Alarm pheromones

Chemical signaling in response to danger

François J. Verheggen* ; Eric Haubruge ; Mark C. Mescher

* Author for correspondence

Running title: Alarm Pheromones

François J. Verheggen & Eric Haubruge

Department of Functional and Evolutionary Entomology

Gembloux Agro-Bio Tech, Liege University

2, passage des Déportés

B-5030 Gembloux, Belgium

Tel. 003281622286 ; Fax. 003281622312 ; mail. entomologie@fsagx.ac.be

Mark C. Mescher

Department of Entomology, Center for Chemical Ecology

The Pennsylvania State University

University Park, PA, 16802 USA

Tel. 0018148654208 ; mail. mcmescher@psu.edu

Summary

Many animals respond to the threat of predation by producing alarm signals that warn other individuals of the presence of danger or otherwise reduce the success of predators. While alarm signals may be visual or auditory as well as chemical, alarm pheromones are common, especially among insects and aquatic organisms. Plants too emit chemical signals in response to attack by insect herbivores that recruit the herbivores' natural enemies and can induce preparations for defense in neighboring plants (or other parts of the same plant). In this chapter we discuss our current understanding of chemical alarm signaling in a variety of animal groups (including social and pre-social insects, marine invertebrates, fish, and mammals) and in plants. We also briefly discuss the exploitation of alarm pheromones as foraging cues for natural enemies. We conclude with a brief discussion of the potential exploitation of alarm signaling to achieve the applied goal of managing pest species.

Key Words *(5 to 10 words, no"of" or "and")*

Alarm pheromone, aphid, ant, honeybee, fish, plant-plant communication, pest management strategy

Introduction

In response to the approach of predators--or other rapid adverse changes in the immediate environment--many organisms emit alarm signals that can alert nearby individuals (conspecifics as well as others) of impending danger. Alarm signaling has frequently been viewed as an evolutionary puzzle because the fitness benefits to individuals receiving the signal are usually apparent while signaling often appears costly for signalers (e.g. Taylor *et al.*, 1990). Genuinely altruistic signaling can presumably evolve where the benefits preferentially fall on conspecifics with higher than average relatedness to the signaler (Sherman, 1977) as suggested by inclusive fitness theory (Hamilton, 1964). But alarm signaling may also directly benefit the fitness of the signaling individual itself, for example if the anti-predator or escape behaviors induced by the call reduce the probability of successful predation (Högstedt, 1983; Sherman, 1985) or attract the predator away from the signaling individual (Charnov and Krebs, 1974). Alarm calls may also have delayed benefits for the signaler, for example by saving the lives of individuals who will reciprocate in the future (Trivers, 1971) or those of potential mates (Witkin and Fitkin, 1979) or other group members in circumstances where group living is beneficial (Smith, 1986).

Alarm signals frequently have visual and auditory components, especially in birds and mammals (e.g. Sherman, 1977; Seyfarth *et al.*, 1980; Leavesley and Magrath, 2005), but chemical alarm signals are also widespread (Wyatt, 2003). Chemical signals involved in communication with other conspecific individuals are called pheromones (from the Greek *pherein*, to transfer), and are thus distinguished from hormones (*hormon*, to excite) which mediate communication within an individual organism (Karlson and Lüscher, 1959). Most alarm pheromones likely have evolved from compounds originally having other functions.

Specifically, it has been proposed that alarm pheromones may evolve either from chemicals involved in defense against predators or from compounds released upon injury (Wyatt, 2003). To the extent that these compounds serve as reliable cues to the presence of predators, potential receivers should evolve to detect them and respond in ways that enhance fitness. The acquisition of a true signaling function then entails further evolutionary elaboration of the cue specifically in response to selection acting on its role in communication (Maynard Smith and Harper, 2003).

A large literature addresses chemical identification of alarm pheromones and their impact on the behavior of nearby individuals. In order to conclude that particular compounds acts as an alarm pheromone, it is generally considered necessary to demonstrate that (i) the chemical(s) is released exclusively under exposure to hazard (e.g. predator attack), (ii) the signal is perceived by conspecifics, and (iii) it induces in the receiving individuals behavioral reactions similar to that induced when directly exposed to the same danger (Wyatt, 2003). The latter criteria is usually the most difficult to demonstrate, as it is not enough to demonstrate a modification in the behavior of the receiving individuals; the changes must clearly be appropriate responses to danger specific threat. Generally, adaptive responses to the reception of an alarm pheromone may be classified as evasive (e.g., receivers flee from the pheromone releaser) or aggressive (receivers move toward the signal and attack or harass the predator). Observed reactions can vary according to the concentration of pheromone released and also with prior experience of the receiver (Howse, 1998).

Alarm pheromones have been documented in both vertebrate and non-vertebrate animals (Wyatt, 2003), and similar types of signaling seem to occur also in plants (Wittstock and Gershenzon, 2002; Heil and Karban, 2010). The chemical composition of alarm pheromones is highly variable: Table 1 presents a partial list of identified examples from animal systems.

Alarm signals may be as simple as a single molecule (e.g. citral in mites, Kuwahara et al., 1979), but can also be complicated chemical mixtures, whose activity is determined by their specific composition, the quantitative proportion of the different compounds, and the stereoisomerism of the dominating substances (Wadhams, 1990).

Table 1 near here

The remainder of this chapter reviews illustrative examples taken drawn from the tremendous diversity of alarm signaling systems that occur in presocial (aphids) and social (ants, termites, honeybees) insects, vertebrate animals, and plants.

Alarm pheromones in insects

Alarm pheromones appear to be the second most commonly produced class of chemical signals used by insects, after sex pheromones (Barbier, 1982). Alarm signaling has evolved in various Arthropod taxa in which the individuals are proximate enough to each other to rapidly communicate. Gregarious and social insects, including Hymenopterans and Hemipterans, have developed a diverse array of chemical compounds that function as releasers of alarm behavior (Table 1). Indeed, alarm pheromones appear to be highly adaptive for species in which individuals form aggregates that can exhibit a collective response to traumatic stimuli (Blum, 1985). In eusocial species, for example, they allow colony resources to be rapidly and efficiently deployed in response to specific threats. Insect alarm pheromones are usually short molecules of low molecular weight and simple structure (e.g., terpenoids or aliphatic ketones and esters). They are thus highly volatile and dissipate rapidly after emission as befits signals that operate over short time frames and at localized spatial scales (Payne, 1974). Various organs can be involved in their production, including anal glands, mandibles, and stings. Although commonly comprising mixtures of several compounds, alarm pheromones tend to be less specialized than other types of pheromones, and few are species specific (Blum, 1985). This relative non-specificity may be an advantage to species that are able to detect alarm signals of other insects sharing vulnerability to a common threat.

In non-eusocial insects the effects of alarm pheromones are generally limited to causing dispersal. The response to alarm signals varies among eusocial species, but commonly involves attraction/recruitment of conspecific workers or soldiers and the adoption of aggressive postures. Below we discuss alarm signaling in aphids, ants, and honeybees.

i. Aphids

Because aphids are important agricultural pests throughout the world, their biology and behavior has been well studied. Aphid alarm signaling was first characterized in the 1970s. In response to predation and other disturbances, aphids secrete droplets from two cornicles situated on the upper surface of the abdomen near the tail that emit an odor repellent to conspecifics (Kislow and Edwards, 1972) (Figure 1). This pheromone induces alate and apterous *Myzus persicae* (Hemiptera, Aphididae) to stop feeding and move away from the signaler or to drop from the host plant—waving their antennae before and during these aversive behaviors. Variation in response to alarm pheromone occurs both within and between species and correlates with to the relative risk of predation and the costs of escape (Pickett *et al.*, 1992).

The active component of the liquid secreted from the cornicles of several economically important species of aphids was found to be a sesquiterpene ($C_{15}H_{24}$) named (E)-7,11-dimethyl-3-methylene-1,6,10-dodecatriene, or more commonly (*E*)-ß-farnesene (Eßf) or trans-ß-farnesene (Bowers *et al.*, 1972) (Table 1). This same compound was subsequently identified in many other aphid species including the green peach aphid *Myzus persicae* Sulzer (Edwards *et al.*, 1973; Wientjens *et al.*, 1973) and the pea aphid *Acyrthosiphon pisum* Harris (Wohlers, 1981).

Germacrene A (Table 1), a biogenetic precursor of many sesquiterpenes, was later isolated from the alfalfa aphid and identified as an alarm pheromone (Bowers *et al.*, 1977b), though it appears to play this signaling role only within the genus *Therioaphis*. Pickett and Griffiths (1980) found *Megoura viciae* to synthesize additional monoterpenes, including α-pinene, ß-pinene and limonene, with (-)-α-pinene having the most significant alarm activity. (Z,E)-α-farnesene and (E,E)-α-farnesene were also reported in several aphid species (Pickett and Griffiths, 1980; Gut and Van Oosten, 1985), but did not show biological activity (Bowers *et al.*, 1977a).

