



Insect alarm pheromones in response to predators: Ecological trade-offs and molecular mechanisms

Saumik Basu^{a,*}, Robert E. Clark^a, Zhen Fu^{a,b}, Benjamin W. Lee^a, David W. Crowder^a

^a Department of Entomology, Washington State University, Pullman, WA, USA

^b Department of Entomology, Texas A&M University, College Station, TX, USA

ARTICLE INFO

Keywords:

Chemical communication
Insect behavior
Kairomones
Molecular ecology
Predator-prey interactions

ABSTRACT

Insect alarm pheromones are chemical substances that are synthesized and released in response to predators to reduce predation risk. Alarm pheromones can also be perceived by predators, who take advantage of alarm cues to locate prey. While selection favors evolution of alarm pheromone signals that are not easily detectable by predators, predator evolution selects for better prey detection ability. Here, we review the diversity of alarm signals, and consider the behavioral and ecological conditions under which they have evolved. We show that components of alarm pheromones are similar across many insects, although aphids exhibit different behavioral responses to alarm cues compared to social insects. The effects of alarm pheromones on prey behavior depend on factors such as the concentration of pheromones and the density of conspecifics. We also discuss the molecular mechanisms of alarm pheromone perception underlying the evolutionary arms race between predators and prey, and the function of olfactory proteins and receptors in particular. Our review provides a novel synthesis of the diversity and function of insect alarm pheromones, while suggesting avenues that might better allow researchers to exploit population-level responses to alarm signaling for the sustainable management of pests and vector-borne pathogens.

1. Introduction

Alarm signaling is a component of anti-predator defense for many birds, mammals, insects, amphibians, gastropods, and plants (Wyatt, 2003; Heil and Karban, 2010). Insects exhibit a great diversity of volatile alarm pheromones, which warn conspecific individuals of predators (Wyatt, 2003; Verheggen et al., 2010). Insect herbivores typically live adjacent to conspecific individuals on shared plants and rely on alarm pheromones to indicate the presence of predators. Insects that detect alarm signals can then engage in defensive behaviors to avoid predators. Yet, predators can take advantage of pheromone cues to locate susceptible prey. This had led to an evolutionary arms race where selection favors evolution of alarm pheromone signals that are not easily detectable by predators, but where predator evolution selects for superior prey detection ability.

Research on insect alarm pheromones has primarily focused on the order Hemiptera, and aphids in particular (Vander moten et al., 2012). Aphids feed in large aggregations and are abundant in many ecosystems. In response to predators, aphids often release waxy droplets from their cornicles that contain complex mixtures of fatty acids (Greenway and

Griffith, 1973). These compounds volatilize rapidly, and recipient aphids perceive the signals using sensory organs (Kislow and Edwards, 1972; Pickett et al., 1992). Once alarm signals are perceived, aphids respond with behaviors that include feeding cessation and movement within or among plants (e.g., Kislow and Edwards, 1972; Nault et al., 1976; Pickett et al., 1992). In other cases, aphid alarm pheromones trigger aggressive behaviors in predators. For example, first instar nymphs of *Ceratovacuna lanigera* are aggressively attacked by syrphid flies when they release pheromones (Arakaki, 1989). Once alarm signals are diminished, however, aphids typically resettle.

Alarm pheromones have also been widely described in social insects since the first report of these compounds in ants by Goetsch (1934). Following this, alarm secretions were found to induce aggressive behavior in conspecific workers of almost all ant species studied (Hölldobler and Wilson, 1990). In ants, alarm pheromones serve two distinct functions, “aggressive alarms”, which promote aggressive responses to antagonists, and “panic alarms”, which promote dispersal from a predation threat (Wilson and Regnier, 1971). In honeybees (*Apis mellifera*), perception of alarm pheromones, which are produced by workers guarding the entrance of hives, can lead to increased movement

* Corresponding author.

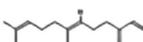
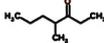
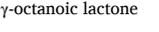
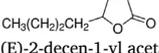
E-mail address: saumik.basu@wsu.edu (S. Basu).

and aggression among nest mates (Vander Meer et al., 1998; Alaux et al., 2009). Honeybees also release alarm pheromones from their stingers when attacking organisms that threaten their hives (Boch et al., 1962; Shearer and Boch, 1965). The release of these pheromones provides orientation information that is used for recruiting other bees within a hive to a threat (Wager and Breed, 2000). Other bee species can also eavesdrop on alarm pheromones produced by other bee species while foraging, which allows foraging individuals to avoid host plants that harbor competitors and predators (Wang et al., 2016).

Although considerable literature has elucidated the chemical composition and behavioral responses of herbivores and predators to

alarm pheromones, the importance of predator-prey co-evolution for pheromone perception is rarely considered in an ecological context. Moreover, pheromone receptors, and their molecular function, remain poorly understood, which limit the ability to exploit predator and prey responses to alarm cues for pest management. To address these knowledge gaps, in this review we discuss the diversity of alarm pheromones as well as the behavioral and ecological factors that affect alarm signaling and perception. We then discuss advances in molecular and biochemical mechanisms of insect alarm pheromone perception. We consider how alarm pheromone signaling has evolved in both prey and predators. Finally, we discuss future directions and applications of alarm

Table 1
Various alarm pheromone components in different insect orders.

Insect orders	Principal components	Response behavior	Functions and other important properties	References
Aphids (Hemipterans)	(E)- β -Farnesene	Escape, dispersion and fright behaviors	EBF is the primary alarm component in most of the aphid species. Once perceived by the receiver it induced escape response by walking away or dropping off the host plant.	Edwards et al. (1973); Francis et al. (2005a, b); Bowers et al. (1977b) Pickett and Griffith (1980) Dawson et al. (1987)
	 Germacrene A	Escape, dispersion and fright behaviors	Germacrene aphid is primarily identified in alfalfa aphid (<i>Therioaphis</i>)	
	 (-)- α -Pinene	Escape, dispersion and fright behaviors	(-)- α -Pinene is the primary alarm compound in vetch aphid <i>Megoura viciae</i>	
	 Isothiocyanate	Escape, dispersion and fright behaviors	Act synergistically with EBF in cruciferous aphids	
Ants (Hymenoptera)	n-undecane	Aggressive behavior	Present in the alarm pheromone of almost all Formicidae species and induce the recruitment and aggression of workers or escape behavior. Found in <i>H. opacior</i> and <i>P. pennsylvanica</i> and show drastically increased mobility. Strongest alarm pheromone component in leaf cutting ant (<i>Attini</i>) along with 2-heptanone Alarm pheromone in leaf cutting ant (<i>Attini</i>) and in other related ant species	Stoeffler et al. (2007) Duffield et al. (1976) Hughes et al. (2001) Hughes et al. (2001)
	 2,5-dimethyl-3-isopentylpyrazine	Fright response or recruitment		
	 4-methyl-3-heptanone			
	 2-heptanone			
Honeybees (Hymenoptera)	 Isopentyl acetate (IPA)	Aggressive behavior and recruitment	Perception of the alarm pheromone increase movement of the workers, guarding through nestmates during against intruder Together with IPA contribute to other behavioral responses Elicit landing aberration indistinguishable from natural alarm foraging response Foraging responses, repel forager from landing on inflorescence	Boch et al. (1962); Shearer and Boch (1965) Pickett et al. (1982) Li et al. (2014) Li et al. (2014)
	 (Z)-11-eicosen-1-ol and 2-heptanone	Aggressive alarm response and recruitment		
	 γ -octanoic lactone	Strongest alarm hormone in <i>A. dorsata</i>		
	 (E)-2-decen-1-yl acetate	Aggressive responses in <i>A. dorsata</i> and <i>A. florea</i>		
				

pheromones for pest and disease management.

2. Diversity and function of insect alarm pheromones

2.1. Alarm pheromones in aphids

The composition of alarm pheromones varies among aphid species that have been studied, ranging from single molecules to complex blends (Vandermorten et al., 2012). Alarm signals are believed to be evolutionarily derived from defensive compounds, or compounds released during injury (Wyatt, 2003; Verheggen et al., 2010). Alarm signals include monoterpenes, short-chain aliphatic hydrocarbons, and sesquiterpenes that differ from other pheromones (Ginzel, 2010). Effects of alarm pheromones on aphid behavior depend on the quantity and ratio of different components and their spatial arrangement (stereoisomerism) (Wadhams, 1990; Verheggen et al., 2010). For example, the pheromone (*E*)-norfarnesene has similar stereochemistry and effectiveness than (*E*)- β -Farnesene, but it is one carbon shorter (Bowers et al., 1977a).

The most well-studied component of aphid alarm pheromones is (*E*)- β -Farnesene, which has been identified in species including *Acyrtosiphon pisum*, *Aphis gossypii*, *Rhopalosiphum maidis*, *Aphis glycine*, and *Aphis craccivora* (Bowers et al., 1972; Edward et al., 1973; Pickett and Griffiths, 1980; Francis et al., 2005b; Verheggen et al., 2010) (Table 1). A study of 23 aphid species showed (*E*)- β -Farnesene was the principle alarm component in 16 (Francis et al., 2005b), but other species like *Megoura viciae* possessed additional monoterpenes (Pickett and Griffiths, 1980). (*E*)- β -Farnesene is also a component of plant volatiles released in response to herbivores (Crock et al., 1997; Turlings and Ton, 2006). One hypothesis is that (*E*)- β -Farnesene synthesis in aphids resulted from natural selection to mimic plants. However, the low levels, instability, and pulsed release of aphid (*E*)- β -Farnesene during attack from predators is probably functionally superior to constitutively emitting plant derived (*E*)- β -Farnesene (Kunert et al., 2010; Vosteen et al., 2016). Moreover, (*E*)- β -Farnesene released by plants may interfere with aphid signals due to habituation (Petrescu et al., 2001), which has been seen in transgenic plants that continuously produce (*E*)- β -Farnesene (Kunert et al., 2010). However, plants often simultaneously secrete sesquiterpene-like compound β -Caryophyllene, which may allow aphids to distinguish between (*E*)- β -Farnesene produced by plants and aphids (Kunert et al., 2010).

