






Review

Life History Traits of the Pentatomidae (Hemiptera) for the Development of Pest Management Tools

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Abstract: Knowledge of the biology of a pest is essential for building sustainable management programmes. Pentatomidae have a hemimetabolous life cycle with egg, nymphal, and adult life stages, which differ in morphological, ecological, and behavioural traits. Some of these traits, such as mating behaviour, pheromones (alarm and aggregation pheromones) and the acquisition of gut symbionts can be targeted for pest management strategies. Here, we review the available literature on these life history traits of the Pentatomidae with potential for use in management programmes. Pheromone-mediated aggregation and the disruption of symbiont acquisition are two important targets for Pentatomidae control. Other traits such as the use of alarm pheromones for enhancing natural enemies and substrate-borne vibration for mating disruption deserve further consideration. Colour vision and flight ability are still poorly studied, despite their potential importance for stink bug management.

Keywords: stink bugs; behaviour; pheromones; symbionts; IPM



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1. Introduction

Pentatomidae, commonly known as shield or stink bugs, is the largest family in the Pentatomoidea, which is known to contain a considerable number of economically important pest species [1–3]. Divided into eight subfamilies, the Pentatomidae represents the third-largest Heteropteran family [1,4]. Pentatomidae are mostly phytophagous and polyphagous, with the exception of predatory species of the subfamily Asopinae [1–4]. Phytophagous pentatomids are a major concern for many agricultural systems, damaging crops through direct feeding and by transmitting plant pathogens [1,3], whereas predatory pentatomids are considered to be beneficial, as they prey on various insect pest species [5]. This review focuses on phytophagous stink bugs.

Chemical control programs have been the principal approach for managing stink bugs [6,7]. Despite these management efforts, populations continue to surpass damage thresholds, and the development of insecticide resistance has been observed [6]. To reduce the use of insecticides, behaviourally based management and monitoring programs need to be further developed. These require knowledge of the biological and behavioural traits of stink bugs [5–8].

The Pentatomidae have hemimetabolous development with an egg, nymphal, and adult stage, and can have multiple generations per year (Figure 1). Five nymphal instars occur in the Pentatomidae. The first instars are generally gregarious, inactive, and remain on top of or near the eggshells. The first instars do not feed on host plants but acquire

specific symbionts by ingesting secretions covering the shells. These bacterial symbionts are thus vertically transmitted from females via the egg surface [9–11]. The acquisition of these symbionts plays a beneficial role in the fitness of the insect host, especially in survival and development, and detoxification of their food [12–14]. As the nymphs pass through instars, they gradually and progressively disperse. The size of the nymphs increases throughout the different stadia and the growth of the wing pads starts during the fourth and fifth instar. During the adult stage, the bug possesses fully developed wings; reproduction begins after the passage to adulthood and completion of sexual maturation, with typical precopulatory and copulatory behaviours combining chemical and vibrational signals [6].