Figure 1 near here

Recently, Francis et al. (2005a) characterized the volatile emissions of 23 aphid species and reported that Eßf was the only volatile chemical emitted in significant amounts by 16 of them. Eßf was a minor component of the volatile emissions of five other species. The remaining two species, *Euceraphis punctipennis* Zetterstedt and *Drepanosiphum platanoides* Schrank, did not release any Eßf, though other terpenes were isolated. In addition to the species examined by Francis *et al.* (2005b), we have identified four additional aphid species that appear to produce Eßf as their only volatile chemical: *Rhopalosiphum maidis* Fitch, *Aphis glycines* Matsumura, *Aphis spiraecola* Pagenstecher and *Brachycaudus persicae* Pesserini (Verheggen, unpublished data).

In *Myzus persicae*, the quantity and mode of action of the alarm pheromone was found to vary with morph and age of aphids (Gut and Van Oosten, 1985). The quantities of Eßf in aphids also increase in relation to increasing body weight (Byers, 2005), but its concentration declines exponentially with increasing body weight. In *Acyrthosiphon pisum*, Verheggen *et al.* (2009) found that exposure to Eßf emitted by other individuals influences the levels of Eßf produced by immature aphids during development.

In addition to its role as an alarm pheromone in aphids, Eßf is also a common component of plant volatiles emissions—including both constitutive volatile blends (e.g. Agelopoulos *et al.*, 2000) and those induced by herbivore feeding (e.g. Turlings and Ton, 2006) or mechanical damage (e.g. Agelopoulos *et al.*, 1999). And Eßf is a constituent of various essential oils found in several plants family such as Asteraceae (Reichling and Becker, 1978; Heuskin *et al.*, 2009). It is thus tempting to speculate that Eßf production by plants functions to repel or habituate aphids or to otherwise interfere with alarm signaling, but there is currently little evidence that such effects occur (Petrescu *et al.*, 2001). Instead, it appears that the presence of other sesquiterpenes—like (-)-ß-caryophyllene—in plant volatile blends allow aphids to distinguish the pure Eßf emitted by conspecifics from Eßf of plant origin (Dawson *et al.*, 1984). On the other hand, other terpenes like α-pinene or isothiocyanates have been reported to enhance the dispersal-inducing activity of Eßf, leading to an increased specificity of the alarm signal in some aphid species (Pickett and Griffiths, 1980; Dawson *et al.*, 1987). Interestingly, Eßf is present in trichomes of wild potato plants where its release under aphid infestation does appear to cause dispersal (Gibson and Pickett, 1983).

The behavioral effect of alarm pheromone on aphids varies across species and also with the amount of pheromone encountered by receiving individuals. Typical responses range from the cessation of feeding and removal of the stylet from host plant tissues to walking, jumping, or falling away from the source of emission (Edwards *et al.*, 1973; Wientjens *et al.*, 1973; Phelan *et al.*, 1976; Montgomery and Nault, 1977a, b, 1978; Roitberg and Myers, 1978; Wohlers, 1980; Clegg and Barlow, 1982; Chau and Mackauer, 1997; Losey and Denno, 1998; Shah *et al.*, 1999; Braendle and Weisser, 2001). In the sugar-cane woolly aphid, *Ceratovacuna lanigera* Zehntner (Homoptera, Pemphigidae), the alarm pheromone reportedly elicited aggressive behavior from conspecifics (Arakaki, 1989). Eßf has also a repellent effect on the landing behavior of alate aphids, which can cause them to choose an alternative host plant (Lambers and Schepers, 1978; Phelan and Miller, 1982; Wohlers, 1982). Field experiments confirmed dispersal behavior of aphids subjected to their alarm pheromone in 41 species (Xiangyu *et al.*, 2002). Kunert *et al.* (2005) also found that Eßf exposure increased the production of winged individuals specialized for dispersal. Once Eßf concentrations decrease, aphids commonly re-infest host plants (Calabrese and Sorensen, 1978). Because the amounts of alarm pheromone emitted by an individual under natural conditions might be too low to warn all nearby conspecifics, two recent studies tested the hypothesis that aphids might amplify the alarm signal by emitting additional Eßf in response to the alarm signals of other individuals but found no evidence for such an effect (Hatano *et al.*, 2008; Verheggen *et al.*, 2008b).

In addition to serving as an alarm signal to conspecifics and other aphids, Eßf is exploited as a foraging cue by predators and parasitoids that feed on aphids. Details are presented in section *iv*.

ii. Ants

The first published observation of an ant alarm pheromone was probably that of Goetsch (1934) who noted that crushed organs were capable of causing aggressive reactions in workers. Following this original observation, all Formicid species were subsequently found to produce and use an alarm pheromone (Hölldobler and Wilson 1990), whose secretion may alert or recruit conspecifics and often stimulates aggressive reactions (Blum 1985 and references therein). Although behavioral responses can differ drastically among ant species, alarm pheromones generally serve two distinct functions (Wilson and Regnier, 1971). The response to “aggressive alarms” is characterized by rapid movements oriented toward the emitter and by aggressive attitudes ranging from mandible and gaster movements to biting or stinging the antagonist (Figure 2). Recruitment of more workers and intensified attacks on intruders are also observed. Responses to “panic alarms” entail escape, dispersion, and flight behaviors. Workers’ displacement speed is increased, as well as the frequency of direction changes. The type of reaction was found to correlate with differences among species in the size and density of colonies, with species having larger and denser colonies being more prone to aggressive responses. For example, *Lasius fuliginosus* forms large subterranean colonies and the general response workers to the alarm pheromone, *n*-undecane (Table 1), entails running toward the pheromone source with mandibles opened (Stoeffler *et al.*, 2007). In contrast, workers of *Hypoponera opacior* and *Ponera pennsylvanica*, which have small colony sizes, drastically increase their mobility but do not run toward the emitter when exposed to the main constituent of their alarm pheromone, 2,5-dimethyl-3-isopentylpyrazine (Duffield *et al.*, 1976).

Figure 2 near here

A variety of natural products and associated behaviors have been highlighted in the different formicid genera, with production sites including mandibular, pygidial, metapleural and Dufour’s glands. Ant alarm pheromones are usually aliphatic carbon chains shorter and more volatile than those characteristic of trail pheromones. These include ketones, alcohols, esters, aldehydes, alkylpyrazines, terpenes, short aliphatic hydrocarbons, and formic acid. As with aphid alarm signals, the alarm pheromones used by ants are thus well suited chemically for their role in mediating effective responses to threats that are highly localized in space in time. Different chemicals often composed the alarm pheromone blend of a single ant species and these components can elicit different behaviors in receiving individuals. Moreover, because of differences in volatility, and perhaps also due to differences in the sensitivity of receiving individuals, the areas over which specific compounds induce active responses can also vary.

Minor workers of *Pheidole embolopyx* respond to encountering intruders of other species by secreting trail and alarm pheromones produced by the pygidial gland (Wilson and Hölldobler, 1985). In combination, these signals announce the presence of the enemy and lead to the recruitment of major workers who mount a sustained attack on the intruders.

The different components of the *Camponotus obscuripes* (Formicinae) alarm pheromone are produced in Dufour's gland and in the poison gland (Fujiwara-Tsujii *et al.*, 2006). The first gland contains a mixture of aliphatic carbon chains of which *n*-undecane represents 90%. Formic acid, a compound commonly used by ants for defense, trail marking, and recruitment, appears to be the only volatile chemical produced in the poison gland. In response to danger, *C. obscuripes* releases a mixture of these substances, each having a different volatility and function. Formic acid, perceived at longer distances, informs other colony members of the presence of a threat and helps them to locate the source of the emission. At shorter range, *n*-Undecane, and other associated saturated hydrocarbons, induce aggression toward antagonists.

Among leaf cutting ants in the genus *Atta,* the mandibular gland secretions of most species contain mixtures of volatile, low-molecular-weight alcohols and ketones, which elicit the alarm response (Blum, 1968). The main volatile components of the mandibular glands of major workers are 4-methyl-3-heptanone (Table 1) and 2-heptanone (Hughes *et al.*, 2001), with the former being most active in eliciting alarm responses (Moser *et al.*, 1968). The latter chemical also occurs commonly in other ant genera (Feener *et al.*, 1996).

iii. Honeybees

A vital role honeybee colony defense is played by so-called guard bees, which patrol the nest entrance and represent the first line of colony defense. These guards are also specialized for the production of alarm pheromone which they release to recruit nestmates from the interior of the colony in case of danger (Boch *et al.*, 1962; Collins *et al.*, 1982). The perception of the pheromone increases workers movement and promotes aggression. Indeed, beekeepers are well acquainted with the banana-like odor released by stressed colonies, and with the fact that one bee sting is likely to be followed by others unless one rapidly moves away from the colony or uses smoke to sedate it. Although there is a striking variation in the intensity of their response (in docile colonies, only a few bees may respond while thousands of stinging individuals may attack in more aggressive colonies), only guarding workers produce the alarm pheromone (Vander Meer *et al.*, 1998; Alaux *et al.*, 2009).