The behavioral responses of aphids to alarm pheromones have primarily been based on studies with (*E*)- β -Farnesene, making it a model system to study insect behavior in response to chemical signals. When under attack from predators, aphids typically release (*E*)- β -Farnesene in pulses, which is followed by an exponential decline in the concentration of pheromones over time, which prevents habituation and distinguishes imminent threats (Schwartzberg et al., 2008; Kunert et al., 2010). For example, *A. pisum* uses an oscillating pheromone signal when under attack from ladybug and lacewing predators (Schwartzberg et al., 2008; Joachim et al., 2013). Aphids have also been shown to be more responsive to the frequency of alarm pheromone release compared to the concentration (Kunert et al., 2005). For example, the frequency of exposure to (*E*)- β -Farnesene is more important than the total amount or the density of aphids for the induction of winged morphs in *A. pisum* (Kunert et al., 2005).

(*E*)- β -Farnesene also facilitates wing induction in aphids and can trigger dispersal behavior (Kunert et al., 2005; Wang et al., 2019). The experimental release of (*E*)- β -Farnesene has been shown to induce behaviors including withdrawal of stylets from plants, walking from threats, and dropping off plants; however, the same signals can attract natural enemies (Hatano et al., 2010; Vandermoten et al., 2012). Transgenic plants releasing (*E*)- β -Farnesene also deter aphid settling on plants (Phelan and Miller, 1982; Kunert et al., 2010; Zhou et al., 2016; Wang et al., 2019).

Responses of aphids to (*E*)- β -Farnesene vary widely based on aphid traits and ecological context. For example, green and red morphs of

A. pisum exhibit different behaviors in response to a ladybird beetle (*Propylea japonica*) (Weisser et al., 1999; Fan et al., 2018). Green morphs tend to respond to (*E*)- β -Farnesene by walking away from the alarm signal, while red morphs tend to drop off a plant (Fan et al., 2018). These differences in behavior of the two morphs may be due to variable predation risk, with red morphs more conspicuous to predators and thus more likely to respond to predation threat (Keiser and Mondor, 2015; Polin et al., 2015). Aphids often produce less alarm pheromones when reared individually than when in aggregations, or when exposed to odor from active aphid colonies (Verheggen et al., 2008b). The biosynthesis of (*E*)- β -Farnesene also depends on aphid age and weight, with pre-reproductive aphids producing more alarm pheromone than post-reproductives, and alarm pheromone production declining with increasing body weight (Mondor et al., 2000). These trends may have evolved given that pre-reproductive and smaller aphids have greater potential fitness.

Despite the central role of (*E*)- β -Farnesene in eliciting aphid behaviors, the biosynthesis of this compound was not well understood until recently. Earlier studies suggested that compounds derived from bacterial endosymbionts or plants could be the precursor from which (*E*)- β -Farnesene is derived. However, recent studies show that neither host plants, nor obligate aphid endosymbionts, contribute to (*E*)- β -Farnesene biosynthesis (Sun and Li, 2017). Rather, (*E*)- β -Farnesene is likely produced *de novo* in a physiological pathway associated with juvenile hormone biosynthesis that shares common intermediate precursors such as farnesyl diphosphate (Mondor et al., 2000; Sun and Li, 2017).

While (*E*)- β -Farnesene is the most well-studied component of aphid alarm pheromones, not all aphids produce this compound, including *Eucerphis punctipennis* and *Drepanosiphum platanoides* (Francis et al., 2005a). Other components identified in aphid alarm pheromone secretions include Germacrene A in *Therioaphis* sp., monoterpenes such as α -pinene, β -pinene, and limonene in *Megoura viciae* (Bowers et al., 1977b; Pickett and Griffiths, 1980). Further work is needed to identify the molecular mechanisms that promote production of these compounds and their role in affecting aphid behavioral responses to predators.

2.2. Alarm pheromones in social insects

Social insects such as ants and bees produce many alarm pheromones as a part of their olfactory communication (Table 1). In many ant species the biosynthesis of these pheromone components can occur in either the Dufour's gland or the poison glands, which are located in the abdomen and stinger, respectively (Fujiwara-Tsujii et al., 2006; Lenz et al., 2013). However, other ant species produce alarm pheromones in the antennal lobe or the mandibles (Blum, 1985; Mizunami et al., 2010). While most ants produce aliphatic carbon chains as part of alarm pheromone blends (Fujiwara-Tsujii et al., 2006), the diversity of pheromone components observed in social insects to date is greater than in aphids (Table 1). For example, the principle components of pheromone blends is often 4-methyl-3-heptanone in leaf cutting ants (*Atta* sp.), pyrazine in fire ants (*Solenopsis invicta*), and 2-heptanone in many other ant species (e.g., Hughes et al., 2001; Vander Meer et al., 2010; Lenz et al., 2013) (Table 1).

Eliciting responses in ants by presenting workers with pheromones has been a mainstay in ant behavioral ecology, as pheromones can modulate aggressive or flee responses. For example, jet ant (*Lasius fuliginosus*) workers respond to alarm pheromone n-undecane by running toward the source (Stoeffler et al., 2007). Conversely, workers of *Hypoponera opacior* and *Ponera pennsylvanica* increase movement in response to 2,5-dimethyl-3-isopentylpyrazine, but run away from the source (Duffield et al., 1976). Response to alarm pheromones can also involve intruders in the territory of the nest. For example, *Pheidole embolopyx* produce alarm pheromones in response to nest intruders, causing workers to mount intense defensive responses (Wilson and Holldobler, 1985). Two species of slave-ants (*Formica cunicularia* and *Formica rufibarbis*) respond to alarm pheromones with aggressive

behavior towards parasites (Tamarri et al., 2009). Recently, Norman et al. (2017) found great variation of alarm pheromone composition among seven species of fungus-growing *Attini* ants, which exhibit differences in behavioral activity of alarm compounds. Alarm pheromone components produced in the mandibles of *Eciton* ant species also exhibit differential aggressive response including frequency of attacks and worker recruitment based on their composition (Lalor and Hughes, 2011; Brückner et al., 2018).

In honeybees (*Apis mellifera*), alarm pheromone released from stingers provides orientation information to bees to locate targets and can alter appetitive stimuli associated with olfactory learning (Wager and Breed, 2000; Urlacher et al., 2010). Honeybee alarm pheromones also play a vital role in establishing intra- and interspecific communications within and between various bee species, promoting plant-pollinator interactions (Wang and Tan, 2019). Conversely, honeybee foragers are capable of detecting hetero-specific alarm pheromone signals through eavesdropping, allowing them to avoid host plants with interspecific competitors. For example, *Apis cerana* can eavesdrop on alarm signals released by two other honeybee species, *Apis dorsata* and *Apis mellifera*, and avoid competition for floral resources (Wang et al., 2016).

The first biologically active alarm pheromone component identified in honeybees was isopentyl acetate (Boch et al., 1962) (Table 1), and later at least over 40 other low molecular weight aliphatic or aromatic components were detected in the secretions of the Koshewnikov gland as complex chemical blends (Hunt, 2007). Certain components of these signals, such as (*Z*)-11-eicosen-1-ol and 2-heptanone in honeybees, are known to alter bee behavior Boch et al. (1962); Shearer and Boch (1965); Pickett et al. (1982) (Table 1). Similarly, recent studies identified three main alarm compounds in giant Asian honeybee, *Apis dorsata*,

γ -octanoic lactone, isopentyl acetate, and (*E*)-2-decen-1-yl acetate, and these compounds induced either defensive behaviors or foraging (Li et al., 2014) (Table 1). However, not all the aliphatic or aromatic secretions in honey bee pheromone blends are believed to elicit alarm responses on their own, although they may work in concert with other chemicals (Hunt, 2007; Li et al., 2014).

3. Molecular mechanism of alarm pheromone perception

Chemoreception in insects is a physiological process whereby environmental stimuli are detected, and the signals are transduced to the central nervous system (Fig. 1). The perception of alarm signals is mediated by chemosensory proteins, including transmembrane odorant receptors (ORs) and secreted odorant-binding proteins (OBPs) on the antennae (Leal, 2013; Zhang et al., 2017). After odorant molecules enter the sensillar lymph, they bind to OBPs, which transport the molecules to ORs on sensory neurons (Sun et al., 2018, Fig. 1). ORs then form heterodimers with highly conserved and co-expressed odorant receptor co-receptor (ORCO) proteins, which serve a chaperone function and contribute to pore formation in ligand-gated ion channels upon ligand binding (Nakagawa et al., 2012; Zhou et al., 2012) (Fig. 1), while also activating sensory neurons in cooperation with OBPs to transduce alarm signals (Benton et al., 2006; Zhang et al., 2017).

