances. Two of these components are secreted by the poison gland: the most volatile component is an attractant that increases the ants linear speed; the other is the trail pheromone. A third component, present on the last abdominal sternite, acts as an attractant, a locostimulant and a synergist for the trail pheromone. The activity of these substances increases with the age of the workers. The poison gland of *Leptothorax distinguenda* contains two pheromone components: one elicits a strong short-term attraction to prey items; the other guides workers from foraging sites to the colony but only weakly. The poison gland of each minor and major worker is the source of the trail pheromone in *Ph. jordanica* Saulcy and *Ph. sinatica* Mayr (Ali & Mashaly, 1997b). In *Ph. embolopyx* (Jackson & Ratrieks, 2006), the trail pheromone is secreted from the poison gland of only minor workers.

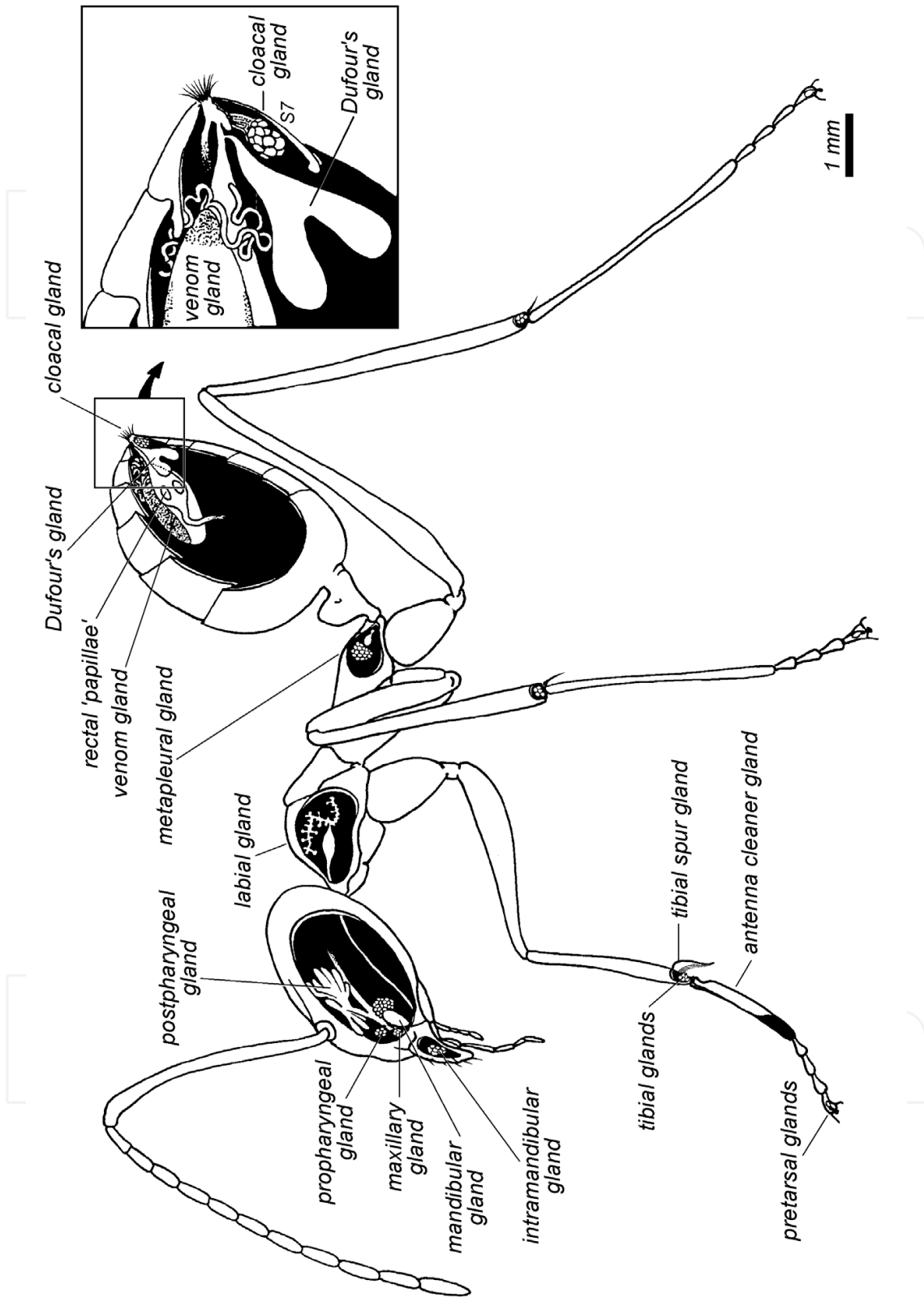


Fig. 1. Schematic drawing of a typical ant worker, showing the location of the various exocrine glands. The inset shows an enlargement of the abdominal tip, with the position of the cloacal gland, venom gland and Dufour's gland indicated (Wenseleers et al., 1998).

Hindgut is found throughout the Formicinae, in *Eciton* and *Neivamyrmex* of the Ecitoninae and in *Diacamma* in the Ponerinae (Hölldobler & Wilson, 1990; Morgan, 2008). Wilson & Pavan (1959) found that the dolichoderine ant *Iridomyrmex humilis* Myer uses Pavan's gland (sternal gland) as a source of the trail pheromone, with the trail substance being secreted via the posterior border of the sixth sternite. Also, the sternal gland is recorded as the source of the trail pheromone in the ant *Dolichoderus thoracicus* Smith (Attygalle et al., 1998) and in *P. tarsata* (Janssen et al., 1999).

The pygidial gland can be found in all subfamilies except the Formicinae. In the Dolichoderinae, the pygidial gland (also known as the anal gland) is usually very large, and is used in defense and alarm (Morgan, 2008). Termite predation by the ponerine ant *Pachycondyla laevigata* is regulated by a recruitment trail pheromone that originates from the pygidial gland and not, as previously assumed, from the hindgut. The pygidial gland opens between the 6th and 7th abdominal terga and is associated