The possibility that an alarm signal, of then unknown nature and origin, could act to alert honeybee workers was first suggested in the early 17th century (Butler, 1609, cited by Wilson 1971). The signal was later proposed to be an odorant (Huber, 1814), who noticed that presenting a honeybee worker's sting (attached to a forceps) to conspecifics changed their behavior changed from “quiet” to “aggressive”. He concluded that “some odors incite honeybees to flee”. It was later established that the honeybee alarm pheromone is produced in the mandibular as well as in the Koshewnikov gland associated with the sting apparatus (Boch *et al.*, 1962; Shearer and Boch, 1965) —though pheromone emission does not require that the sting be used.

Boch et al. (1962) first identified isopentyl acetate (previously called iso-amyl acetate) (Table 1) as a biologically active alarm pheromone associated with the sting (The use of smoke by beekeepers suppresses the activation of antennal receptors of isopentyl acetate, and therefore reduces nestmate recruitment (Visscher *et al.*, 1995). Subsequently, over 20 additional volatile aliphatic and aromatic active compounds, of low molecular weight, have been identified in the alarm pheromone blend (Hunt, 2007). In addition to isopentyl acetate, (Z)-11-eicosen-1-ol is thought to play an essential role (Boch *et al.*, 1962; Pickett *et al.*, 1982). Although both these compounds individually induce alarm responses in bee workers, when presented together they elicit behavioral responses comparable to the intact sting (Pickett *et al.*, 1982). Not all components of the pheromone blend in honeybees induce alarm behavior, some have other specialized functions including flight induction (e.g. benzyl acetate), and recruitment (e.g. 1-butanol, 1-octanol, hexyl acetate), while others play multiple roles (e.g. 1-hexanol, butyl acetate, isopentyl acetate, 2-nonanol) (Wager and Breed, 2000). Shearer and Boch (1965) reported alarm activity of 2-heptanone (Table 1) isolated from honeybee mandibular glands. With increasing age, the size of the gland and the amount of 2-heptanone increases (Vallet *et al.*, 1991). When filter paper treated with 2-heptanone is placed at the hive entrance, bees nearby become greatly agitated, assuming a characteristic aggressive posture and running toward the emission source in jerky circles or short zigzags.

Contrary to longstanding expectations, the honeybee alarm pheromone blend does not seem to be implicated in target localization (Free, 1961; Wager and Breed, 2000).

iv. Alarm pheromones used as kairomones by natural enemies

Semiochemicals provide a powerful way for organisms to communicate and coordinate their behaviors. But they also represent opportunities for other organisms to intercept and exploit such signals. Indeed, there are numerous examples of natural enemies having learned or evolved to use the pheromones of their prey as foraging cues (Vet and Dicke, 1992).

Figure 3 near here

For example, aphid natural enemies rely on semiochemicals, especially the aphid alarm pheromone, to locate aphid colonies (Figure 3). Previous studies have demonstrated this phenomenon in lady beetles, Coccinella sp., Adalia sp. and Harmonia sp. (e.g. Nakamuta, 1991; Francis *et al.*, 2004; Verheggen *et al.*, 2007); hoverflies (e.g. Verheggen *et al.*, 2008a; Almohamad *et al.*, 2009; Verheggen *et al.*, 2009); ground beetles (Kielty *et al.*, 1996); lacewings (Boo *et al.*, 1998; Zhu *et al.*, 1999); and parasitic wasp adults and larvae (Beale *et al.*, 2006).

Ant parasitoids also use alarm pheromone components to locate their specific hosts. Individuals of *Apocephalus paraponerae* (Diptera: Phoridae), which parasitizes workers of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae) locate fighting or injured workers of this host species by using 4-methyl-3-heptanone and 4-methyl-3-heptanol (Feener *et al.*, 1996). The cursorial spider *Habronestes bradleyi* (Araneae, Zodariidae), a specialist predator of the meat ant *Iridomyrmex purpureus*, likewise locates workers of its prey by using their alarm pheromone, which consists mainly of 6-methyl-5-hepten-2-one and is frequently released during territorial disputes among conspecifics (Allan *et al.*, 1996).

Alarm pheromones in marine invertebrates

Alarm behaviors in aquatic invertebrates are also commonly mediated by chemical signals, and a growing number of aquatic organisms have been shown to display antipredator behavior in response to injury-released chemical cues from conspecifics, including mollusks (e.g. Spinella et al., 1993), flatworms (e.g. Wisenden and Millard, 2001), annelids (e.g. Watson et al., 2005) and echinoderms (e.g. Vadas and Elner, 2003).

The first report of a chemical alarm cue in a platyhelminth was the demonstration that predator avoidance behavior in a free-living flatworm, *Dugesia dorotocephala*, could be induced by chemical cues released from injured conspecifics (Wisenden and Millard, 2001). Despite their relatively simple nervous system, Planaria are apparently also capable of learned risk association, as following simultaneous exposure to the conspecific alarm signal and sunfish odor cues, they subsequently respond to the sunfish odor alone as an indicator of danger (Wisenden and Millard, 2001). Green sea urchins, *Lytechinus variegates*, employ a two-phased response to cues from damaged conspecifics entailing an initial rapid but ephemeral alarm response followed by a more sustained flight phase, which induces urchins to disperse (Vadas and Elner, 2003). Chemical alarm substances have also been documented in Gastropods. The snail *Littorina littorea*, common periwinkle, shows crawl-out responses (i.e., movement out of the water) in response to chemical stimuli from injured individuals (Jacobsen and Stabell, 1999). The first cnidarian pheromone to be documented was anthopleurine (Table 1), which is released from wounded tissues of the sea anemone

Anthopleura elegantissima—for example during attack by the nudibranch *Aeolidia papillosa*—and evokes rapid withdrawal in nearby conspecifics (Howe and Sheikh, 1975).

Alarm pheromones in fish

Many fishes use alarm pheromones to warn conspecifics of potential threats in the surrounding environment (reviewed by Smith in 1992). The first suggestion that Ostariophysan fishes (the second largest superorder of fish) might exhibit a fright reaction in response to some signal from wounded conspecifics, and that this might reduce the receivers' vulnerability subsequent predation, was made by von Frisch (1938). Pfeiffer (Pfeiffer, 1963, 1977, 1978) subsequently documented alarm signaling in several Ostariophysan species. The secretion of the signals involves specialized epidermal cells that contain the alarm pheromone. When these cells are broken, as during predation events, this substance is released into the surrounding water (Figure 4). Thus, senders cannot actively release their alarm substance (Smith, 1992), but the restricted context in which they are emitted reliably informs conspecifics of the presence of a predator. Fathead minnows (*Pimephales promelas*) and finescale dace (*Chrosomus neogaeus*) also exhibited significant antipredator responses (increased shoaling and decreased area of movement) when exposed to conspecific skin extract (Brown *et al.*, 2000). Similar reactions were observed in response to hypoxanthine-3-N-oxide (Table 1), one of several molecules thought to function as a chemical alarm signal in Ostariophysan species (Brown *et al.*, 2000). Complementary studies subsequently found that exposure to low concentrations of hypoxanthine-3-N-oxide may cause fish to increase vigilance towards secondary (i.e. visual) risk assessment cues, leading to an increased alarm response in case of predator attack (Brown *et al.*, 2004). The fish fright reaction can also be detected visually by other nearby individuals leading to the rapid propagation of the alarm response through a group (Smith, 1992).

Figure 4 near here

In the Percid fishes, physical injury also appears to be required for release of the active alarm pheromone component, and exposure to water that previously contained an injured individual leads to reduced movement (“freezing”) and periods of inactivity in the receiver (Crane *et al.*, 2009). Fish alarm pheromones do not appear to be species specific, and generally usually induce equivalent alarm responses in other species (Smith, 1982). For example, the pumpkinseeds, *Lepomis gibbosus* (Acanthopterygii), exhibit antipredator responses when exposed to hypoxanthine-3-N-oxide, the putative Ostariophysan alarm pheromone (Golub *et al.*, 2005). This similarity of intra- and interspecific reactions in fishes, suggests corresponding similarities in signaling chemistry and reception mechanisms. This has led to some controversy as to whether alarm signals in fish should strictly be classed as pheromones or as allelochemicals (Burnard *et al.*, 2008).

Alarm pheromones in mammals

Mammals make wide use of pheromones to mark territories, attract mates, and coordinate group behavior. Chemical alarm signaling also occurs, but though many territorial and sexual pheromones have been identified in mammals, relatively little progress has been made in the chemical identification and functional analysis of mammal alarm pheromones (Hauser *et al.*, 2005). It is commonly thought that mammal alarm pheromones are volatile, and it is hypothesized that they may be low molecular weight compounds, such as fatty acids or steroids. The perception of these alarm signal seems to be mediated by an auxiliary olfactory sense organ called the vomeronasal organ (VON), or Jacobson's organ (Dulac and Axel, 1998).