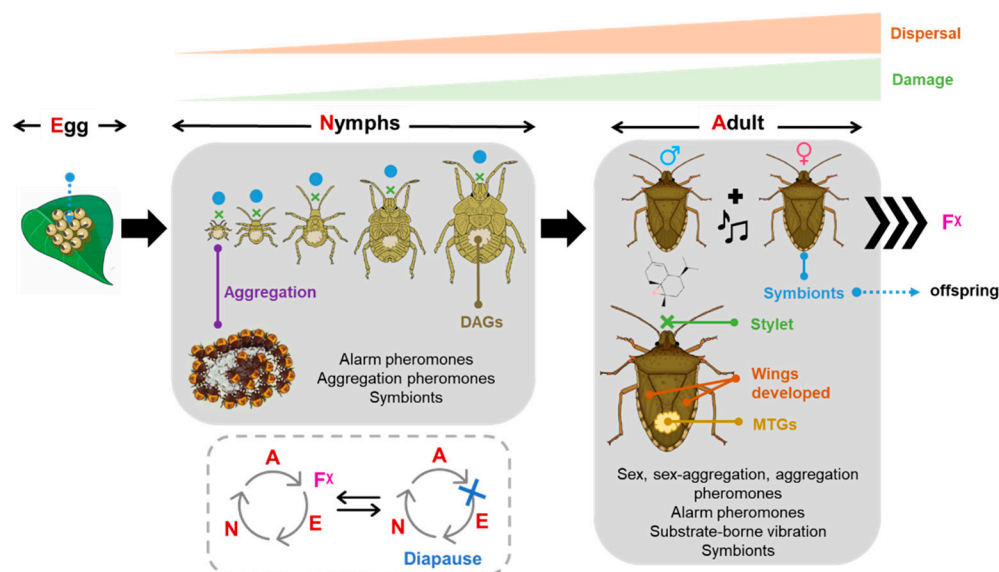


Figure 1. Schematic drawing showing various traits associated with the life cycle of the Pentatomidae, which can be targeted for pest management. The chemical molecule represents the sex, sex–aggregation or aggregation pheromones, and the musical note represents the vibrational signals (F^x: number of generations; DAGs: dorsal abdominal scent glands; MTGs: metathoracic scent glands).

Pentatomids are well known for producing a wide variety of chemicals during their life cycle, such as sex, alarm, and aggregation pheromones [15–17]. Sex–aggregation pheromones are defined as compounds that are produced by one sex that attract both sexes for mating purposes, whereas sex pheromones attract only the opposite sex. Compounds that are produced by one sex that attract both sexes, including nymphs, for behaviours other than mating are considered aggregation pheromones [18]. In all pentatomid species for which pheromones (sex, sex–aggregation, aggregation) have been identified, males are responsible for production [16,17]. However, the distinction between sex–aggregation and aggregation pheromone can be difficult and requires rigorous bioassays demonstrating the behavioural responses of conspecifics to specific compounds [16]. Thus, in cases where there was not sufficient empirical work to determine which designation is correct, we refer to these as aggregation pheromones.

Traits other than chemical signals can also be considered when developing control strategies (Figure 1). Recent advances in understanding the vertical transmission of symbionts and manipulation of transmission offer new possibilities for controlling Pentatomidae [19]. For example, the removal of symbionts can lead to a strong negative effect on insect fitness [10,12,20–24]. Furthermore, several studies have been conducted on vibratory communication (closely associated with stink bug courtship) in order to develop pest control methods that exploit this communication mode [25].

Recent advances in understanding stink bug biology through their symbionts, pheromones, and other traits (e.g., colour vision, flying behaviour) offer new opportunities for the development of integrated pest management tactics. However, their utilisation is still

limited to a few stink bug species, and the complexity and time required to develop commercial applications of these behavioural tools remains a major challenge. Here, we summarise the currently available knowledge of the mating behaviour, alarm and aggregation pheromones, and symbionts within the Pentatomidae, with emphasis on their potential to be exploited for the development of stink bug pest management tactics.

2. Vibratory and Pheromone Signals in Stink Bug Mating

Substrate-borne vibrations are prevalent in insects [26–29]. In the Pentatomidae, these have been described in 36 species [30,31]. Substrate-borne communication has been well studied in the model species *Nezara viridula* (L.), where it is closely associated with their mating behaviour [30,32].

In stink bugs, mating behaviour is mediated by chemical and vibrational signals and involves long-range mate location and close-range courtship behaviour [30–34]. This bimodal communication starts at long distance with the emission of the male pheromone which attracts females towards the chemical signal and can result in aggregations of females on the same host plant or in areas surrounding the calling males [33]. At close range, the male pheromone stimulates the female to start her vibratory calling (e.g., Female Calling Song, FCS). The FCS triggers the male to search for the calling female [35,36]. The male walks on the plant towards the source of vibration and answers with his calling and courtship songs (e.g., Male Calling Song, MSC and Male Courtship Song, MCrS) [37]. The rhythmic FCS repetitions create a vibrational signal which guides the male towards the female, even when complex plant architecture is involved [36]. The vibratory signals of stink bugs are characterised by low frequencies (around 100 Hz) with narrow spectral peaks which are well tuned with the resonance properties of host plants, which act as low-pass filters [38,39]. These characteristics enable short-range communication and facilitate mate location [35,36].