While cellular and molecular mechanisms of alarm signaling have been assessed for a few insects, genome and RNA-seq sequencing have promoted identification and characterization of multiple ORs and OBPs recently (Zhou et al., 2010; Sun et al., 2012; Zhang et al., 2017). For example, in *A. pisum*, perception of (*E*)- β -Farnesene is mediated by coordinated action of one OR (ApisOR5), which is expressed in type B neurons housed in large placoid sensilla in the sixth antennal segment,

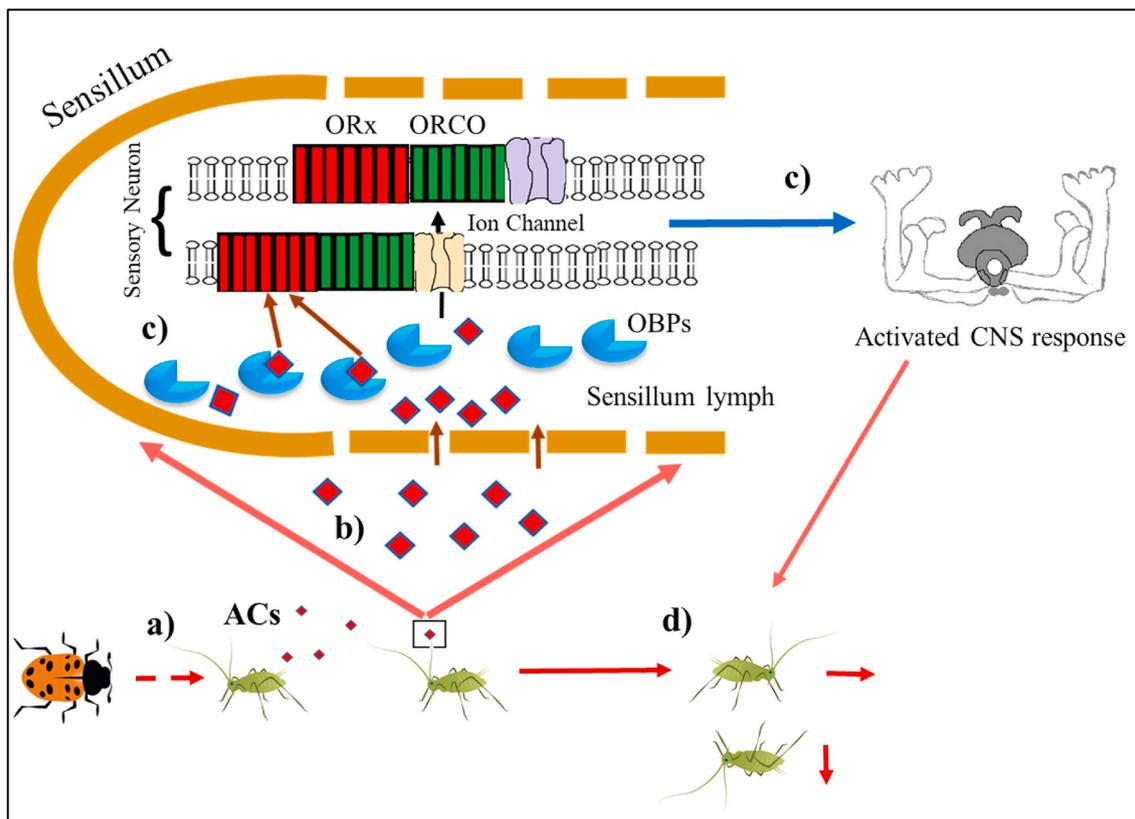


Fig. 1. Schematic representation of alarm pheromone perception by aphid antennae: (a) In response to natural enemy attack, aphids to release alarm compounds (ACs) as waxy droplets from cornicles; (b) volatilized ACs enter the insect sensilla, located on six antennal segment through cuticular pores, bind and ferried by odorant binding proteins (OBPs) housed in sensillum lymph to odorant receptor complex (ORx/ORCO) located on the dendritic membrane of sensory neurons; (c) alarm signal for impending danger is transduced from peripheral sensory neurons to central nervous system (CNS) which (d) promotes escape responses in con-specifics like running and dropping from hosts. Insect brain image modified from Gerber et al. (2017).

and two OBPs (ApisOBP3, ApisOBP7), which are expressed in the sensillum lymph (Zhang et al., 2017, Fig. 1). In *A. pisum* individuals, among over 60 odorants tested, only (*E*)- β -Farnesene and geranyl acetate elicited electrophysiological responses to ApisOR5 (Zhang et al., 2017). Moreover, when ApisOBP3 and ApisOBP7 were silenced in *A. pisum* using RNAi, aphids did not respond to (*E*)- β -Farnesene, confirming the role of these OBPs in detecting and responding to (*E*)- β -Farnesene (Zhang et al., 2017). Similarly, in *Rhopalosiphum padi*, both RpadOBP3 and RpadOBP7 are associated with (*E*)- β -Farnesene perception (Fan et al., 2017). In eusocial insects, OBPs have been shown to play a crucial role in alarm signaling by binding and transporting pheromone compounds to their olfactory systems (Pelosi et al., 2018; Song et al., 2018). Similar to OBPs, ORs have been identified from honeybees (Wanner et al., 2007; Karpe et al., 2017) and ants (e.g., Pask et al., 2017; Slone et al., 2017; Yan et al., 2017). In these insects, these receptors are required for chemical perception and can mediate certain social behaviors such as pollinator attraction to plants (Fleischer and Krieger, 2018).

Insect OBPs have also been characterized through investigation of their binding affinity and using molecular docking experiments with bioactive components. However, transmembrane ORs have proven to be challenging to express and purify in heterologous systems, and crystal structures for ORs have not yet been determined (Ventur and Zhou, 2018). Some OBPs that have been assessed across aphid species, such as OBP3, such that they are highly conserved (Northey et al., 2016) (Fig. S1). Additionally, Tyr30, which is located close to the predicted ligand binding site of OBP3 and plays an important role in ligand binding (Northey et al., 2016), was conserved across all 8 OBP3 sequences we aligned (Fig. S1). Other residues that could function in ligand interactions in aphids, including Phe5, Val27, and Tyr105, are also conserved (Fig. S1). However, similar OBPs may have unique functions in different aphid species; assays show that OBP3 in *N. ribisnigri* binds only to (*E*)- β -Farnesene, but the same OBP in *M. viciae* can respond to a mixture of different alarm molecules including (*E*)- β -Farnesene, (-)- α -pinene, β -pinene, and limonene, with (-)- α -pinene the most active (Northey et al., 2016).

Molecular binding assays between OBPs and aphid-derived alarm pheromone molecules indicate the potential to develop pest control strategies by exploiting the specificity of alarm communication and by altering arms race between predators and prey. For example, given that particular ORs and OBPs show a strong affinity toward (*E*)- β -Farnesene and mediate alarm pheromone signaling, they may be targets for aphid management (Fan et al., 2017; Ventur and Zhou, 2018). OBPs might also be used to recruit predatory insects to prey aggregations (Verheggen et al., 2008a; Vandermoten et al., 2011). For example, among five OBPs identified from adult lacewings (*Chrysopa pallens*), three OBPs (CpalOBP3, CpalOBP6, and CpalOBP10) were shown to be involved in the detection and transport of signals produced by plant volatiles and aphid alarm signals that indicated locations of prey; higher expression of these OBPs in both male and female antennae altered lacewing behavior and resulted in increased oviposition on plants with active aphid colonies (Li et al., 2017).

4. Alarm pheromone as kairomones for natural enemies

Alarm pheromones can recruit predators to prey and act as kairomones, chemical signals that are beneficial to a signal receiver but detrimental to the emitter (Nordlund and Lewis, 1976). However, studies assessing effects of alarm pheromones on predator-prey interactions are mixed, even for (*E*)- β -Farnesene, with predators responding strongly in some ecological contexts but not others (Table S1). Alarm pheromones often serve as foraging cues to predators when high enough concentrations are present (Hatano et al., 2008; Vandemorten et al., 2012; Vosteen et al., 2016). However, the short distance transmission of alarm pheromones often makes it difficult for predators to use them for prey detection (Joachim et al., 2015; Vosteen

et al., 2016). Although multiple prey species, such as *A. pisum*, *M. persicae*, and *M. viciae* emit low levels of (*E*)- β -Farnesene under natural conditions in the absence of any stress factor, most other aphids do not emit detectable (*E*)- β -Farnesene in undisturbed colonies (Francis et al., 2000; Acar et al., 2001; Joachim and Weisser, 2013). Consequently, for predators to find prey, aphids have to already be emitting warning signals. Importantly, (*E*)- β -Farnesene's low persistence means plant-emitted volatiles are typically more reliable signals of herbivores (Joachim et al., 2015).

4.1. Alarm pheromones as kairomones for prey location

Responses of predators to pheromones can vary even among species with similar foraging strategies. For example, the amount of (*E*)- β -Farnesene released by *A. pisum* is less than 50 ng when under attack from lacewings (*Chrysoperla carnea*) and multiple ladybird beetle species, which was below thresholds needed to trigger predator responses in the laboratory (Schwartzberg et al., 2008; Joachim and Weisser, 2013; Joachim et al., 2015; Vosteen et al., 2016). Moreover, while generalist parasitoids such as *Aphidius colemani* and *Lysiphlebus testaceipes* showed no response to high concentrations of (*E*)- β -Farnesene, the generalist wasps *Aphidius ervi* and *Praon valucere*, and the specialists *Diaeretiella rapae* and *Aphidius uzbekistanicus*, were attracted to high (*E*)- β -Farnesene amounts (0.3–30 μ g) (Du et al., 1998; Heuskin et al., 2011; Ameixa and Kindlman, 2012). Under field conditions, such concentrations may only occur in the largest aphid colonies that are most attractive to parasitoids. Hoverfly (*Episyrphus balteatus*) larvae, in contrast, use both low and high levels of (*E*)- β -Farnesene as signaling cues (Francis et al., 2005b; Verheggen et al., 2008a; Leroy et al., 2010; Heuskin et al., 2012).

Beyond testing single chemical or blends, aphid tissue has been used to test the response of different predator species to alarm signals. For example, an ant (*Lasius niger*), the lady beetles *Adalia bipunctata* and *Harmonia axyridis*, the parasitoid *Lysiphlebus testaceipes*, and marmalade hoverfly (*Episyrphus balteatus*) were attracted to crushed aphids with stored alarm compounds (Francis et al., 2004, 2005b; Grasswitz and Paine, 1992; Verheggen et al., 2007, 2012). Such studies have also shown that volatiles other than (*E*)- β -Farnesene play a role in attracting predators. For instance, in *M. viciae*, the main alarm component is β -pinene, and (*E*)- β -Farnesene is only present in low quantities, but predators are attracted to crushed aphids (Francis et al., 2005a). Other predatory arthropods also exploit alarm pheromones as prey-finding cues. For example, cursorial spider (*Habronestes bradleyi*), a specialist predator of the ant *Iridomyrmex purpureus*, is attracted by naturally occurring amounts of alarm pheromone 6-methyl-5-hepten-2-one that is emitted by ant workers (Allan et al., 1996). Upon receiving alarm signals released by western flower thrip, *Frankliniella occidentalis*, the predator mite *Amblyseius cucumeris* and another natural enemy minute pirate bug, *Orius tristicolor* were found to increase forage and use the alarm pheromone as host finding cue (kairomone) (Teerling et al., 1993).