with a distinct cuticular structure that obviously serves as a glandular applicator (Hölldobler et al., 1980). The existence of a trail pheromone in a postpygidial gland of an *Aenictus* species has been demonstrated, and the substances have been identified as methyl anthranilate and methyl nicotinate. The pheromone consists of two parts: a primer effect, caused by methyl nicotinate, which prepares workers to follow trails but is not itself followed, and a releaser effect, caused by methyl anthranilate, which causes trail-following only in conjunction with the primer substance (Oldham et al., 1994).

The anatomy of the gaster of *Crematogaster* ants prevents them from laying trails from abdominal glands; therefore, they have adopted another system in which they use glands in the hind tibia with a duct to the tarsi to lay the secretion by the feet (Leuthold 1968). The same results were found by Fletcher & Brand (1968); Ayre (1969); Ali & Mashaly (1997a); and Morgan et al. (2004) while working with *C. peringueyi* Emery, *C. lineolata*, *C. inermis* and *C. castanea*, respectively.

Hölldobler & Palmer (1989) discovered special exocrine glands in the distal tarsomere of the hindlegs of *Amblyopone australis* workers, whereas foragers of *Amblyopone* mark their trails by setting "footprints" with secretions from these tarsal glands. Workers of the ant *Am. reclinata* employ solitary prey retrieval when the prey is small, but they recruit nestmates to large prey. In the latter case, the scout forager paralyzes the prey with its powerful sting and quickly returns to the nest. During this homeward journey, the scout deposits a trail pheromone, which originates from the well-developed footprint glands (pretarsal gland) in its hindlegs. Recruited workers follow this trail to reach the prey, which is later jointly dragged to the nest (Billen et al., 2005).

2.5.3.2 Optimum dose

It is well established that a specific concentration of trail pheromones is important because concentrations that are too high or too low elicit either no response or repellency (Barlin et al., 1976). Ants are able to optimize their foraging behavior by selecting the most rewarding source, due only to a modulation of the quantity of pheromone laid on a trail (Traniello & Robson, 1995).