Interference of stink bug communication using substrate-borne vibratory signals has been explored for pest management [25,40]. For example, a few studies have been conducted that explore the use of vibratory signals as a repellent, a mating disruption strategy, and for population monitoring. A vibratory disturbance of 100 Hz can affect communication between males and females of *N. viridula* by decreasing the number of males responding to female calling songs and by reducing the number of males responding to the courtship song [41]. Although disturbance did not affect the production of female calling songs or the location of females by males, females changed the rhythm and the dominant frequency of their songs to avoid overlap with artificial external disturbances. Similar results have also been observed in *Euchistus heros* (F.) [42]. Although the properties of the plant tissues strongly influence vibrational transmission, other factors can also significantly disturb transmission processes. Several studies demonstrated that biotic noise could modify the temporal structure, the frequency, or the amplitude of signals and negatively affect the behavioural responses of conspecifics [41,43,44]. Other abiotic factors such as wind and raindrops have also been suggested as a source of disturbance for stink bug vibratory communication [30].



Substrate-borne vibrations not only affect communication between partners but can also affect the reproductive behaviour of insects [45]. Pure tone vibrations (75–200 Hz) mechanically transmitted to plants significantly (>90%) decreased copulation in *E. heros* by inhibiting male calling and searching for females [46]. In addition, a reduction in fecundity and fertility has also been observed in females exposed to background noise for 24 h, despite the fact that they had been mated. Although this hypothesis remains to be tested, the authors suggested that the background noise could induce stress, resulting in shorter copulation periods and/or a reduction in the efficiency of sperm transfer. A recent study [47] investigated the potential of female rival signals for mating disruption in *E. heros*, *Chinavia ubica* (Rolston) and *Chinavia impicticornis* (Stål). In the presence of rival female signals, fewer males were able to reach females, and a significant reduction in copulating

pairs was observed. These results suggest that female rival signals could be used to disrupt mating of stink bugs.

Indirect effects of vibratory signals, such as the attraction of parasitoids and predators, may also contribute to the regulation of stink bug populations. Predators and parasitoids can use stimuli associated with stink bug prey/hosts to search for and locate stink bugs [26]. For example, the egg parasitoid *Telenomus podisi* (Ashmead) has been shown to be attracted to vibratory signals from *E. heros* [48,49]. Laumann et al. [49] demonstrated that *T. podisi* remained for longer on leaves vibrated by natural or artificial female songs, compared to non-vibrated leaves or leaves vibrated by male songs. These studies suggest that the in situ behavioural response to host female vibratory signals increases the probability of *T. podisi* locating host eggs. Nevertheless, attraction of natural enemies to synthetic vibrational and pheromonal signals does not necessarily imply parasitism. An additional concern is that negative consequences for biological control (i.e., attracting and misleading with no reward) can also be observed [50]. Thus, caution needs to be taken when using these stimuli in pest control.

The detection and monitoring of insect communication with automatic acoustic devices has been investigated in a few species [25,51,52]. For example, algorithms using Gaussian mixture models (GMM), or probabilistic neural networks (PNN) have been used for the identification and detection of Cicadidae [53], as well as the vibratory signals produced by red palm weevils [54]. In both studies, the mathematical models were over 94% accurate. Other methods such as linear prediction cepstral coefficient feature vectors and a multilayer perceptron classifier have also shown potential for vibratory discrimination of leafhoppers [55]. Similarly, the incorporation of an automatic acoustic device has been proposed for stink bug identification and detection [56]. PNN and GMM models were able to identify and discriminate the vibratory signals of *Euschistus servus* (Say) and *N. viridula* species from incidental noise (e.g., locomotion, feeding or tunnelling) with an accuracy, in most cases, higher than 90%. Although this study was conducted under laboratory conditions, thus excluding abiotic noises such as wind and vibrations by other organisms, the results suggest that the method has potential for monitoring stink bugs and improving levels of control realised by pest management programmes.