Although some predator species fail to show responses to alarm pheromone in the field, more sensitive measures demonstrate their capacity to respond. For example, while *Chrysoperla carnea* larvae and adults failed to show attractant behavior to high or low amounts of (*E*)- β -Farnesene (Joachim et al., 2015), electroantennography studies show that adults can detect and respond to (*E*)- β -Farnesene (Zhu et al., 1999). In contrast, *Chyropa cognata* showed neither electroantennography nor attraction to (*E*)- β -Farnesene even at high amounts (10 mg) (Boo et al., 1998). Similarly, in the field two ladybird species (*Coleomegilla maculata* and *Harmonia axyridis*) did not show any behavioral response to releases of (*E*)- β -Farnesene, but abundance increased in (*E*)- β -Farnesene treated fields (Zhu et al., 1999; Cui et al., 2012; Leroy et al., 2012). Larvae of another ladybird species (*A. bipunctata*) also have the ability to detect aphid prey from short-range, which is believed to be mediated by (*E*)- β -Farnesene (Francis et al., 2004; Hemptinne et al., 2000).

Research on parasitoids may shed insight into the role of alarm pheromones as kairomones. In the field, increased numbers of aphid

parasitoids were detected in yellow traps using (*E*)- β -Farnesene, and there is evidence of parasitoids learning to associate (*E*)- β -Farnesene with hosts (Cui et al., 2012). The parasitoid *A. uzbekistanicus*, for example, was only initially attracted to synthetic (*E*)- β -Farnesene at high levels (5.7 μ g), but females with oviposition experience responded to lower levels (1.4 μ g) (Micha and Wyss, 1996). Female parasitoids of cabbage aphid (*Diaeretiella rapae*) with oviposition experience also preferred aphids with cornicle secretions over non-secreting aphids, but naïve parasitoid females failed to distinguish between these aphid types (Moayeri et al., 2014). For some parasitoids, contact with non-volatile components other than (*E*)- β -Farnesene from aphid secretions can promote host specificity. For example, physical contact of the parasitoid *L. testaceipes* with cornicle secretions or body fluid increased oviposition on *R. padi* (Grasswitz and Paine, 1992). Moreover, the wasps *A. ervi* and *A. uzbekistanicus* only engage in oviposition responses during physical contact with aphid cornicle secretions, with no response occurring to volatile emissions alone (Battaglia et al., 2000; Micha and Wyss, 1996). These results suggest that parasitoid wasps use a broad complex of volatile and tactile chemical signals, of which (*E*)- β -Farnesene plays an important role to locate hosts.

4.2. Alarm pheromones as kairomones for prey avoidance or mutualisms

Alarm pheromones can act as warning signals for predators to avoid certain types of prey, such as those herbivores that are chemically-defended and toxic. For example, aphids that feed on cruciferous plants (Brassicaceae) containing glucosinolates have a biochemical ability to degrade glucosinolate to volatile isothiocyanate (Table 1), which is toxic to predators (Francis et al., 2004; Jones et al., 2001). It is documented that isothiocyanates act synergistically with (*E*)- β -Farnesene to mediate alarm signaling in cruciferous aphids, and therefore may function to deter predators (Dawson et al., 1987). This suggests that alarm pheromone blends may evolve to both provide signals that promote anti-predator behaviors in aphids, by including compounds such as (*E*)- β -Farnesene, while also deterring prey, by including compounds such as isothiocyanates. Isothiocyanates thus act as herbivore-induced plant volatiles (HIPV) by promoting repellent behaviors in predators, while also deterring prey when acting with (*E*)- β -Farnesene.

In addition to natural enemies, insects that form mutualistic relationships with aphids can be attracted to alarm signals. Argentine ants (*Linepithema humile*), for example, double their visitation to *C. populicola* aphid colonies when exposed to aphid cornicle secretions (Mondor and Addicott, 2007). Electroantennograms could be used to further probe electrophysiological responses of various insects to their alarm pheromones, and investigate olfactory discriminations of alarm signals by other insects (Du et al., 2019). For example, the black garden ant (*Lasius niger*) responds to lower doses of (*E*)- β -Farnesene in electroantennogram studies, but scout ants fail to show any response unless high concentrations are applied in the field (Verheggen et al., 2012). Adult ants of the species *Formica subsericea* (Say) also only respond to (*E*)- β -Farnesene from poplar leaf aphid (*Chaitophorus populicola*) at high concentrations (Nault et al., 1976).

5. Alarm pheromone emission: costs and benefits

Releases of alarm pheromones have a trade-off. On one hand, they signal impending threats from predation. On the other, the release of aphid alarm pheromone as a sticky cornicle secretion contains a high amount of triglyceride (Greenway and Griffiths, 1973) that is energetically costly to produce and risks attracting predators (Vandemorten et al., 2012). For an aphid cohort, alarm pheromones protect individuals that belong to the same colony rather than the emitter. Hence, the release of alarm pheromones by individual aphids following attack can benefit entire colonies (Edwards, 1966; Mondor and Roitberg, 2004; Wu et al., 2010). This may be selected for because many aphids are

parthenogenetic, where individuals in the same colony have the same genotype (Dedryver et al., 2013). Consequently, even though producing alarm pheromone may increase predation risk for an individual, it provides an inclusive fitness benefit (Robertson et al., 1995).

The production of aphid alarm pheromones has physiological and behavioral costs. The primary component of cornicle droplets that contain alarm pheromones are derived from lipids, which are limited in aphids due to their phloem-based diet (Callow et al., 1973). Biosynthesis of (*E*)- β -Farnesene is also linked with juvenile hormone production (Van Oosten et al., 1990), and synthesis of (*E*)- β -Farnesene affects development and can delay aphid reproduction (Mondor and Roitberg, 2003). For instance, lower fecundity of *Aphis gossypii* was observed after exposure to synthetic alarm pheromone (Su et al., 2006). Thus, there is a selective advantage in minimizing the emissions of (*E*)- β -Farnesene from aphids where the risk of predation is low (Outreman et al., 2010). For example, *A. pisum* regulates the amount of (*E*)- β -Farnesene in alarm secretion, with lower quantities emitted in smaller colonies than in larger colonies (Verheggen et al., 2010). The amount of (*E*)- β -Farnesene released also decreased in later instars and adults, ensuring enhanced protection for pre-compared to post-reproductive life stages (Mondor et al., 2000).

Behavioral responses to (*E*)- β -Farnesene depend on factors including life stage (Losey and Denno, 1998a,b), genotype (Braendle and Weisser, 2001), and environmental context (Dill et al., 1990). In *A. pisum*, *Myzus persicae*, and *Diuraphis noxia*, early instars are less sensitive to (*E*)- β -Farnesene than late instars because young individuals are more susceptible to starvation when they fall from the host plant (Montgomery and Nault, 1978; Roitberg and Myers, 1978a,b; Shah et al., 1999). Winged morphs of *M. persicae* are also more sensitive than wingless morphs to (*E*)- β -Farnesene (Visser and Piron, 1997). Additionally, host-adapted *A. pisum* populations from four different hosts differed in their defensive behaviors after (*E*)- β -Farnesene perception, suggesting that host shifts can lead to ecological specialization (Kunert et al., 2010). These differences in alarm response may arise from differing selection pressure on aphid species, morphs, and clones.

6. Effect of aphid alarm pheromones on vector-borne pathogen transmission

Many aphids transmit plant viruses, and changes in behavior due to alarm pheromones may affect virus acquisition and transmission. For example, winged adults of *Myzus persicae* respond more strongly to (*E*)- β -Farnesene compared to wingless adults, nymphs, or post-reproductive adults (Montgomery and Nault, 1978). This could affect the spread of pathogens, as winged adults are most capable of long-distance dispersal. Application of alarm pheromones in the field can also hamper aphid colonization on hosts and affect aphid longevity (Xiangyu et al., 2002). In turn, several attempts have been made to synthesize (*E*)- β -Farnesene for management of aphid vectors (Nishino et al., 1976; Bowers et al., 1977b; Dawson et al., 1982, 1988).

Chemical modification and application of (*E*)- β -Farnesene decreased settling and fitness of *M. persicae* on plants, which reduced transmission of *beet yellow virus* and *potato virus Y* (Dawson et al., 1982). *Myzus persicae* and *Macrosiphum euphorbiae* populations have also been lowered by application of synthetic (*E*)- β -Farnesene, but this increased transmission of *potato virus Y* (Lin et al., 2016). These results may have been caused by the fact that *potato virus Y* is a non-persistent virus that is retained in aphid stylets, and increased aphid movement in response to (*E*)- β -Farnesene may increase virus transmission even if aphid abundance decreases (Bragard et al., 2013; Lin et al., 2016). The application of (*E*)- β -Farnesene can also affect the transmission of pea enation mosaic virus by *A. pisum* (Lee et al., unpublished data).

7. Applications and future directions

Much of the research on alarm pheromones in insect herbivores may

be directly applicable to pest management. For example, the natural release of (*E*)- β -Farnesene from the glandular trichome of wild potatoes repels aphids (Gibson and Pickett, 1983; Beale et al., 2006). However, there are contradictory results regarding the defensive role of (*E*)- β -Farnesene against aphids. In transgenic *Arabidopsis*, constitutive releases of (*E*)- β -Farnesene failed to affect the settling or performance of the green peach aphid (*Myzus persicae*) (Kunert et al., 2010). Yet, even if alarm cues fail to have direct effects on aphids, releases of these cues can potentially increase the attraction of aphid predators and increase biological control (Du et al., 1998; Verheggen et al., 2007, 2008; Zhu et al., 1999; Vosteen et al., 2016). However, to make progress in these areas we suggest three promising directions for alarm pheromone research. First, alarm pheromones can be engineered for developing sustainable pest management programs. Second, more work is needed to identify molecular mechanisms related to alarm pheromone signaling. Third, recent advances in molecular biology techniques should allow for better manipulation of alarm pheromones. We expand on each of these ideas in the sections to follow.