Using extract of whole gasters, Van Vorhis et al. (1981) demonstrated for *I. humilis* Mayer that the optimum activity was found in response to a trail containing 0.1 - 1.0 ant equivalent

per 50 cm. The activity dropped when the concentration was lower or higher than the optimal concentration. When the concentration was increased to 5 ant equivalents per 5 cm trail, not only did the trail-following activity decrease but also the mean lateral distance from the trail at which ants exhibited trail following increased. *Myrmica rubra* L. workers responded actively to a synthetic pheromone concentration ranging from 10^{-2} - 10^2 ng per 30 cm trail (one poison gland produced 508 ng 3-ethyle-2,5dimthylepyrazine), whereas at concentrations lower than 10^{-2} ng, the workers had difficulty detecting the trail.

Morgan et al. (1990) found that the highest activity in *T. impurum* Foerster was at a concentration of 0.1 poison gland equivalent / 30 cm trail. The activity decreased at a concentration of 1 and 0.01 poison gland / 30 cm trail and subsequently completely disappeared at the concentration of 0.001 gland. In *Ph.jordanica*, *Ph. sinaitica* and *Ph. sp.*, the workers induced the highest activity between one and 5 gaster equivalent/30 cm trail (Ali & Mashaly, 1997b). In *Paratrechina longicornis* and *P. vividula*, the optimum dose of the trail-following was found to be 1 gaster equivalent / 30 cm trail (Mashaly et al., 2008). In *M. lepineyi* and *M. bicolor*, the optimal dose was found to be 1.0 and 0.1 poison gland equivalent/30 cm trail, respectively (Mashaly et al., 2010). The optimum concentration was 1.0 and 0.1 gaster equivalent (GE)/30 cm trail in *M. niloticum*, 1.0 GE in *M. najrane* and 5.0 GE in *M. mayri* (Mashaly, 2010). In *M. meridionalis* and *M. foreli*, the optimum concentration of trail pheromone was found to be 1 gland equivalent/30 cm trail (Mashaly, 2011). In *P. sennaarensis*, the optimum concentration of trail pheromone was found to be 0.1 gland equivalent/40 cm trail (Mashaly et al., 2011).

2.5.3.3 Trail longevity

Pheromones are released mainly from exocrine glands as liquids that evaporate into the surrounding air. The distance through which a pheromone may transmit a message is a function of the volatility of the compound, its chemical stability in air, the rate of diffusion, the olfactory efficiency of the receiver, and wind speed and direction (Fitzgerald & Underwood, 1998). In ants, trail longevity varies from minutes in *Aphaenogaster albisetosus* (Hölldobler et al., 1995), to 2 h in *M. lepineyi* and *M. bicolor* (Mashaly et al., 2010), to 1 h in *M. niloticum*, *M. mayri*, and *M. najrane* (Mashaly, 2010), to 105 mins in *P. longicornis* and *P. vividula* (Mashaly et al., 2008), to 1 hr in *M. meridionalis* and *M. foreli* (Mashaly, 2011) and to several weeks in some *Eciton* species (Torgerson & Akre, 1970). Short-lived trails can rapidly modulate recruitment to ephemeral food sources, whereas long-lived trails will be more suited to persistent, or recurrent, food sources (Fitzgerald & Underwood, 1998). The activity of the optimal dose trail pheromone in *P. sennaarensis* decreased to half of the original activity level after approximately 30 min, and it completely disappeared after 1 h (Mashaly et al., 2011).

2.5.3.4 Specificity of trail pheromones

No matter which gland they use, the myrmicines investigated to date show a strong variability of intra- and intergeneric trail specificity, ranging from a total or a partial specificity to a complete anonymity of signals (Traniello & Robson, 1995). For example, odor trail pheromones are completely species-specific between *T. caespitum* Linne, 1758, and *T. guineense* Bernard, 1953, but the latter could follow trails of other myrmicine genera (Blum & Ross., 1965). Workers of *C. scutellaris* Olivier, 1792 follow the trails of *C. laestrygon* Emery, 1869, but the latter always prefer their own trace (Gobin & Billen., 1994). A partial specificity