Sex and aggregation pheromones have been identified in approximately 50 species where the pattern of responses is divided between those that appear to attract only females, and those that attract both sexes, as well as nymphs when this has been tested (Table 1) [16,17,57,58]. The only exception is for *Piezodorus hybneri* (Westwood); its pheromone appears to be bifunctional, acting either as a sex or aggregation pheromone, depending on the time of the year [59,60]. In comparison, sex-aggregation pheromones have only been identified for a few species (Table 1). To date, only male stink bugs have been observed to produce these pheromones. Sex pheromones have been described in various Pentatomidae tribes and consist, in general, of a blend of at least two compounds. For example, among the An-testinii tribe, methyl (*E,Z,Z*)-2,4,6-decatrienoate was identified as the main sex pheromone compound in *Thyanta perditor* (F.) and *Thyanta pallidovirens* (Stål), along with the sesquiterpenes (+)- α -curcumene, (-)-zingiberene, and (-)- β -sesquiphellandrene [61,62]. Similar methyl esters have been reported to act as sex pheromones in other tribes. In the Carpocorini tribe, methyl 2,6,10-trimethyltridecanoate has been identified as a sex pheromone for *E. heros* [63–65], *Euschistus obscurus* (Palisot) [63,64] and *Agroecus griseus* (Dallas) [66]. In Edessinae, the only known sex pheromone is for *Edessa meditabunda* (Fabricius), where methyl 4,8,12-trimethylpentadecanoate and methyl 4,8,12-trimethyltetradecanoate constitute the major and minor compounds in this species, respectively [67]. Other compounds such as sesquiterpenoids have been reported to act as sex pheromones in Pentatomidae. For example, the sex pheromone of *Tibraca limbativentris* (Stål) is a mixture (7:3) of two isomers of 1,10-bisaboladien-3-ol (i.e., zingiberenol) [68,69], where the main compound alone and the mixture are attractive to females in the field [70]. An isomer of zingiberenol has also been described in the sex pheromone of *Oebalus pœcilus* (Dallas) [71].

Table 1. Defensive compounds and alarm pheromones (D), sex pheromones (S), aggregation pheromones (Ag), and sex–aggregation pheromones (SAg) identified in phytophagous Pentatomidae (list adapted and updated from Borges and Blassioli-Moraes [17] and Weber et al. 2018 [16]. For each of these pheromones, information regarding the life stage and the sex emitting the pheromones is indicated. For the alarm pheromones,  and  indicate adults and nymphs, respectively, whereas the sex, sex–aggregation and aggregation pheromones are emitted by males (“M”). Information regarding the life stage and the sex (males (M); females (F); nymphs (n)) of responder(s) to the alarm, sex, aggregation, or sex–aggregation pheromones are also listed if behavioural studies have been conducted, with red, green, and grey indicating the degree of response (red = does not respond to the pheromone, green = responds to the pheromone, grey = response has not been tested). In terms of compounds listed for each pheromone, only the most abundant compound is listed for the alarm pheromones, except for species in which bioassays have been conducted. For these species, all the compounds (as well as the instar and sex emitter) are listed, and the most abundant compound is underlined. For the sex pheromones, aggregation pheromones and sex–aggregation pheromones all compounds assayed are listed.