7.1. Alarm pheromone for pest management

The ability of insect alarm pheromones to attract predators may be exploited to make baits or traps. For example, expression of (*E*)- β -Farnesene synthase gene in *Arabidopsis thaliana* increased aphid parasitoid attraction towards plants (Beale et al., 2006). Similarly, synthetic 4-methyl-3-heptanone, a component of alarm pheromone used by grass-cutting ants, can trap and control these insects (Hughes et al., 2002). However, most of the studies focused on the attractant properties of alarm pheromone on predators have been conducted under controlled laboratory conditions, and field trials are needed for validation. Therefore, there are ample opportunities for chemical ecologists and entomologists to develop various sustainable pest management strategies exploiting natural enemy behavioral responses to alarm pheromones.

7.2. Molecular and biochemical research related to alarm signaling

Recent research on various aspects of insect alarm pheromones have

provided insight into insect behavior and predator-prey interactions. However, several questions have yet to be answered regarding the detailed mechanisms mediating insect alarm pheromone signaling in terms of the components of the machinery, diversity of alarm signaling, signal perception, and other downstream processes. With recent development of various molecular and biochemical techniques, various new components associated with alarm signaling have been identified and characterized in various insect species. The evolution of alarm pheromone responses integrates two different categories: (i) perception of alarm compounds by olfactory proteins (molecular- and physiological level), and (ii) their impact on the behavior on predator-prey dynamics (population and community level) (Fig. 2). Interrelation of both these interactions at multiple levels ultimately contribute to biological complexity of alarm signaling (Fig. 2).

Beside alarm pheromones, we should also consider effects of plant derived volatiles that contain alarm components on insect predators. Although we have limited knowledge about the role of different enzymes involved in mono- and sesquiterpene biosynthesis in insects, the biosynthetic pathways for similar compounds have been well characterized in plants. For example, the biosynthesis of both alarm pheromone and juvenile hormones in insects are believed to share some common enzymes and intermediates with plant compounds, and thus there is potential to characterize the biosynthesis, storage, and regulation of alarm pheromones in plants to understand insects. However, the biosynthesis enzymes involved in (*E*)- β -Farnesene production are quite divergent in both plants and insects, suggesting that compounds from plants may not always have the expected effects on insect herbivores or their predators. Thus, future research using modern molecular approaches such as genome and/or RNA sequencing should focus on identifying divergence in alarm components between insects and plants.

7.3. Advanced molecular biology techniques may facilitate alarm pheromone research

Our understanding of molecular and biochemical recognition of alarm pheromone binding proteins and receptors are limited, and future research should identify and characterize various components of alarm

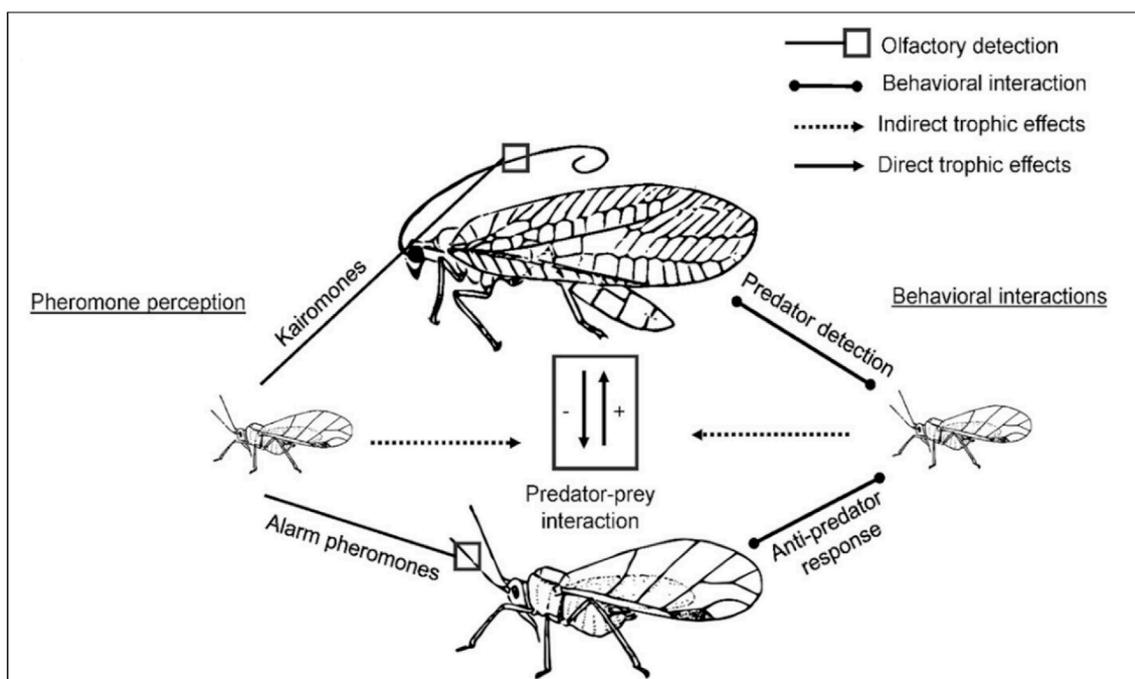


Fig. 2. Diagram of interactions across multiple levels of biological complexity. Two broad categories have been considered: perception of volatile compounds by odorant binding proteins (molecular- and physiological level), and the impact of behavior on predator-prey dynamics (population and community-level interactions).

signaling pathways and signaling mechanisms. Advancement in “omics” technologies (genomics, transcriptomics, proteomics) could guide research to explore different understudied areas of alarm signaling mechanisms. For example, genome editing tools such as CRISPR-Cas9 have been used for *in vivo* functional characterization of genes that are involved in alarm signaling reception and transduction (Guo et al., 2020). Moreover, the use of transgenic plants expressing dsRNAs against various alarm components, or directly feeding aphids with artificial diet containing dsRNA, could revolutionize our understanding of the mechanisms of insect alarm-pheromone mediated signaling in various insects.

8. Conclusions

Recent research related to the biosynthesis, diversity, perception, regulation, and function of insect alarm pheromones has increased our knowledge on behavioral responses of prey and predators, as well as the ecological trade-offs, biochemical, and molecular details of alarm signaling. Various aspects of alarm pheromone research have also enhanced our knowledge of the chemical ecology of alarm pheromones and their role in mediating intra- and interspecific interactions between predators and prey. Available research shows that insect colony size, structure, and composition regulate production and release of insect alarm pheromones, but more research is needed to investigate the socio-ecological and evolutionary contexts of alarm pheromone production by individual insects. Assessing the balance between eco-physiological costs and inclusive fitness benefits or aggressive behavior require further research as well. Moreover, the use of alarm pheromones as kairomones by predators may provide novel avenues for pest management. Overall, a thorough understanding of the biosynthesis, diversity, perception, regulation, and function of insect alarm pheromone signaling, and the ecology of interactions with their predators, will enable us to generate various novel and advanced strategies to control different insect pests and vector-borne pathogens.

Acknowledgements

This research was supported by USDA-NIFA Grants 2016-67011-24693, 2017-67013-26537, and 2019-67011-29602. We also thank S. Fuzz and M. Asche for assistance creating figures.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ibmb.2020.103514>.

References

Acar, E.B., Medina, J.C., Lee, M.L., Booth, G.M., 2001. Olfactory behavior of convergent lady beetles (Coleoptera: coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: aphididae). *Can. Entomol.* 133, 389–397.

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., Robinson, G.E., 2009. Honey bee aggression supports a link between gene regulation and behavioral evolution. *Proc. Natl. Acad. Sci. U.S.A.* 106, 15400–15405.

Allan Rachel, A., Elgar Mark, A., Capon Robert, J., 1996. Exploitation of an ant chemical alarm signal by the zodariid spider *Habronestes bradleyi* Walckenaer. *Proc. Roy. Soc. Lond. B.* 263, 69–73.

Ameixa, O.M.C.C., Kindlmann, P., 2012. Effect of synthetic and plant-extracted aphid pheromones on the behaviour of *Aphidius colemani*. *J. Appl. Entomol.* 136, 292–301.

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.

Battaglia, D., Poppy, G., Powell, W., Romano, A., Tranfaglia, A., Pennacchio, F., 2000. Physical and chemical cues influencing the oviposition behaviour of *Aphidius ervi*. *Entomol. Exp. Appl.* 94, 219–227.

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., Zhang, Y., 2006. Aphid alarm pheromone produced by transgenic plants affects aphid and parasitoid behavior. *Proc. Nat. Acad. Sci. USA* 103, 10509–10513.

Benton, R., Sachse, S., Michnick, S.W., Vossahl, L.B., 2006. Atypical membrane topology and heteromeric function of *Drosophila* odorant receptors *in vivo*. *PLoS Biol.* 4, e20.

Blum, M.S., 1985. Alarm pheromones. In: Kerkut, G.A., Gilbert, L.I. (Eds.), *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Pergamon Press, New York, USA, pp. 193–224.

Boch, R., Shearer, D.A., 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.

Boo, K.S., Chung, I.B., Han, K.S., Pickett, J.A., 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., Dutky, S.R., 1972. Aphid alarm pheromone: isolation, identification, synthesis. *Science* 177, 1121–1122.

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

Bowers, W.S., Nishino, C., Montgomery, M.E., Nault, L.R., Nielson, M.W., 1977b. Sesquiterpene progenitor, germacrene A: an alarm pheromone in aphids. *Science* 196, 680–681.

Braendle, C., Weisser, W.W., 2001. Variation in escape behavior of red and green clones of the pea aphid. *J. Insect Behav.* 13.