Although, infochemicals appear to play a smaller role in communication between humans than in other mammals, the ability to produce and perceive pheromones has also been demonstrated in humans (McClintock, 1998). The existence of a human alarm pheromone has not been demonstrated, but it has been suggested that humans can detect differences between a neutral scent and a scent associated with frightened individuals (Ackerl *et al.*, 2002).

Chemical alarm signaling has been demonstrated in mice (Rottman and Snowdown, 1972). When exposed to the odor of a stressed conspecific, mice behaved aversively to the source of the odor, even though they responded positively to the sender's odor prior to the introduction of the stress. Stressed male Wistar rats release a volatile alarm pheromone , from the perianal region that elicits defensive and risk-assessment behavior in receiving individuals, characterized by hyperthermia, increased freezing, sniffing, and walking as well as a decreased resting behavior (Kikusui *et al.*, 2001; Inagaki *et al.*, 2009). So far, the chemical structure of this pheromone has not been elucidated.

Odor-induced fear responses have also been documented in cattle and shown to be at least partly mediated by olfactory cues in the urine of stressed individuals (Boissy *et al.*, 1998).

Alarm signals in plants

Plants actively respond to damage induced by infesting arthropods by inducing direct defenses such as toxins and antifeedants (Gatehouse, 2002). But, they also typically release blends of volatile compounds from damaged tissues—as well as systemically—that appear to play a variety of signaling functions (Farmer, 2001). For example, these herbivore-induced plant volatiles can directly repel foraging herbivores, such as ovipositing butterflies and moths and host-seeking aphids (Dicke and Vet, 1999). Herbivore-induced volatiles also serve as key foraging cues for natural enemies of the feeding herbivores, including insect predators and parasitoids (e.g. Turlings *et al.*, 1998) and even for insectivorous birds (Mäntylä *et al.*, 2008). Moreover, these signals can convey complex and highly specific information about the status of emitting plants. For example, the highly specialized parasitoid wasp *Cotesia congregata* can consistently distinguish among volatile blends elicited by the feeding of two closely related caterpillar species and preferentially responds to the odors of plants infested by its host (De Moraes *et al.*, 1998).

There has been a longstanding debate about the extent to which damage-induce plant volatiles might also be important in signaling between neighboring plants (Farmer, 2001; Karban, 2008; Heil and Karban, 2010), but a number of recent studies suggests that these compounds play an important role in signaling between damaged and undamaged tissues of individual plants (e.g. Arimura *et al.*, 2000; Dolch and Tscharntke, 2000; Karban and Maron, 2002; Karban *et al.*, 2003; Engelberth *et al.*, 2004), and particularly in overcoming potential constraints on the internal (vascular) transmission of wound signals imposed by plants' modular architecture (Karban *et al.*, 2006; Frost *et al.*, 2007; Heil and Silva Bueno, 2007; Rodriguez-Saona *et al.*, 2009).

Conclusion: potential applications of alarm pheromones

In addition to obviously intriguing questions about the evolution of alarm signaling within individuals species and differences in the way they function between taxa, understanding this class of semiochemical-mediated interactions also has potential for application to the management of pest species. Sex pheromones, mainly of Lepidopteran insects, have frequently been incorporated into management strategies (Copping, 2001). While few alarm pheromones have been employed in this context, some efforts have been made to incorporate them in push-pull strategies as behavior-manipulating stimuli to make the protected resource unattractive to the pest (Cook *et al.*, 2007). And honeybee alarm pheromone can be used to repel *Apis mellifera* from oilseed rape before insecticide applications (Free *et al.*, 1985).

A good deal of research has addressed the potential use of aphid alarm pheromone as a control mechanism. Following identification of the aphid alarm pheromone—(E)-ß-farnesene in most species of Aphidinae—researchers began discussing the possibility of using this semiochemical to repel aphids (Bowers *et al.*, 1972), encouraged by the relative ease of extracting and purifying (E)-ß-farnesene from plant material (Heuskin *et al.*, 2009). Early attempts to employ (E)-ß-farnesene in the field were unsuccessful, however, as aphids recolonized host-plants very rapidly following exposure (Calabrese and Sorensen, 1978). Later, slow-release formulations of *Hemizygia petiolata* (Lamiaceae) containing high levels of (E)-ß-farnesene were successfully employed to reduce pea aphid populations in field experiments (Bruce *et al.*, 2005). The increased aphid mobility induced by (E)-ß-farnesene exposition could also increase aphid exposure to insecticides and fungal control agents (Griffiths and Pickett, 1980). Similarly, application of farnesol and nerolidol, components of the two-spotted mite (*Tetranychus urticae*) alarm pheromone, increased mite mobility and subsequent exposure to co-applied acaricides, leading to enhanced control relative to the application of acaricides alone (Copping, 2001).

Studies on the role of (E)-ß-farnesene in interspecific interactions in natural systems also suggest its potential application to the control of aphid population mechanisms. As noted above, Gibson and Pickett (1983) demonstrated the ability of wild potatoes to repel aphids by naturally releasing (E)-ß-farnesene from their glandular trichomes. And works on the perception of the aphid alarm pheromone by predators highlights of its potential to increase aphid apparency to natural enemies (Du *et al.*, 1998; Zhu *et al.*, 1999; Verheggen *et al.*, 2007; Almohamad *et al.*, 2008; Verheggen *et al.*, 2008a). Beale et al. (2006) exploited this potentital by incorporating an Eßf synthase gene into the genome of *Arabidopsis thaliana*, and demonstrated increased attraction of aphid parasitoids to the modified plants.

Because alarm pheromones can be attractants for certain organisms, they also have potential for use in baits or traps. Hughes and colleagues (2002) showed that an alarm pheromone produced by grass-cutting ants, 4-methyl-3-heptanone, has significant potential to improve the efficacy of baits used for the control of these insects, since individuals receiving the signal tend to move toward the source of emission.

Far fewer studies have addressed practical applications of non-insect alarm pheromones. However, alarm signals might well have applications in the control of aquatic pests. For example, the search for a method to decrease the decline of Britain’s native white-clawed crayfish (*Austropotamobius pallipes*) caused by the presence of the induced signal crayfish (*Pacifastacus leniusculus*), originally from North America, has given rise to speculation that *P. leniusculus* pheromones (including sex, stress and alarm pheromones) might improve the efficiency of existing baits (Stebbing *et al.*, 2003).

Reference list

Ackerl, K., Atzmueller, M., and Grammer, K. (2002). The scent of fear. *Neuroendocrinol. Lett.* 23**,** 79-84.

Agelopoulos, N. G., Chamberlain, K., and Pickett, J. A. (2000). Factors affecting volatile emissions of intact potato plants, Solanum tuberosum : Variability of quantities and stability of ratios. *J. Chem. Ecol.* 26.

Agelopoulos, N. G., Hooper, A. M., Maniar, S. P., Pickett, J. A., and Wadhams, L. J. (1999). A novel approach for isolation of volatile chemicals released by individual leaves of a plant in situ. *J. Chem. Ecol.* 25**,** 1411-1425.

Alaux, C., Sinha, S., Hasadsri, L., Hunt, G. J., Guzman-Novoa, E., DeGrandi-Hoffman, G., Uribe-Rubio, J. L., Southey, B. R., Rodriguez-Zas, S., and Robinson, G. E. (2009). Honey bee aggression supports a link between gene regulation and behavioral evolution. *P.N.A.S.* 106**,** 15400-15405.

Allan, R. A., Elgar, M. A., and Capon, R. J. (1996). Exploitation of an ant chemical alarm signal by the zodariid spider Habronestes bradleyi Walckenaer. *P. Roy. Soc. B-Biol. Sci.* 263**,** 69-73.

Almohamad, R., Verheggen, F. J., Francis, F., Lognay, G., and Haubruge, E. (2008). Emission of alarm pheromone by non-preyed aphid colonies. *J. Appl. Entomol.* 132**,** 601-604.

Almohamad, R., Verheggen, F. J., and Haubruge, E. (2009). Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. *B.A.S.E.* 13**,** 467-481.

Arakaki, N. (1989). Alarm pheromone eliciting attack and escape responses in the sugar-cane woolly aphid, Ceratovacuna-lanigera (Homoptera, Pemphigidae). *J. Ethol.* 7**,** 83-90.

Arimura, G.-I., Ozawa, R., Shimoda, T., Nishioka, T., Boland, W., and Takabayashi, J. (2000). Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406**,** 512–515.

Barbier, M. (1982). Les phéromones. Aspects biochimiques et biologiques. Masson.