Pheromone ¹	Emitter	Responder	Compounds ²	References
Dinidorinae: Dinidorini				
<i>Aspongopus</i> sp.				
D			(E)-2-Hexenal	[72]
D			<i>Coridus janus</i> (E)-2-Hexenal	[73]
D			<i>Cyclopelta siccifolia</i> (E)-2-Hexenal	[74]
Discocephalinae: Discocephalini				
<i>Antiteuchus innocens</i>				
D			Undecane (M, F)	[75]
D			Undecane (1st–5th instar)	[75]
Discocephalinae: Ochlerini				
<i>Lincus malevolus</i>				
D			Undecane (M, F); (E)-4-oxo-2-decenal (F)	[76]
<i>Lincus spurcus</i>				
D			Undecane (M, F)	[76]
D			Undecane (5th instar)	[77]
Edessinae				
<i>Edessa meditabunda</i>				
S	M	M, F, n	Methyl 4,8,12-trimethylpentadecanoate	[67,78]
D			Undecane (1st–2nd instar)	[79]
<i>Edessa rufomarginata</i>				
D			Undecane	[80]
Pentatominae: Aeliini				
<i>Aelia fieberi</i>				
D			(E)-2-Decenal (M, F)	[81]
Pentatominae: Antestiini				
<i>Plautia stali</i>				
Ag	M	M, F, n	Methyl (2E,4E,6Z)-2,4,6-decatrienoate	[82]
<i>Thyanta custator accera</i>				
?	M		Methyl (2E,4Z,6Z)-2,4,6-decatrienoate; (+)- α -curcumene; (–)-zingiberene; (–)- β -sesquiphellandrene	[61]

Table 1. Cont.


















Pheromone ¹	Emitter	Responder	Compounds ²	References
			<i>Thyanta pallidovirens</i>	
S	M	M, F, n	Methyl (2E,4Z,6Z)-2,4,6-decatrienoate; (+)- α -curcumene; (-)-zingiberene; (-)- β -sesquiphellandrene	[61,83]
D			Tridecane (M, F)	[61]
D			Tridecane (1st–2nd instar)	[84]
			<i>Thyanta perditor</i>	
S	M	M, F, n	Methyl (2E,4E,6Z)-2,4,6-decatrienoate	[62]
D			Tridecane (M, F)	[62]
D			Tridecane (1st–2nd instar)	[79]
			Pentatominae: Bathycoliini	
			<i>Bathycolia distincta</i>	
D		M, F, n	(E)-2-Hexenal; 4-oxo-(E)-2-hexenal; (E)-2-decenal; (E)-2-decenyl acetate; tridecane; dodecane	[85]
			Pentatominae: Cappaeni	
			<i>Caura rufiventris</i>	
D			Tridecane	[72]
			<i>Halyomorpha halys</i>	
Ag	M	M, F, n	Isomers of murgantiol (10,11-Epoxy-1- bisabolen-3-ol)	[86,87]
D			Tridecane (M, F)	[86,88–91]
D			Tridecane (3rd–5th instar)	[86,88]
D	M, F, n	M, F, n	(E)-2-Decenal	[92]
			<i>Veterna patula</i>	
D			Tridecane	[72]
			Pentatominae: Carpocorini	
			<i>Agroecus griseus</i>	
S	M	M, F, n	Methyl 2,6,10 trimethyltridecanoate	[66]
D			Tridecane	[66,93]
D			Tridecane (1st–5th instar)	[66]
			<i>Carpocoris fuscispinus</i>	
D			Tridecane (M, F)	[94]
			<i>Cosmopepla bimaculate</i>	
D			Tridecane (M, F)	[95]
			<i>Euschistus biformis</i>	
D			Tridecane	[96]
			<i>Euschistus conspersus</i>	
Ag	M	M, F, n	Methyl (2E,4Z)-2,4-decadienoate; methyl (2E,4E)-decadienoate; geranylacetone	[97]
D			Tridecane (1st–2nd instar)	[84]
			<i>Euschistus heros</i>	
S	M	M, F, n	Methyl 2,6,10 trimethyltridecanoate; methyl (2E,4Z)-2,4-decadienoate; methyl 2,6,10-trimethyldodecanoate	[63,65,98]
D		M, F, n	(E)-2-Hexenal; 4-oxo-(E)-2-hexenal; hexenoic acid; (E)-2-hexenyl acetate; 2-octenal; (E)-2-octen-1-ol; nonanal; (E)-2-heptenyl acetate; (E)-2-decenal; (E)-2-octenyl acetate; tridecane; tetradecane; (E)-2-decenyl acetate; tridecanal; tetradecanal; pentadecane	[99–101]
D			Tridecane (1st–4th instar); tetradecanal (5th instar)	[79,96,99]

Table 1. Cont.