Bragard, C., Caciagli, P., Lemaire, O., Lopez-Moya, J.J., MacFarlane, S., Peters, D., Susi, P., Torrance, L., 2013. Status and prospects of plant virus control through interference with vector transmission. *Annu. Rev. Phytopathol.* 51, 177–201.

Brückner, A., Hoenle, P.O., von Beeren, C., 2018. Comparative chemical analysis of army ant mandibular gland volatiles (Formicidae: dorylinae). *Peer J.* 6.

Callow, R.K., Greenway, A.R., Griffiths, D.C., 1973. Chemistry of the secretion from the cornicles of various species of aphids. *J. Insect Physiol.* 19, 737–748.

Crock, J., Wildung, M., Creteau, R., 1997. Isolation and bacterial expression of a sesquiterpene synthase cDNA clone from peppermint (*Mentha piperita*, L.) that produces the aphid alarm pheromone (E)-beta-farnesene. *Proc. Natl. Acad. Sci. U.S.A.* 94, 12833–12838.

Cui, L.-L., Francis, F., Heuskin, S., Lognay, G., Liu, Y.-J., Dong, J., Chen, J.-L., Song, X.-M., Liu, Y., 2012. The functional significance of E- β -Farnesene: does it influence the populations of aphid natural enemies in the fields? *Biol. Contr.* 60, 108–112.

Dawson, G.W., Griffiths, D.C., Pickett, J.A., Plumb, R.T., Woodcock, C.M., Zhang, Z.N., 1988. Structure/activity studies on aphid alarm pheromone derivatives and their field use against transmission of *Barley yellow dwarf virus*. *Pestic. Sci.* 22, 17–30.

Dawson, G.W., Griffiths, D.C., Pickett, J.A., Smith, M.C., Woodcock, C.M., 1982. Improved preparation of (E)- β -farnesene and its activity with economically important aphids. *J. Chem. Ecol.* 8, 1111–1117.

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

Dedryver, C.-A., Le Gallic, J.-F., Mahéo, F., Simon, J.-C., Dedryver, F., 2013. The genetics of obligate parthenogenesis in an aphid species and its consequences for the maintenance of alternative reproductive modes. *Heredity* 110, 39–45.

Dill, L.M., Fraser, A.H.G., Roitberg, B.D., 1990. The economics of escape behaviour in the pea aphid, *Acyrtosiphon pisum*. *Oecologia* 83, 473–478.

Du, Y., Grodowitz, M.J., Chen, J., 2019. Electrophysiological responses of eighteen species of insects to fire ant alarm pheromone. *Insects* 10.

Du, Y., Poppy, G.M., Powell, W., Pickett, J.A., Wadhams, L.J., 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., Wheeler, J.W., 1976. Alkylpyrazine alarm pheromones in primitive ants with small colonial units. *Comp. Biochem. Physiol. B Comp. Biochem.* 54, 439–440.

Edwards, J.S., 1966. Defense by smear: supercooling in the cornicle wax of aphids. *Nature* 211, 73–74.

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

Fan, J., Xue, W., Duan, H., Jiang, X., Zhang, Y., Yu, W., Jiang, S., Sun, J., Chen, J., 2017. Identification of an intraspecific alarm pheromone and two conserved odorant-binding proteins associated with (E)- β -farnesene perception in aphid *Rhopalosiphum padi*. *J. Insect Physiol.* 101, 151–160.

Fan, L.-P., Ouyang, F., Su, J.-W., Ge, F., 2018. Adaptation of defensive strategies by the pea aphid mediates predation risk from the predatory lady beetle. *J. Chem. Ecol.* 44, 40–50.

Fleischer, J., Krieger, J., 2018. Insect pheromone receptors - key elements in sensing intraspecific chemical signals. *Front. Cell. Neurosci.* 12, 425.

Francis, F., Haubruge, E., Gaspar, C., 2000. Influence of host plants on specialist/generalist aphids and on the development of *Adalia bipunctata* (Coleoptera: coccinellidae). *Eur. J. Entomol.* 97, 481–485.

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

Francis, F., Martin, T., Lognay, G., Haubruge, E., 2005a. Role of (E)- β -farnesene in systematic aphid prey location by *Episyrphus balteatus* larvae (Diptera: syrphidae). *Eur. J. Entomol.* 102, 431–436.

Francis, F., Vanderloten, S., Verheggen, F., Lognay, G., Haubruge, E., 2005b. Is the (E)- β -farnesene only volatile terpenoid in aphids? *J. Appl. Entomol.* 129, 6–11.

Fujiwara-Tsujii, N., Yamagata, N., Takeda, T., Mizunami, M., Yamaoka, R., 2006. Behavioral responses to the alarm pheromone of the ant *Camponotus obscuripes* (Hymenoptera: formicidae). *Zool. Sci.* 23, 353–359.

Gerber, B., Aso, Y., 2017. In: Menzel, R. (Ed.), *Learning and Memory: A Comprehensive Reference*, vol. 1. Elsevier, Oxford, pp. 463–473.