Beale, M. H., Birkett, M. A., Bruce, T. J. A., Chamberlain, K., Field, L. M., Huttly, A. K., Martin, J. L., Parker, R., Phillips, A. L., Pickett, J. A., Prosser, I. M., Shewry, P. R., Smart, L. E., Wadhams, L. J., Woodcock, C. M., and Zhang, Y. H. (2006). Aphid alarm pheromone produced by transgenic plants affects aphid and parasitoid behavior. *P.N.A.S.* 103**,** 10509-10513.

Blum, M. S. (1968). Alarm pheromones. *Annu. Rev. Entomol.* 14**,** 157-180.

Blum, M. S. (1985). Alarm pheromones. *In* "Comprehensive Insect physiology, Biochemistry and Pharmacology" (G. A. Kerkut, L. I. Gilbert, Ed.), pp. 193-224. Pergamon Press,

Boch, R., Shearer, D. A., and Stone, B. C. (1962). Identification of iso-amyl acetate as an active component in the sting pheromone of the honey bee. *Nature*. 195**,** 1018-1020.

Boissy, A., Terlouw, C., and Le Neindre, P. (1998). Presence of cues from stressed conspecifics increases reactivity to aversive events in cattle: Evidence for the existence of alarm substances in urine. *Physiol. Behav.* 63**,** 489-495.

Boo, K. S., Chung, I. B., Han, K. S., Pickett, J. A., and Wadhams, L. J. (1998). Response of the lacewing Chrysopa cognata to pheromones of its aphid prey. *J. Chem. Ecol.* 24**,** 631-643.

Bowers, W. S., Nault, L. R., Webb, R. E., and Dutky, S. R. (1972). Aphid alarm pheromone: Isolation, identification, synthesis. *Science*. 177**,** 1121-1122.

Bowers, W. S., Nishino, C., Montgomery, M. E., and Nault, L. R. (1977a). Structure-activity-relationships of analogs of aphid alarm pheromone, (E)-beta-farnesene. *J. Insect Physiol.* 23**,** 697-701.

Bowers, W. S., Nishino, C., Montgomery, M. E., Nault, L. R., and Nielson, M. W. (1977b). Sesquiterpene progenitor, Germancrene A : An alarm pheromone in aphids. *Science*. 196**,** 680-681.

Braendle, C., and Weisser, W. W. (2001). Variation in escape behavior of red and green clones of the pea aphid. *J. Insect Behav.* 14**,** 497-509.

Brown, G. E., Adrian, J. C., Smyth, E., Leet, H., and Brennan, S. (2000). Ostariophysan alarm pheromones: Laboratory and field tests of the functional significance of nitrogen oxides. *J. Chem. Ecol.* 26**,** 139-154.

Brown, G. E., Poirier, J. F., and Adrian, J. C. (2004). Assessment of local predation risk: the role of subthreshold concentrations of chemical alarm cues. *Behav. Ecol.* 15**,** 810-815.

Bruce, T. J. A., Birkett, M. A., Blande, J., Hooper, A. M., Martin, J. L., Khambay, B., Prosser, I., Smart, L. E., and Wadhams, L. J. (2005). Response of economically important aphids to components of Hemizygia petiolata essential oil. *Pest Manag. Sci.* 61**,** 1115-1121.

Burnard, D., Gozlan, R. E., and Griffiths, S. W. (2008). The role of pheromones in freshwater fishes. *J. Fish Biol.* 73**,** 1-16.

Byers, J. A. (2005). A cost of alarm pheromone production in cotton aphids, Aphis gossypii. *Naturwissenschaften*. 92**,** 69-72.

Calabrese, E. J., and Sorensen, A. J. (1978). Dispersal and recolonization by Myzus-persicae following aphid alarm pheromone exposure. *Ann. Entomol. Soc. Am.* 71**,** 181-182.

Charnov, E. L., and Krebs, J. R. (1974). The evolution of alarm calls, altruism or manipulation? *Am. Nat.* 109.

Chau, A., and Mackauer, M. (1997). Dropping of pea aphids from feeding site: A consequence of parasitism by the wasp, Monoctonus paulensis. *Entomol. Exp. Appl.* 83**,** 247-252.

Clegg, J. M., and Barlow, C. A. (1982). Escape behavior of the pea aphid Acyrthosiphon pisum (Harris) in response to the alarm pheromone and vibration. *Can. J. Zoo.* 60**,** 2245-2252.

Collins, A. M., Rinderer, T. E., Harbo, J. R., and Bolten, A. B. (1982). Colony defense by Africanized and European honeybees. *Science*. 218**,** 72-74.

Cook, S. M., Khan, Z. R., and Pickett, J. A. (2007). The use of Push-Pull strategies in integrated pest managment. *Annu. Rev. Entomol.* 52**,** 375-400.

Copping, L. G. (2001). The biopesticide manual. British Crop Protection Council.

Crane, A. L., Woods, D., and Mathis, A. (2009). Behavioural responses to alarm cues by free-ranging rainbow darters (Etheostoma caeruleum). *Behaviour*. 146**,** 1565-1572.

Dawson, G. W., Griffiths, D. C., Pickett, J. A., Smith, M. C., and Woodcock, C. M. (1984). Natural inhibition of the aphid alarm pheromone. *Entomol. Exp. Appl.* 36**,** 197-199.

Dawson, G. W., Griffiths, D. C., Pickett, J. A., Wadhams, L. J., and Woodcock, C. M. (1987). Plant-derived synergists of alarm pheromone from turnip aphid, Lipaphis (Hyadaphis) erysimi (Homoptera, Aphididae). *J. Chem Ecol.* 13**,** 1663-1671.

De Moraes, C. M., Lewis, W. J., Paré, P. W., Alborn, H. T., and Tumlinson, J. H. (1998). Herbivore-infested plants selectively attract parasitoids. *Nature*. 393**,** 570-573.

Dicke, M., Agrawal, A. A., and Bruin, J. (2003). Plants talk, but are they deaf? *Trends Plant Sci.* 8**,** 403-405.

Dicke, M., and Vet, L. E. M. (1999). Plant–carnivore interactions: evolutionary and ecological consequences for plant, herbivore and carnivore. *In* "Herbivores: Between Plants and Predators" (H. Olff, V. K. Brown, R. H. Drent, Ed.), pp. 483-520. Blackwell Science, Oxford.

Dolch, R., and Tscharntke, T. (2000). Defoliation of alders (Alnus glutinosa) affects herbivory by leaf beetles on undamaged neighbours. *Oecologia*. 125**,** 504-511.

Du, Y., Poppy, G. M., Powell, W., Pickett, J. A., Wadhams, L. J., and Woodcock, C. M. (1998). Identification of semiochemicals released during aphid feeding that attract parasitoid Aphidius ervi. *J. Chem. Ecol.* 24**,** 1355-1368.

Duffield, R. M., Blum, M. S., and Wheeler, J. W. (1976). Alkylpyrazine alarm pheromones in primitive ants with small colonial units. *Comp. Biochem. Physiol. B*. 54**,** 439-440.

Dulac, C., and Axel, R. (1998). Expression of candidate pheromone receptor genes in vomeronasal neurons. *Chem. Senses*. 23**,** 467-475.

Edwards, L. J., Siddall, J. B., Dunham, L. L., Uden, P., and Kislow, C. J. (1973). Trans-beta-farnesene, alarm pheromone of the green peach aphid, Myzus persicae (Sulzer). *Nature*. 241**,** 126-127.

Engelberth, J., Alborn, H. T., Schmelz, E. A., and Tumlinson, J. H. (2004). Airborne signals prime plants against insect herbivore attack. *P.N.A.S.* 101**,** 1781–1785.

Farmer, E. (2001). Surface-to-air signals. *Nature* 411**,** 854–856.

Feener, D. H., Jacobs, L. F., and Schmidt, J. O. (1996). Specialized parasitoid attracted to a pheromone of ants. *Anim. Behav.* 51**,** 61-66.

Francis, F., Lognay, G., and Haubruge, E. (2004). Olfactory responses to aphid and host plant volatile releases: E-B-Farnesene an effective kairomone for the predator Adalia bipunctata. *J. Chem. Ecol.* 30**,** 741-755.

Francis, F., Vandermoten, S., Verheggen, F., Lognay, G., and Haubruge, E. (2005a). Is the (E)-b-Farnesene only volatile terpenoid in aphids ? *J. Appl. Entomol.* 129**,** 6-11.

Francis, F., Vandermoten, S., Verheggen, F., Lognay, G., and Haubruge, E. (2005b). Is the (E)-b-Farnesene only volatile terpenoid in aphids ? *Journal of Applied Entomology*. 129**,** 6-11.

Free, J. B. (1961). The stimuli releasing the stinging response of honeybees. *Anim. Behav.* 9**,** 193-196.