Pheromone ¹	Emitter	Responder	Compounds ²	References
?	M		<i>Euschistus ictericus</i> Methyl (2E,4Z)-2,4-decadienoate; methyl (2E,4E)-decadienoate	[97]
S	M	M, F, n	<i>Euschistus obscurus</i> Methyl (2E,4Z)-2,4-decadienoate; methyl 2,6,10-trimethyltridecanoate; methyl 2,6,10-trimethyldodecanoate; methyl (2E,4E)-decadienoate	[63,64]
Ag	M	M, F, n	<i>Euschistus politus</i> Methyl (2E,4Z)-2,4-decadienoate; methyl (2E,4E)-decadienoate	[97]
Ag	M	M, F, n	<i>Euschistus servus</i> Methyl (2E,4Z)-2,4-decadienoate; methyl (2E,4E)-decadienoate; geranylacetone	[97]
D			(E)-2-Hexenal	[102]
Ag	M	M, F, n	<i>Euschistus tristigmus</i> Methyl (2E,4Z)-2,4-decadienoate; geranylacetone; decanoic acid	[97]
D			Hexanal	[102]
D			Tridecane (1st–5th instar)	[79]
D			<i>Dichelops melacanthus</i> Tridecane (M, F); 4-oxo-(E)-2-hexenal (M, F)	[99,100,103]
D			4-Oxo-(E)-2-hexenal (5th instar)	[99]
Ag	M	M, F, n	<i>Dolycoris baccarum</i> α -Bisabolol *; trans- α -bergamotene *; (S)- β -bisabolene *	[104]
D			Tridecane (M, F); hexenal	[105,106]
Ag	M	M, F, n	<i>Mormidea v-luteum</i> Isomers of zingiberenol (cis-(1S,4R,1'S)-zingiberenol; trans-(1R,4R,1'S)-zingiberenol); murgantiol *; sesquiperitol	[107]
S	M	M, F, n	<i>Oebalus poecilus</i> Isomer of zingiberenol ((1S,4R,1'S)-4-(1',5'-dimethylhex-4'-enyl)-1-methylcyclohex-2-en-1-ol)	[71]
D			<i>Oebalus pugnax</i> Tridecane	[108]
S	M	M, F, n	<i>Tibraca limbativentris</i> Isomers of zingiberenol ((3S,6S,7R)-1,10-bisaboladien-3-ol; (3R,6S,7R)-1,10-bisaboladien-3-ol); sesquiperitol	[68,69]
Pentatominae: Eysarcorini				
Ag	M	M ⁽³⁾ , F, n	<i>Eysarcoris lewisi</i> Sesquisabinen-1-ol	[109,110]
?	M		<i>Eysarcoris parvus</i> (Z)-exo- α -Bergamotene	[111]
Pentatominae: Halyini				
D			<i>Apodiphus amygdali</i> 4-Oxo-(E)-2-hexenal	[112]
D			4-Oxo-(E)-2-hexenal (1st–5th instar)	[112]
D			<i>Brochymena quadripustulata</i> (E)-2-Hexenal	[113]
D			<i>Erthesina fullo</i> Tridecane (M, F)	[114]
D			<i>Poecilometris strigatus</i> (E)-2-Hexenal; (E)-2-octenal	[115]

Table 1. Cont.


