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

- GINZEL, M.D., 2010. Olfactory signals. In: Breed, M.D., Moore, J. (Eds.), *Encyclopedia of Animal Behavior*. Academic Press, Oxford, pp. 584–588.
- GOETSCH, W., 1934. Untersuchungen über die zusammenarbeit im ameisenstaat. *Z. Morph. u. Ökol. Tiere* 28, 319–401.
- GRASSWITZ, T.R., PAINE, T.D., 1992. Kairomonal effect of an aphid cornicle secretion on *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: aphididae). *J. Insect Behav.* 5, 447–457.
- GREENWAY, A.R., GRIFFITHS, D.C., 1973. A comparison of triglycerides from aphids and their cornicle secretions. *J. Insect Physiol.* 19, 1649–1655.
- GUO, X., YU, Q., CHEN, D., WEI, J., YANG, P., YU, J., WANG, X., KANG, L., 2020. 4-Vinylanisole is an aggregation pheromone in locusts. *Nature* 584, 584–588.
- HATANO, E., KUNERT, G., MICHAUD, J.P., WEISSER, W.W., 2008. Chemical cues mediating aphid location by natural enemies. *Eur. J. Entomol.* 105, 797–806.
- HATANO, E., KUNERT, G., WEISSER, W.W., 2010. Aphid wing induction and ecological costs of alarm pheromone emission under field conditions. *PLoS One* 5, e11188.
- HEIL, M., KARBAN, R., 2010. Explaining evolution of plant communication by airborne signals. *Trends Ecol. Evol.* 25, 137–144.
- HEMPTINNE, J.-L., GAUDIN, M., DIXON, A.F.G., LOGNAY, G., 2000. Social feeding in ladybird beetles: adaptive significance and mechanism. *Chemoecology* 10, 149–152.
- HEUSKIN, Stéphanie, LORGE, S., GODIN, B., LEROY, P., FRÈRE, I., VERHEGGEN, F.J., HAUBRUGE, E., WATHELET, J.-P., MESTDAGH, M., HANCE, T., LOGNAY, G., 2011. Optimisation of a semiochemical slow-release alginate formulation attractive towards *Aphidius ervi* Haliday parasitoids. *Pest Manag. Sci.* 68, 127–136.
- HEUSKIN, Stéphanie, LORGE, S., LOGNAY, G., WATHELET, J.-P., BÉRA, F., LEROY, P., HAUBRUGE, E., BROSTAUX, Y., 2012. A semiochemical slow-release formulation in a biological control approach to attract hoverflies. *J. Environ. Prot. Ecol.* 3, 72–85.
- HÖLDOBLER, B., WILSON, E.O., 1990. *The Ants*. Springer-Verlag, Berlin Heidelberg.
- HUGHES, W.O.H., HOWSE, P.E., 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., 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.
- JOACHIM, C., HATANO, E., DAVID, A., KUNERT, M., LINSE, C., WEISSER, W.W., 2013. Modulation of aphid alarm pheromone emission of pea aphid prey by predators. *J. Chem. Ecol.* 39, 773–782.
- JOACHIM, C., VOSTEEN, I., WEISSER, W.W., 2015. The aphid alarm pheromone (E)- β -farnesene does not act as a cue for predators searching on a plant. *Chemoecology* 25, 105–113.
- JOACHIM, C., WEISSER, W.W., 2013. Real-Time Monitoring of (E)- β -Farnesene emission in colonies of the pea aphid, *Acyrtosiphon pisum*, under lacewing and ladybird predation. *J. Chem. Ecol.* 39, 1254–1262.
- JONES, A.M.E., BRIDGES, M., BONES, A.M., COLE, R., ROSSITER, J.T., 2001. Purification and characterisation of a non-plant myrosinase from the cabbage aphid *Brevicoryne brassicae* (L.). *Insect Biochem. Mol. Biol.* 31, 1–5.
- KARPE, S.D., JAIN, R., BROCKMANN, A., SOWDHAMINI, R., 2016. Identification of complete repertoire of *Apis florea* odorant receptors reveals complex orthologous relationships with *Apis mellifera*. *Genome Biol. Evol.* 8, 2879–2895.
- KEISER, C.N., MONDOR, E.B., 2015. Cues of predation risk induce instar- and genotype-specific changes in pea aphid colony spatial structure. *Ethology* 121, 144–151.
- KISLOW, C.J., EDWARDS, L.J., 1972. Repellent odour in aphids. *Nature* 235, 108–109.
- KUNERT, G., OTTO, S., RÖSE, U.S.R., GERSHENZON, J., WEISSER, W.W., 2005. Alarm pheromone mediates production of winged dispersal morphs in aphids. *Ecol. Lett.* 8, 596–603.
- KUNERT, G., REINHOLD, C., GERSHENZON, J., 2010. Constitutive emission of the aphid alarm pheromone, (E)- β -farnesene, from plants does not serve as a direct defense against aphids. *BMC Ecol.* 10, 23.
- LALOR, P.F., HUGHES, W.O.H., 2011. Alarm behaviour in eciton army ants. *Physiol. Entomol.* 36, 1–7.
- LEAL, W.S., 2013. Odorant reception in insects: roles of receptors, binding proteins, and degrading enzymes. *Annu. Rev. Entomol.* 58, 373–391.
- LENZ, E.L., KRASNEC, M.O., BREED, M.D., 2013. Identification of undecane as an alarm pheromone of the ant *Formica argentea*. *J. Insect Behav.* 26, 101–108.
- LEROY, P.D., VERHEGGEN, F.J., CAPELLA, Q., FRANCIS, F., HAUBRUGE, E., 2010. An introduction device for the aphidophagous hoverfly *Episyrphus balteatus* (De Geer) (Diptera: syrphidae). *Biol. Contr.* 54, 181–188.
- LEROY, P.D., SCHILLINGS, T., FARMAKIDIS, J., HEUSKIN, S., LOGNAY, G., VERHEGGEN, F.J., YVES BROSTAUX, Y., HAUBRUGE, E., FRANCIS, F., 2012. Testing semiochemicals from aphid, plant and conspecific: attraction of *Harmonia axyridis*. *Insect Sci.* 19, 372–382.
- LI, J., WANG, Z., TAN, K., QU, Y., NIEH, J.C., 2014. Effects of natural and synthetic alarm pheromone and individual pheromone components on foraging behavior of the giant Asian honey bee, *Apis dorsata*. *J. Exp. Biol.* 217, 3512–3518.
- LI, Z.-Q., ZHANG, S., CAI, X.-M., LUO, J.-Y., DONG, S.-L., CUI, J.-J., CHEN, Z.-M., 2017. Three odorant binding proteins may regulate the behavioural response of *Chrysopa pallens* to plant volatiles and the aphid alarm pheromone (E)- β -farnesene. *Insect Mol. Biol.* 26, 255–265.
- LIN, F.-J., BOSQUÉE, E., LIU, Y.-J., CHEN, J.-L., YONG, L., FRANCIS, F., 2016. Impact of aphid alarm pheromone release on virus transmission efficiency: when pest control strategy could induce higher virus dispersion. *J. Virol. Methods* 235, 34–40.
- LOSEY, J.E., DENNO, R.F., 1998a. Interspecific variation in the escape responses of aphids: effect on risk of predation from foliar-foraging and ground-foraging predators. *Oecologia* 115, 245–252.
- LOSEY, J.E., DENNO, R.F., 1998b. The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecol. Entomol.* 23, 53–61.
- MICHA, S.G., WYSS, U., 1996. Aphid alarm pheromone (E)- β -farnesene: a host finding kairomone for the aphid primary parasitoid *Aphidius uzbekistanicus* (Hymenoptera: aphidiinae). *Chemoecology* 7, 132–139.
- MIZUNAMI, M., YAMAGATA, N., NISHINO, H., 2010. Alarm pheromone processing in the ant brain: an evolutionary perspective. *Front. Behav. Neurosci.* 4.
- MOAYERI, H.R.S., RASEKH, A., ENKEGAARD, A., 2014. Influence of cornicle droplet secretions of the cabbage aphid, *Brevicoryne brassicae*, on parasitism behavior of naïve and experienced *Diaeretiella rapae*. *Insect Sci.* 21, 56–64.
- MONDOR, E.B., ADDICOTT, J.F., 2007. Do exaptations facilitate mutualistic associations between invasive and native species? *Biol. Invasions* 9, 623–628.
- MONDOR, E.B., BAIRD, D.S., SLESSOR, K.N., ROITBERG, B.D., 2000. Ontogeny of alarm pheromone secretion in pea aphid, *Acyrtosiphon pisum*. *J. Chem. Ecol.* 26, 2875–2882.
- MONDOR, E.B., ROITBERG, B.D., 2004. Inclusive fitness benefits of scent-marking predators. *Proc. Biol. Sci. Lond. B. (Suppl.)* 271, S341–S343.
- MONDOR, E.B., ROITBERG, B.D., 2003. Age-dependent fitness costs of alarm signaling in aphids. *Can. J. Zool.* 81, 757–762.
- MONTGOMERY, M.E., NAULT, L.R., 1978. Effects of age and wing polymorphism on the sensitivity of *Myzus persicae* to alarm pheromone. *Ann. Entomol. Soc. Am.* 71, 788–790.
- NAKAGAWA, T., PELLEGRINO, M., SATO, K., VOSSHALL, L.B., TOUHARA, K., 2012. Amino acid residues contributing to function of the heteromeric insect olfactory receptor complex. *PLoS One* 7, e32372.
- NAULT, L.R., MONTGOMERY, M.E., BOWERS, W.S., 1976. Ant-aphid association: role of aphid alarm pheromone. *Science* 192, 1349–1351.
- NISHINO, C., BOWERS, W.S., MONTGOMERY, M.E., NAULT, L.R., 1976. Aphid alarm pheromone mimics the nor-farnesenes. *Appl. Entomol. Zool.* 11, 340–343.
- NORDLUND, D.A., LEWIS, W.J., 1976. Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. *J. Chem. Ecol.* 2, 211–220.
- NORMAN, V.C., BUTTERFIELD, T., DRIJFHOUT, F., TASMAN, K., HUGHES, W.O.H., 2017. Alarm pheromone composition and behavioral activity in fungus-growing ants. *J. Chem. Ecol.* 43, 225–235.
- NORTHEY, T., VENTHUR, H., DE BIASIO, F., CHAUVIAC, F.-X., COLE, A., RIBEIRO, K.A.L., GROSSI, G., FALABELLA, P., FIELD, L.M., KEEP, N.H., ZHOU, J.-J., 2016. Crystal structures and binding dynamics of odorant-binding protein 3 from two aphid species *Megoura viciae* and *Nasonovia ribisnigri*. *Sci. Rep.* 6.
- OUTREMAN, Y., KUNERT, G., SIMON, J.-C., WEISSER, W.W., 2010. Ecological costs of alarm signaling in aphids. In: Kindlmann, P., Dixon, A.F.G., Michaud, J.P. (Eds.), *Aphid Biodiversity under Environmental Change: Patterns and Processes*. Springer Netherlands, Dordrecht, pp. 171–181.
- PASK, G.M., SLONE, J.D., MILLAR, J.G., DAS, P., MOREIRA, J.A., ZHOU, X., BELLO, J., BERGER, S.L., BONASIO, R., DESPLAN, C., REINBERG, D., LIEBIG, J., ZWIEBEL, L.J., RAY, A., 2017. Specialized odorant receptors in social insects that detect cuticular hydrocarbon cues and candidate pheromones. *Nat. Commun.* 8, 297.
- PELOSI, P., IOVINELLA, I., ZHU, J., WANG, G., DANI, F.R., 2018. Beyond chemoreception: diverse tasks of soluble olfactory proteins in insects. *Biol. Rev. Camb. Phil. Soc.* 93, 184–200.
- PETRESCU, A.S., MONDOR, E.B., ROITBERG, B.D., 2001. Subversion of alarm communication: do plants habituate aphids to their own alarm signals? *Can. J. Zool.* 79, 737–740.
- PHELAN, P.L., MILLER, J.R., 1982. Post-landing behavior of alate *Myzus persicae* as altered by (E)- β -Farnesene and three carboxylic acids. *Entomol. Exp. Appl.* 32, 46–53.
- PICKETT, J.A., GRIFFITHS, D.C., 1980. Composition of aphid alarm pheromones. *J. Chem. Ecol.* 6, 349–360.
- PICKETT, J.A., WADHAMS, L.J., WOODCOCK, C.M., HARDIE, J., 1992. The chemical ecology of aphids. *Annu. Rev. Entomol.* 37, 67–90.
- PICKETT, J.A., WILLIAMS, I.H., MARTIN, A.P., 1982. (Z)-11-eicosen-1-ol, an important new pheromonal component from the sting of the honey bee *Apis mellifera* L. (Hymenoptera, Apidae.). *J. Chem. Ecol.* 8, 163–175.
- POLIN, S., GALIC, J.-F.L., SIMON, J.-C., TSUCHIDA, T., OUTREMAN, Y., 2015. Conditional reduction of predation risk associated with a facultative symbiont in an insect. *PLoS One* 10, e0143728.
- ROBERTSON, I.C., ROITBERG, B.D., WILLIAMSON, I., SENGER, S.E., 1995. Contextual chemical ecology: an evolutionary approach to the chemical ecology of insects. *Am. Entomol.* 41, 237–240.
- ROITBERG, B.D., MYERS, J.H., 1978a. Adaptation of alarm pheromone responses of the pea aphid *Acyrtosiphon pisum* (Harris). *Can. J. Zool.* 56, 103–108.
- ROITBERG, B.D., MYERS, J.H., 1978b. Effect of adult Coccinellidae on the spread of a plant virus by an aphid. *J. Appl. Ecol.* 15, 775–779.
- SCHWARTZBERG, E.G., KUNERT, G., STEPHAN, C., DAVID, A., RÖSE, U.S.R., GERSHENZON, J., BOLAND, W., WEISSER, W.W., 2008. Real-time analysis of alarm pheromone emission by the pea aphid (*Acyrtosiphon pisum*) under predation. *J. Chem. Ecol.* 34, 76–81.
- SHAH, P.A., PICKETT, J.A., VANDENBERG, J.D., 1999. Responses of Russian wheat aphid (Homoptera: aphididae) to aphid alarm pheromone. *Environ. Entomol.* 28, 983–985.
- SHEARER, D.A., BOCH, R., 1965. 2-Heptanone in the mandibular gland secretion of the honey bee. *Nature* 206, 530.
- SLONE, J.D., PASK, G.M., FERGUSON, S.T., MILLAR, J.G., BERGER, S.L., REINBERG, D., LIEBIG, J., RAY, A., ZWIEBEL, L.J., 2017. Functional characterization of odorant receptors in the ponerine ant, *Harpegnathos saltator*. *Proc. Natl. Acad. Sci. U.S.A.* 114, 8586–8591.
- SONG, X.M., ZHANG, L.Y., FU, X.B., WU, F., TAN, J., LI, H.L., 2018. Various bee pheromones binding affinity, exclusive chemosensillar localization, and key amino acid sites reveal the distinctive characteristics of odorant-binding protein 11 in the eastern honey bee, *Apis cerana*. *Front. Physiol.* 9, 422.
- STOEFFLER, M., MAIER, T.S., TOLASCH, T., 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.