was also found within the genus *Solenopsis* Westwood, 1840, with some species following each other's artificial trails and others being highly selective in their response (Barlin et al., 1976). Interspecific trail-following tests in three sympatric species, *M. capitatus*, *M. minor* and *M. wasmanni*, showed that workers of each species are able to recognize and follow artificial trails obtained from the Dufour's gland secretions of the others (Grasso et al., 2002). There is no species specificity among *M. niloticum*, *M. najrane* and *M. mayri* in their trail pheromones (Mashaly, 2010). Also, the response of the two Messor ants *M. meridionalis* and *M. foreli* to extracts of their trail pheromones, presented as a point source, is clearly non species-specific (Mashaly, 2011). *P. sennaarensis* and *Tapinoma simrothi* each respond to the trail pheromones of the other species, as well as their own (Mashaly et al., 2011).

2.5.3.5 Trail pheromone structures

Tumlinson et al. (1971) identified methyle, 4-methylepyrrole-2-carboxylate, a poison gland substance of *A. texana*. This compound was the first ant trail pheromone to be identified. The trail pheromone in *A. sexdens arbropilosa* Forel was identified as 3-ethyl-2,5-dimethylepyrazine and methyl 4-methylpyrrole-2-carboxylate (Cross et al., 1979). The same substance was identified as the pheromone in *Acromyrmex octospinosus* (Cross et al., 1982). However, 3-ethyl-2,5-dimethylpyrazine (EDMP) (B) was identified as the trail pheromone of *A. sexdens rubropilosa* (Cross et al., 1979) and *Atta sexdens sexdens* (Evershed & Morgan, 1983). Using older gas chromatographic techniques with packed columns, Evershed & Morgan (1983) showed only M4MPC was found in *A. octospinosus* but that both EDMP and M4MPC were present in workers of *A. cephalotes*, *A. sexdens sexdens* and *A. sexdens rubropilosa*, although the ratio differed considerably, with the compound that had been identified as the trail pheromone in that species being present in a much larger proportion. A ratio for EDMP:M4MPC of 14:1 was found for *A. sexdens sexdens*.

M. pharaonis has been found to produce two trail substances from the poison gland, which were identified to be *Monomorine I* (3-butyl-5-methyl-octahydroindolizine) and *Monomorine III* [2-(5-hexenyl) 5-pentylpyrrolidine] (Ritter et al., 1973). However, the true pheromone was identified as faranal [(3S, 4R)-(6E, 10Z)-3, 4, 7, 11-tetramethyl-6,10-tridecadienal], which was secreted from the Dufour's gland and was shown to be much more active than the monomorines (Ritter et al., 1980). *M. niloticum* and *M. najrane* both contain mixtures of alkyl- and alkenyl-pyrrolidines and -pyrrolines in their venom glands, but no Dufour gland volatile compounds have been detected. *M. mayri* showed neither Dufour gland compounds nor venom components detectable by gas chromatography (Mashaly et al., 2010).

The trail pheromone of *T. caaspitum* was found to be secreted from the poison gland and was identified as a mixture of 2,5-dimethylpyrazine and 3-ethyl-2,5-dimethylpyrazine (7:3). Morgan et al. (1990) stated that *T. impurum* Foerster used methyl-2-hydroxy-6-methylbenzoate (methyl 6-methyl salicylate) as a trail pheromone secreted from the poison gland. Morgan et al. (2004) identified (*R*)-2-dodecanol as the major component of the trail pheromone secreted from the tibial gland of the ant *C. castanea*. The major compounds in the poison gland of *Pogonomyrmex vermiculatus* were found to be the alkylpyrazines, 2,5-dimethylpyrazine, 2,3,5-trimethylpyrazine, and 3-ethyl-2,5-dimethylpyrazine. In behavioral bioassays, poison gland extracts and the mixture of pyrazines produced a trail pheromone effect (Torres-Contreras et al., 2007).