Free, J. B., Pickett, J. A., Ferguson, A. W., Simpkings, J. R., and Smith, M. C. (1985). Reppelling honeybees with alarm pheromones. *J. Agr. Sci.* 105**,** 255-260.

Frost, C. J., Appel, H. M., Carlson, J. E., De Moraes, C. M., Mescher, M. C., and Schultz, J. C. (2007). Within-plant signaling by volatiles overcomes vascular constraints on systemic signaling and primes responses against herbivores. *Ecol. Lett.* 10**,** 490–498.

Fujiwara-Tsujii, N., Yamagata, N., Takeda, T., Mizunami, M., and Yamaoka, R. (2006). Behavioral responses to the alarm pheromone of the ant Camponotus obscuripes (Hymenoptera: Formicidae). *Zool. Sci.* 23**,** 353-358.

Gatehouse, J. A. (2002). Plant resistance toward insect herbivores : a dynamic interaction. *New Phytol.* 156**,** 145-169.

Gibson, R. W., and Pickett, J. A. (1983). Wild potato repels aphids by release of aphid alarm pheromone. *Nature*. 302**,** 608-609.

Goetsch, W. (1934). Untersuchungen über di Zusammenarbeit im Ameisenstaat. *Zoomorphology*. 28**,** 319-401.

Golub, J. L., Vermette, V., and Brown, G. E. (2005). Response to conspecific and heterospecific alarm cues by pumpkinseeds in simple and complex habitats: field verification of an ontogenetic shift. *J. Fish Biol.* 66**,** 1073-1081.

Griffiths, D. C., and Pickett, J. A. (1980). A potential application of aphid alarm pheromones. *Entomol. Exp. Appl.* 27**,** 199-201.

Gut, J., and Van Oosten, A. M. (1985). Functional-significance of the alarm pheromone composition in various morphs of the green peach aphid, Myzus persicae. *Entomol. Exp. Appl.* 37**,** 199-204.

Hamilton, W. D. (1964). The Genetical Evolution of Social Behaviour. *J. Theor. Biol.* 7**,** 1-16.

Hatano, E., Kunert, G., Bartram, S., Boland, W., Gershenzon, J., and Weisser, W. W. (2008). Do aphid colonies amplify their emission of alarm pheromone? *J. Chem Ecol.* 34**,** 1149-1152.

Hauser, R., Wiergowski, M., Marczak, M., Karaszewski, B., and Wodniak-Ochocinska, L. (2005). Alarm pheromones as an exponent of emotional state shortly before death - Science fiction or a new challenge? *Forensic Sci. Int.* 155**,** 226-230.

Heil, M., and Karban, R. (2010). Explaining evolution of plant communication by airborne signals. *Trends Ecol. Evol.* 25**,** 137-144

Heil, M., and Silva Bueno, J. C. (2007). Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *P.N.A.S.* 104**,** 5467–5472.

Heuskin, S., Godina, B., Leroy, P., Capella, Q., Wathelet, J. P., Verheggen, F., Haubruge, E., and Lognay, G. (2009). Fast gas chromatography characterisation of purified semiochemicals from essential oils of Matricaria chamomilla L. (Asteraceae) and Nepeta cataria L. (Lamiaceae). *J. Chromatogr. A* 1216**,** 2768-2775.

Högstedt, G. (1983). Adaptation unto death: function of fear screams. *Am. Nat.* 121**,** 562-570.

Hölldobler, B., and Wilson , E. O. (1990). The ants. Springer-Verlag, Berlin.

Howe, N. R., and Sheikh, Y. M. (1975). Anthopleurine: a sea anemone alarm pheromone. *Science*. 189**,** 386-388.

Howse, P. E. (1998). Pheromones and Behaviour. *In* "Insect pheromones and their use in pest management" (P. E. Howse, I. Stevens, O. Jones, Ed.). Chapman and Hall, Huber, F. (1814). Nouvelles observations sur les abeilles 2nd Edt. Paris & Genève, Librairie Paschoud.

Hughes, W. O. H., Howse, P. E., and Goulson, D. (2001). Mandibular gland chemistry of grass-cutting ants: Species, caste, and colony variation. *J. Chem Ecol.* 27**,** 109-124.

Hughes, W. O. H., Howse, P. E., Vilela, E. F., Knapp, J. J., and Goulson, D. (2002). Field evaluation of potential of alarm pheromone compounds to enhance baits for control of grass-cutting ants (Hymenoptera : Formicidae). *J. Econ. Entomol.* 95**,** 537-543.

Hunt, G. J. (2007). Flight and fight: A comparative view of the neurophysiology and genetics of honey bee defensive behavior. *J. Insect Physiol.* 53**,** 399-410.

Inagaki, H., Nakamura, K., Kiyokawa, Y., Kikusui, T., Takeuchi, Y., and Mori, Y. (2009). The volatility of an alarm pheromone in male rats. *Physiol. Behav.* 96**,** 749-752.

Jacobsen, H. P., and Stabell, O. B. (1999). Predator-induced alarm responses in the common periwinkle, Littorina littorea: dependence on season, light conditions, and chemical labelling of predators. *Mar. Biol.* 134**,** 551-557.

Karban, R. (2008). Plant behaviour and communication. *Ecol. Lett.* 11**,** 727–739.

Karban, R., and Maron, J. (2002). The fitness consequences of interspecific eavesdropping between plants. *Ecol. Lett.* 83**,** 1209–1213.

Karban, R., Maron, J., Felton, G. W., Ervin, G., and Eichenseer, H. (2003). Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. *Oikos* 100**,** 325-332.

Karban, R., Shiojiri, K., Huntzinger, M., and McCall, A. C. (2006). Damage-induced resistance in sagebrush: volatiles are key to intra- and interplant communication. *Ecology*. 87**,** 922–930.

Karlson, P., and Lüscher, M. (1959). 'Pheromones': a new term for a class of biologically active substances. *Nature*. 4653**,** 55-56.

Kielty, J. P., Allen-Williams, L. J., Underwood, N., and Eastwood, E. A. (1996). Behavioral responses of three species of ground beetle (Coleoptera: Carabidae) to olfactory cues associated with prey and habitat. *J. Insect Behav.* 9**,** 237-250.

Kikusui, T., Takigami, S., Takeuchi, Y., and Mori, Y. (2001). Alarm pheromone enhances stress-induced hyperthermia in rats. *Physiol. Behav.* 72**,** 45-50.

Kislow, C. J., and Edwards, L. J. (1972). Repellent odor in aphids. *Nature*. 235**,** 108-109.

Kunert, G., Otto, S., Röse, U. S. R., Gershenzon, J., and Weisser, W. W. (2005). Alarm pheromone mediates production of winged dispersal morphs in aphids. *Ecol. Lett.* 8**,** 596-603.

Kuwahara, Y., Fukami, H., Ishii, S., Matsumoto, K., and Wada, Y. (1979). Pheromone study on acarid mites. II. Presence of the alarm pheromone in the mold mite, Tyrophagus putrescentiae (Schrank) (Acarina: Acaridae) and the site of its production. *Japanese Journal of Sanitary Zoology*. 30**,** 309-314.

Lambers, D. H. R., and Schepers, A. (1978). Effect of trans-beta-farnesene, used as a repellant against landing aphid alatae in seed potato growing. *Potato Res.* 21**,** 23-26.

Leavesley, A. J., and Magrath, R. D. (2005). Communicating about danger: urgency alarm calling in a bird. *Anim. Behav.* 70**,** 365-373.

Losey, J. E., and Denno, R. F. (1998). The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecol. Enomol.* 23**,** 53-61.

Mäntylä, E., Alessio, G. A., Blande, J. D., Heijari, J., and Holopainen, J. K. (2008). From Plants to Birds: Higher Avian Predation Rates in Trees Responding to Insect Herbivory. *PLoS ONE*. 3**,** e2832.

Maynard Smith, J., and Harper, D. (2003). Animal Signals. Oxford University Press.

McClintock, M. K. (1998). On the nature of mammalian and human pheromones. *In* "Olfaction and Taste Xii - an International Symposium" (C. Murphy, Ed.), Vol. 855, pp. 390-392. New York Acad Sciences, New York.

Montgomery, M. E., and Nault, L. R. (1977a). Aphid alarm pheromones - dispersion of Hyadaphis erysimi and Myzus persicae (Hemiptera - Aphididae). *Ann. Entomol. Soc. Am.* 70**,** 669-672.

Montgomery, M. E., and Nault, L. R. (1977b). Comparative response of aphids to alarm pheromone, (E)-beta-farnesene. *Entomol. Exp. Appl.* 22**,** 236-242.

Montgomery, M. E., and Nault, L. R. (1978). Effects of age and wing polymorphism on sensitivity of Myzus persicae to alarm pheromone. *Ann. Entomol. Soc. Am.* 71**,** 788-790.