- Su, J., Zhu, S., Zhang, Z., Ge, F., 2006. Effect of synthetic aphid alarm pheromone (E)-beta-farnesene on development and reproduction of *Aphis gossypii* (Homoptera: aphididae). *J. Econ. Entomol.* 99, 1636–1640.
- Sun, Y.F., Biasio, F.D., Qiao, H.L., Iovinella, I., Yang, S.X., Ling, Y., Riviello, L., Battaglia, D., Falabella, P., Yang, X.L., Pelosi, P., 2012. Two odorant-binding proteins mediate the behavioural response of aphids to the alarm pheromone (E)-beta-farnesene and structural analogues. *PLoS One* 7, e32759.
- Sun, Z.-J., Li, Z.-X., 2017. Host plants and obligate endosymbionts are not the sources for biosynthesis of the aphid alarm pheromone. *Sci. Rep.* 7.
- Sun, J.S., Xiao, S., Carlson, J.R., 2018. The diverse small proteins called odorant-binding proteins. *Open Biol* 8, 180208.
- Tamarri, V., Castracani, C., Grasso, D.A., Visicchio, R., Moli, F.L., Mori, A., 2009. The defensive behaviour of two Formica slave-ant species: coevolutionary implications with their parasite *Polyergus rufescens* (Hymenoptera, Formicidae). *Ital. J. Zool.* 76, 229–238.
- Teerling, C.R., Pierce, H.D., Borden, J.H., Gillespie, D.R., 1993. Identification and bioactivity of alarm pheromone in the western flower thrips, *Frankliniella occidentalis*. *J. Chem. Ecol.* 19, 681–697.
- Turlings, T.C., Ton, J., 2006. Exploiting scents of distress: the prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests. *Curr. Opin. Plant Biol.* 9, 421–427.
- Urlacher, E., Francés, B., Giurfa, M., Devaud, J.-M., 2010. An alarm pheromone modulates appetitive olfactory learning in the honeybee (*Apis Mellifera*). *Front. Behav. Neurosci.* 4.
- Vander Meer, R.K., Breed, M.D., Espelie, K.E., Winston, M.L., 1998. Pheromone Communication in Social Insects. Ants, wasps, bees and termites. Westview, Boulder, CO, p. 258.
- Vander Meer, R.K., Preston, C.A., Choi, M.-Y., 2010. Isolation of a pyrazine alarm pheromone component from the fire ant, *Solenopsis invicta*. *J. Chem. Ecol.* 36, 163–170.
- Vandermoten, S., Francis, F., Haubruge, E., Leal, W.S., 2011. Conserved odorant-binding proteins from aphids and eavesdropping predators. *PLoS One* 6, e23608.
- Vandermoten, S., Mescher, M.C., Francis, F., Haubruge, E., Verheggen, F.J., 2012. Aphid alarm pheromone: an overview of current knowledge on biosynthesis and functions. *Insect Biochem. Mol. Biol.* 42, 155–163.
- Van Oosten, A.M., Gut, J., Harrewijn, P., Piron, P.G.M., 1990. Role of farnesene isomers and other terpenoids in the development of different forms of the aphids *Aphis fabae* and *Myzus persicae*. *Acta Phytopathol. Entomol. Hung.* 25, 331–342.
- Venthur, H., Zhou, J.-J., 2018. Odorant receptors and odorant-binding proteins as insect pest control targets: a comparative analysis. *Front. Physiol.* 9.
- Verheggen, François J., Arnaud, L., Bartram, S., Gohy, M., Haubruge, E., 2008a. Aphid and plant volatiles induce oviposition in an aphidophagous hoverfly. *J. Chem. Ecol.* 34, 301–307.
- Verheggen, F.J., Diez, L., Sablon, L., Fischer, C., Bartram, S., Haubruge, E., Detrain, C., 2012. Aphid alarm pheromone as a cue for ants to locate aphid partners. *PLoS One* 7.
- Verheggen, F.J., Fagel, Q., Heuskin, S., Lognay, G., Francis, F., 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., Mescher, M.C., 2010. Alarm Pheromones—Chemical Signaling in Response to Danger. *Vitam. Horm. Elsevier*, pp. 215–239.
- Verheggen, F.J., Mescher, M.C., Haubruge, E., Moraes, C.M., Schwartzberg, E.G., 2008b. Emission of alarm pheromone in aphids: a non-contagious phenomenon. *J. Chem. Ecol.* 34, 1146–1148.
- Visser, J.H., Piron, P.G.M., 1997. Olfactory antennal responses to plant volatiles in apterous virginoparae of the vetch aphid *Megoura viciae*. *Entomol. Exp. Appl.* 77, 37–46.
- Vosteen, I., Weisser, W.W., Kunert, G., 2016. Is there any evidence that aphid alarm pheromones work as prey and host finding kairomones for natural enemies? *Ecol. Entomol.* 41, 1–12.
- Wadhams, L.J., 1990. The use of coupled gas chromatography: electrophysiological techniques in the identification of insect pheromones. In: McCaffery, A.R., Wilson, I. D. (Eds.), *Chromatography and Isolation of Insect Hormones and Pheromones*, Chromatographic Society Symposium Series. Springer US, New York, NY, pp. 289–298.
- Wager, B.R., Breed, M.D., 2000. Does honey bee sting alarm pheromone give orientation information to defensive bees? *Ann. Entomol. Soc. Am.* 93, 1329–1332.
- Wang, Q., Zhou, J.-J., Liu, J.-T., Huang, G.-Z., Xu, W.-Y., Zhang, Q., Chen, J.-L., Zhang, Y.-J., Li, X.-C., Gu, S.-H., 2019. Integrative transcriptomic and genomic analysis of odorant binding proteins and chemosensory proteins in aphids. *Insect Mol. Biol.* 28, 1–22.
- Wang, Z., Tan, K., 2019. Honey Bee Alarm pheromone mediates communication in plant–pollinator–predator interactions. *Insects* 10, 366.
- Wang, Z., Wen, P., Qu, Y., Dong, S., Li, J., Tan, K., Nieh, J.C., 2016. Bees eavesdrop upon informative and persistent signal compounds in alarm pheromones. *Sci. Rep.* 6.
- Wanner, K.W., Nichols, A.S., Walden, K.K.O., Brockmann, A., Luetje, C.W., Robertson, H. M., 2007. A honey bee odorant receptor for the queen substance 9-oxo-2-decenoic acid. *Proc. Natl. Acad. Sci. U.S.A.* 104, 14383–14388.
- Weisser, W.W., Braendle, C., Minoretti, N., 1999. Predator-induced morphological shift in the pea aphid. *Proc. Roy. Soc. Lond. B.* 266, 1175–1181.
- Wilson, E.O., Hoellndobler, B., 1985. Caste-specific techniques of defense in the polymorphic ant *Pheidole embolopyx* (Hymenoptera: formicidae). *Insectes Soc.* 32, 3–22.
- Wilson, E.O., Regnier, F.E., 1971. The evolution of the alarm-defense system in the formicine ants. *Am. Nat.* 105, 279–289.
- Wu, G.-M., Boivin, G., Brodeur, J., Giraldeau, L.-A., Outreman, Y., 2010. Altruistic defence behaviours in aphids. *BMC Evol. Biol.* 10, 19.
- Wyatt, T.D., 2003. *Pheromones and Animal Behaviour: Communication by Smell and Taste*. Cambridge University Press, Cambridge, UK ; New York.
- Xiangyu, J.G., Zhang, F., Fang, Y.L., Kan, W., Zhang, G.X., Zhang, Z.N., 2002. Behavioural response of aphids to the alarm pheromone component (E)-beta-farnesene in the field. *Physiol. Entomol.* 27, 307–311.
- Yan, H., Opachaloemphan, C., Mancini, G., Yang, H., Gallitto, M., Mlejnek, J., Leibholz, A., Haight, K., Ghaninia, M., Huo, L., Perry, M., Slone, J., Zhou, X., Traficante, M., Penick, C.A., Dolezal, K., Gokhale, K., Stevens, K., Fetter-Pruneda, I., Bonasio, R., Zwiebel, L.J., Berger, S.L., Liebig, J., Reinberg, D., Desplan, C., 2017. An engineered orco mutation produces aberrant social behavior and defective neural development in ants. *Cell* 170, 736–747.e9.
- Zhang, R., Wang, B., Grossi, G., Falabella, P., Liu, Y., Yan, S., Lu, J., Xi, J., Wang, G., 2017. Molecular basis of alarm pheromone detection in aphids. *Curr. Biol.* 27, 55–61.
- Zhou, H., Chen, L., Liu, Y., Chen, J., Francis, F., 2016. Use of slow-release plant infochemicals to control aphids: a first investigation in a Belgian wheat field. *Sci. Rep.* 6.
- Zhou, J.-J., Vieira, F.G., He, X.-L., Smadja, C., Liu, R., Rozas, J., Field, L.M., 2010. Genome annotation and comparative analyses of the odorant-binding proteins and chemosensory proteins in the pea aphid *Acyrtosiphon pisum*. *Insect Mol. Biol.* 19 (2), 113–122.
- Zhou, X., Slone, J.D., Rokas, A., Berger, S.L., Liebig, J., Ray, A., Reinberg, D., Zwiebel, L. J., 2012. Phylogenetic and transcriptomic analysis of chemosensory receptors in a pair of divergent ant species reveals sex-specific signatures of odor coding. *PLoS Genet.* 8, e1002930.
- Zhu, J., Cossé, A.A., Obrycki, J.J., Boo, K.S., 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.