Ali et al. (2007) stated that four Old World species of *Pheidole* ants contain different mixtures of farnesene-type hydrocarbons in their poison apparatus, and the mixture is different between the minor and major workers within a species. The poison glands of minor workers of *Ph. pallidula* contain 3-ethyl-2,5-dimethylpyrazine. No pyrazine compounds were found in the major workers of *Ph. pallidula* or the minor workers of *Ph. sinaitica*. The poison glands of the major workers of *Ph. sinaitica* contained larger amounts of tetra-substituted pyrazines. No pyrazines were found in the poison reservoirs of the major or minor workers of *Ph. teneriffana* or *Ph. megacephala*.

2.5.3.6 Trail pheromones and ant control

Ant control often relies on contact insecticides that are used as barrier treatments (Klotz et al., 2002). These chemical sprays provide only partial ant control because they kill or repel foragers but have little impact on the queens (Rust et al., 1996). Foragers constitute only a small fraction of the worker force and are quickly replaced by nest mates that reach maturity during the treatment period. Additionally, the degradation of these chemicals commonly occurs within 30 days of application, negating any residual effects (Rust et al., 1996) and increasing the need for reapplication. Granular treatments for ant control are commercially available for use in agricultural systems, especially nursery operations (Costa et al., 2001). Solid baits, typically targeting protein-feeding ants, have been somewhat successful (Tollerup et al., 2005). However, many pest species, including the Argentine ant, primarily forage for sugars (Klotz et al., 2002), which necessitates the development of liquid baits (Rust et al., 2004). For these reasons, more effective and environmentally sound ant control practices are needed for vineyards, especially for managers developing sustainable farming practices.

Three Thai herbs, namely, tuba root (*Derris elliptica* Benth.), yam bean seeds (*Pachyrhizus erosus* L.) and tea seed cake (*Camellia* sp.), were found to be an efficient control against adult workers of the Pharaoh ant (*M. pharaonis* L.). The results showed that the tuba root extracts exhibited LC₅₀ against adult workers at approximately 0.22 % w/v; yam bean seed extracts showed LC₅₀ against adult workers of approximately 0.35 % w/v; and tea seed cake extracts showed LC₅₀ against adult worker of approximately 0.55 % w/v after 24 hours of exposure (Tangchitphinitkan et al., 2007).

In a study to develop a novel control method of the invasive Argentine ant *Linepithema humile* (Mayr). A year-long treatment of small areas (100 m² plots of urban house gardens) with synthetic trail pheromone, insecticidal bait or both was conducted. The ant population could be maintained at lower than or similar to the initial level only by combined treatment with synthetic trail pheromone and insecticidal bait. In fact, the ant population was nearly always lowest in the combination treatment plots. Throughout the study period, the ant population in the plots treated with either the synthetic trail pheromone or insecticidal bait remained similar to that of the no-treatment plots (Sunamura et al., 2011).

3. Conclusion

Trail-following investigations may improve our understanding of the chemical communication system employed by pest species. Except for sex pheromones, the use of pheromones in pest management has been largely unexplored. A high concentration of trail pheromone disrupts trail following and foraging in ants; therefore, synthetic trail pheromones could be a novel control agent for pest ants.

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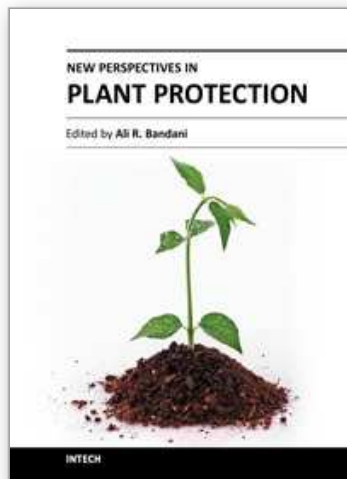
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Crop losses by pests (insects, diseases and weeds) are as old as plant themselves but as agriculture are intensified and cropping patterns including the cultivation of high yielding varieties and hybrids are changing over time the impact of the pests becoming increasingly important. Approximately less than 1000 insect species (roughly 600-800 species), 1500 -2000 plant species, numerous fungal, bacterial and nematode species as well as viruses are considered serious pests in agriculture. If these pests were not properly controlled, crop yields and their quality would drop, considerably. In addition production costs as well as food and fiber prices are increased. The current book is going to put Plant Protection approaches in perspective.

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