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

Nakamuta, K. (1991). Aphid alarm pheromone component, (E)-beta-farnesene, and local search by a predatory lady beetle, Coccinella septempunctata Bruckii mulsant (Coleoptera, Coccinellidae). *App. Entomol. Zool.* 26**,** 1-7.

Payne, T. L. (1974). Pheromone perception. *In* "Pheromones" (M. C. Birch, Ed.). North-Holland Publishing Company,

Petrescu, A. S., Mondor, E. B., and Roitberg, B. D. (2001). Subversion of alarm communication: Do plants habituate aphids to their own alarm signals? *Can. J. Zool.* 79**,** 737-740.

Pfeiffer, W. (1963). The fright reaction of North American fish. *Can. J. Zoo.* 41**,** 69-77.

Pfeiffer, W. (1977). The distribution of fright reaction and alarm substance cells in fishes. *Copeia*. 653-665.

Pfeiffer, W. (1978). Heterocyclic compounds as releasers of the fright reaction in the giant danio Danio malabaricus (Jerdon) (Cyprinidae, Ostariophysi, Pisces). *J. Chem Ecol.***,** 665-673.

Phelan, P. L., and Miller, J. R. (1982). Post-landing behavior of alate Myzus persicae as altered by (E)-beta-farnesene and 3-carboxylic acids. *Entomol. Exp. Appl.* 32**,** 46-53.

Phelan, P. L., Montgomery, M. E., and Nault, L. R. (1976). Orientation and locomotion of the apterous aphids dislodged from their hosts by alarm pheromone. *Ann. Entomol. Soc. Am.* 69**,** 1153-1156.

Pickett, J. A., and Griffiths, D. C. (1980). Composition of aphid alarm pheromones. *J. Chem Ecol.* 6**,** 349-360.

Pickett, J. A., Wadhams, L. J., Woodcock, C. M., and Hardie, J. (1992). The chemical ecology of aphids. *Annu. Rev. Entomol.* 37**,** 67-90.

Pickett, J. A., Williams, I. H., and Martin, A. P. (1982). (Z)-11-Eicosen-1-ol, an important new pheromonal component from the sting of the honeybee, *Apis mellifera* L. (Hymenoptera, Apidae). *Journal of Chemical Ecology*. 8**,** 163-175.

Reichling, J., and Becker, H. (1978). Essential oil of Radix chamomillae (Matricaria chamomilla L.). *Z. Naturforsch. C.* 33**,** 589-591.

Rodriguez-Saona, C. R., Rodriguez-Saona, L. E., and Frost, C. J. (2009). Herbivore-induced volatiles in the perennial shrub, Vaccinium corymbosum, and their role in inter-branch signaling. *J. Chem Ecol.* 35**,** 163-175.

Roitberg, B. D., and Myers, J. H. (1978). Adaptation of alarm pheromone responses of pea aphid Acyrthosiphon pisum (Harris). *Can. J. Zoo.* 56**,** 103-108.

Rottman, S. J., and Snowdown, C. T. (1972). Demonstration and analysis of an alarm pheromone in mice *J. Comp. Physiol. Psycol.* 81**,** 483-490.

Seyfarth, R. M., Cheney, D. L., and Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*. 210**,** 801-803.

Shah, P. A., Pickett, J. A., and Vanderberg, J. D. (1999). Responses of Russian wheat aphid (Homoptera : Aphididae) to aphid alarm pheromone. *Environ. Entomol.* 28**,** 983-985.

Shearer, D. A., and Boch, R. (1965). 2-Heptanone in the mandibular gland secretion of the honeybee. *Nature*. 205**,** 530.

Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science*. 197**,** 1246-1253.

Sherman, P. W. (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behav. Ecol. Sociobiol.* 17**,** 313-323.

Smith, M. C. (1982). Reaction of Percina nigrofasciata, Ammocrypta beani, and Etheostoma swaini (Percidae, Pisces) to conspecific and intergeneric skin extracts. *Can. J. Zoo.* 60**,** 1067-1072.

Smith, R. J. F. (1986). Evolution of alarm signals; role of benefits derived from retaining group members of territorial neighbors. *Am. Nat.* 128**,** 604-610.

Smith, R. J. F. (1992). Alarm signals in fishes. *Rev. Fish Biol.* 2**,** 33-63.

Spinella, A., Alvarez, L. A., Passeggio, A., and Cimino, G. (1993). New 3-alkylpyridines from 3 mediterranean Cephalaspidean mollusks - Structure, ecological role and taxonomic relevance. *Tetrahedron*. 49**,** 1307-1314.

Stebbing, P. D., Watson, G. J., Bentley, M. G., Fraser, D., Jennings, R., Rushton, S. P., and Sibley, P. J. (2003). Reducing the threat: The potential use of pheromones to control invasive signal crayfish. *Bulletin Francais de la Peche et de la Pisciculture*. 219-224.

Stoeffler, M., Maier, T. S., Tolasch, T., and Steidle, J. L. M. (2007). Foreign-language skills in rove-beetles? Evidence for chemical mimicry of ant alarm pheromones in myrmecophilous Pella beetles (Coleoptera : Staphylinidae). *J. Chem Ecol.* 33**,** 1382-1392.

Taylor, R. J., Balph, D. F., and Balph, M. H. (1990). The evolution of alarm calling: a cost-benefit analysis. *Anim. Behav.* 39**,** 860-868.

Trivers, R. L. (1971). The Evolution of Reciprocal Altruism. *Q. Rev. Biol.* 46**,** 35-57.

Turlings, T. C. J., Bernasconi, M., Bertossa, R., Bigler, F., Caloz, G., and Dorn, S. (1998). The induction of volatile emissions in maize by three herbivore species with different feeding habits: Possible consequences for their natural enemies. *Biol. Control*. 11**,** 122-129.

Turlings, T. C. J., and Ton, J. (2006). Exploiting scents of distress : the prospect of manipulating herbivore-induce plant odour to enhance the control of agricultural pests. *Curr. Opin. Plant Biol.* 9**,** 421-427.

Vadas, R. L., and Elner, R. W. (2003). Responses to predation cues and food in two species of sympatric, tropical sea urchins. *Mar. Ecol.* 24**,** 101-121.

Vallet, A., Cassier, P., and Lensky, Y. (1991). Ontogeny of the fine-structure of the mandibular glands of the honeybee (Api mellifera L) workers and the pheromonal activity of 2-heptanone. *J. Insect Physiol.* 37**,** 789-804.

Vander Meer, R. K., Breed, M. D., Espelie, K. E., and Winston , M. L. (1998). Pheromone Communication in Social Insects Ants, Wasps, Bees, and Termites Westview Press

Verheggen, F. J., Arnaud, L., Bartram, S., Gohy, M., and Haubruge, E. (2008a). Aphid and plant volatiles induce oviposition in an aphidophagous hoverfly. *J. Chem Ecol.* 34**,** 301-307.

Verheggen, F. J., Fagel, Q., Heuskin, S., Lognay, G., Francis, F., and Haubruge, E. (2007). Electrophysiological and behavioral responses of the multicolored asian lady beetle, Harmonia axyridis pallas, to sesquiterpene semiochemicals. *J. Chem Ecol.* 33**,** 2148-2155.

Verheggen, F. J., Haubruge, E., De Moraes, C. M., and Mescher, M. C. (2009). Social enviroment influences aphid production of alarm pheromone. *Behav. Ecol.* 20**,** 283-288.

Verheggen, F. J., Mescher, M. C., Haubruge, E., De Moraes, C. M., and Schwartzberg, E. G. (2008b). Emission of alarm pheromone in aphids: A non-contagious phenomenon. *J. Chem Ecol.* 34**,** 1146-1148.

Vet, L. E. M., and Dicke, M. (1992). Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37**,** 141-172.

Visscher, P. K., Vetter, R. S., and Robinson, G. E. (1995). Alarm pheromone perception in honey-bees is decreased by smoke (Hymenoptera, Apidae). *J. Insect Behav.* 8**,** 11-18.

von Frisch, K. (1938). Zur psychologie des Fische-Schwarmes. *Naturwissenschaften*. 26**,** 601-606.

Wadhams, L. J. (1990). The use of coupled gas chromatography : electrophysiological techniques in the identification of insect pheromones. *In* "Chromatography and isolation of insect hormones and pheromones" (A. R. McCaffery, A. R. Wilson, Ed.), pp. 289-298. Plenum, New York/London.

Wager, B. R., and Breed, M. D. (2000). Does honey bee sting alarm pheromone give orientation information to defensive bees? *Ann. Entomol. Soc. Am.* 93**,** 1329-1332.

Watson, G. J., Hamilton, K. M., and Tuffnail, W. E. (2005). Chemical alarm signalling in the polychaete Nereis (Neanthes) virens (Sars) (Annelida : Polychaeta). *Anim. Behav.* 70**,** 1125-1132.

Wientjens, W. H., Lakwijk, A. C., and Vanderma, T. (1973). Alarm pheromone of grain aphids. *Experientia*. 29**,** 658-660.

Wilson , E. O. (1971). The insect societies. Oxford University Press, London.

Wilson , E. O., and Hölldobler, B. (1985). Caste-specific techniques of defense in the polymorphic antPheidole embolopyx (Hymenoptera: Formicidae). *Insect. Soc.* 32**,** 3-22.

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

Wisenden, B. D., and Millard, M. C. (2001). Aquatic flatworms use chemical cues from injured conspecifics to assess predation risk and to associate risk with novel cues. *Anim. Behav.* 62**,** 761-766.

Witkin, S. R., and Fitkin, M. S. (1979). Chickadee alarm calls: does mate investment pay dividends? *Anim. Behav.* 27**,** 1275-1276.

Wittstock, U., and Gershenzon, J. (2002). Constitutive plant toxins and their role in defense against herbivores and pathogens. *Curr. Opin. Plant Biol.* 5**,** 300-3007.

Wohlers, P. (1980). Escape responses of pea aphids, Acyrthosiphon pisum, to alarm pheromones and additional stimuli. *Entomol. Exp. Appl.* 27**,** 156-168.

Wohlers, P. (1981). Effect of the alarm pheromone (E)-beta-farnesene on dispersal behaviour of the pea aphid Acyrthosiphon pisum. *Entomologia Experimentalis et Applicata*. 29**,** 117-124.

Wohlers, P. (1982). Effect of alarm pheromone (E)-beta-farnesene on aphid behavior during flight and after landing on plants. *Z. Angewandte Entomol.* 93**,** 102-108.

Wyatt, T. D. (2003). Pheromones and Animal Behaviour. The press syndicate of the university of Cambridge, Oxford.

Xiangyu, J. G., Zhang, F., Fang, Y. L., Kan, W., Zhang, G. X., and Zhang, Z. N. (2002). Behavioural response of aphids to the alarm pheromone component (E)-beta-farnesene in the field. *Physiol. Entomol.* 27**,** 307-311.

Zhu, J. W., Cossé, A. A., Obrycki, J. J., Boo, K. S., and Baker, T. C. (1999). Olfactory reactions of the twelve-spotted lady beetle, Coleomegilla maculata and the green lacewing, Chrysoperla carnea to semiochemicals released from their prey and host plant : electroantennogram and behavioral responses. *J. Chem. Ecol.* 25**,** 1163-1177.

Figure 1 A

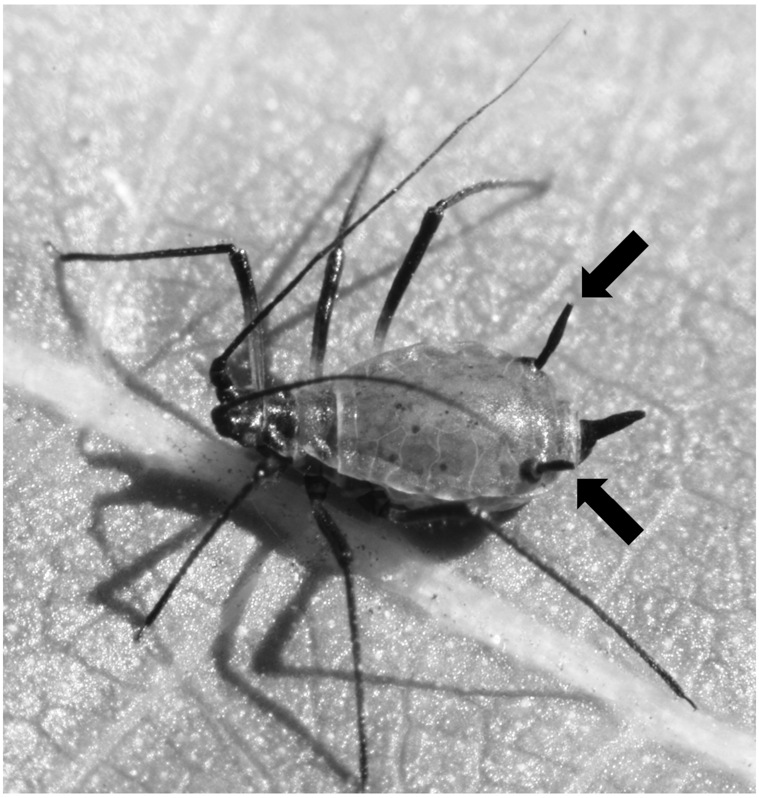

Figure 1B

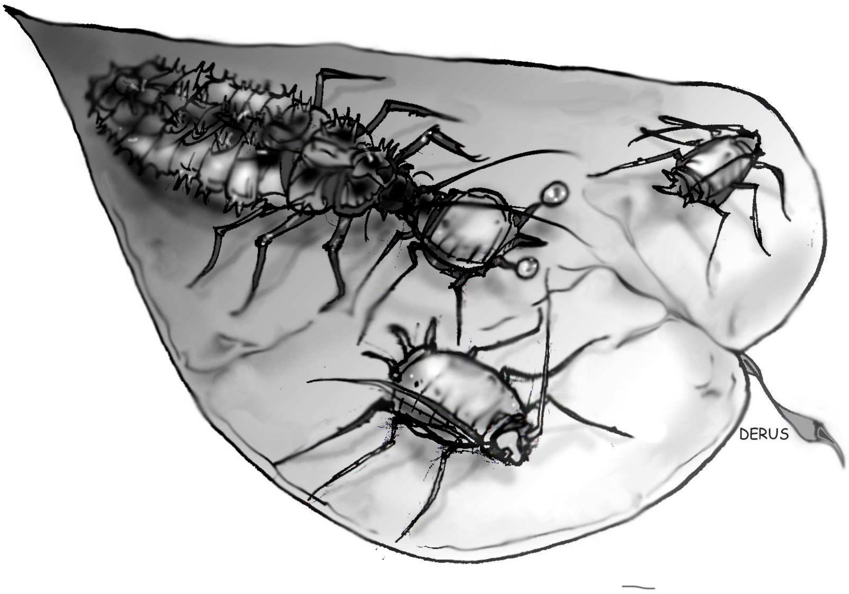

Figure 2

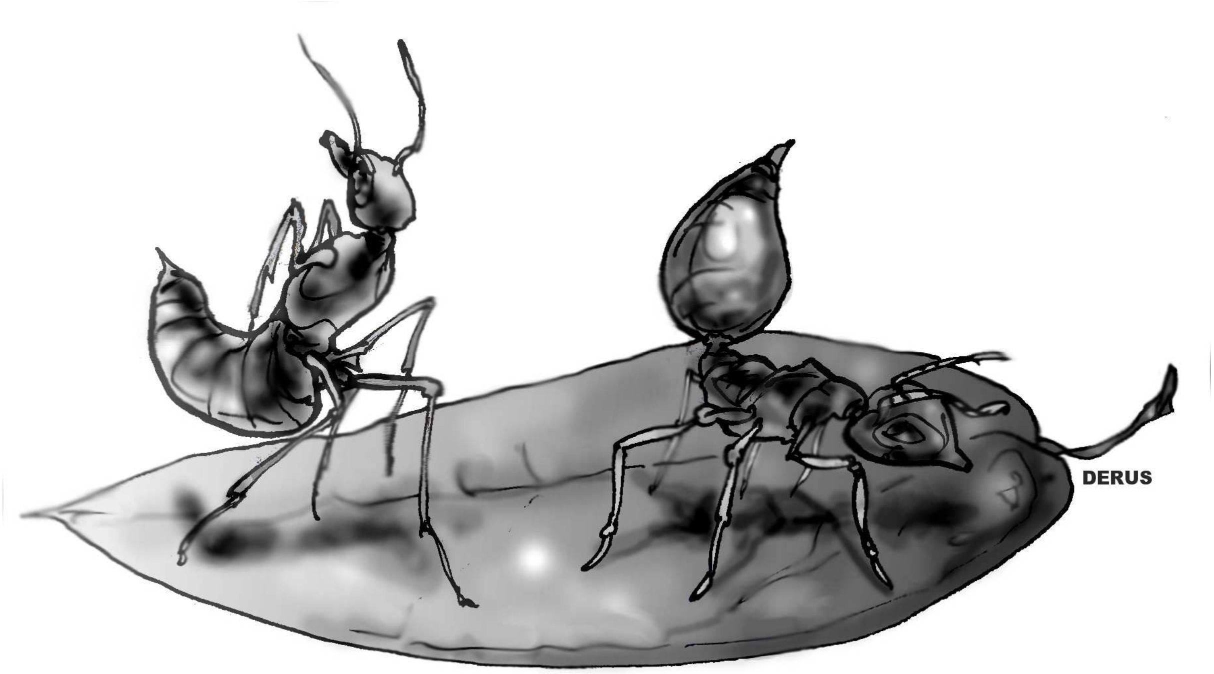

Figure 3

Figure 4