Pheromone ¹	Emitter	Responder	Compounds ²	References
			Pentatominae: Myrocheini <i>Delegorguella lautus</i>	
D			Tridecane	[72]
			Pentatominae: Nezarini <i>Chinavia aseada</i>	
?	M		<i>cis</i> -(Z)-Bisabolene epoxide; <i>trans</i> -(Z)-bisabolene epoxide; (Z)- α -bisabolene	[116]
D			(Z)-4-Nonenal	[102]
D			Tridecane (1st–2nd instar)	[79]
			<i>Chinavia hilaris</i>	
S	M	M, F, n	<i>cis</i> -(Z)-Bisabolene epoxide; <i>trans</i> -(Z)-bisabolene epoxide	[117]
D			(E)-2-Hexenal	[102]
D			Tridecane (1st–2nd instar)	[84]
			<i>Chinavia impicticornis</i>	
S	M	M, F, n	<i>trans</i> -(Z)-Bisabolene epoxide; <i>cis</i> -(Z)-bisabolene epoxide	[118]
D			Tridecane (M); 4-oxo-(E)-2-hexenal (F)	[99,118]
D			4-Oxo-(E)-2-hexenal (5th instar)	[99]
			<i>Chinavia marginata</i>	
?	M		<i>trans</i> -(Z)-Bisabolene epoxide; <i>cis</i> -(Z)-bisabolene epoxide	[119]
			<i>Chinavia ubica</i>	
S	M	M, F, n	<i>trans</i> -(Z)-Bisabolene epoxide; <i>cis</i> -(Z)-bisabolene epoxide	[118]
D			Tridecane (M, F)	[99,100,118]
D			4-Oxo-(E)-2-hexenal (5th instar)	[99]
			<i>Chlorochroa ligata</i>	
S	M	M ⁽³⁾ , F, n	Methyl (E)-6,2,3-dihydrofarnesoate; methyl farnesoate; methyl (E)-5-2,6,10-trimethyl-5,9-undecadienoate	[120,121]
D			Tridecane (M, F)	[122]
D			Tridecane (5th instar)	[122]
			<i>Chlorochroa sayi</i>	
S Ag	M	M, F, n	Methyl geranate; methyl citronellate; methyl farnesoate	[120,123]
D			Tridecane (M, F)	[122]
D			4-Oxo-(E)-2-hexenal (5th instar)	[122]
			<i>Chlorochroa uhleri</i>	
Ag	M	M, F, n	Methyl geranate; methyl citronellate; methyl farnesoate	[120,121]
D			Tridecane (M, F)	[122]
			<i>Nezara antennata</i>	
?	M		(Z)- α -Bisabolene; <i>trans</i> -(Z)-bisabolene epoxide; <i>cis</i> -(Z)-bisabolene epoxide; (E)-nerolidol	[116]
D			(E)-2-Decenal (M, F)	[81]
			<i>Nezara viridula</i>	
Ag	M	M, F, n	<i>trans</i> -(Z)-Bisabolene epoxide; <i>cis</i> -(Z)-bisabolene epoxide; (Z)- α -bisabolene; (E)-nerolidol	[98,116,124–128]
D		M, F, n	Tridecane; (E)-2-decenal; (E)-2-decenyl acetate; (E)-2-hexenal; (E)-2-hexenyl acetate; dodecane	[124,129–131]
D		n	4-Oxo-(E)-2-decenal (1st instar); tetradecane (2nd instar); tridecane (2nd–5th instar); (E)-2-hexenal	[79,84,132,133]

Table 1. Cont.




















Pheromone ¹	Emitter	Responder	Compounds ²	References
D			<i>Palomena viridissima</i> Unknown carbonyl compound	[106]
S	M	M, F, n	Pentatominae: Pentatomini <i>Pallantia macunaima</i> (6R,10S)-Pallantione	[134]
D			Tridecane (M, F)	[93,135]
D			(E)-4-Oxo-2-hexenal (1st instar) Tridecane (2nd–5th instar)	[135]
P	M	M, F, n	<i>Pellaea stictica</i> Isomers of 2,4,8,13-tetramethyltetradecan-1-ol	[136,137]
D			(Z)-4-tridecene	[93]
D			<i>Rhaphigaster nebulosa</i> Tridecane (M, F)	[138]
S	M	M, F, n	Pentatominae: Piezodorini <i>Piezodorus guildinii</i> (7R)-(+)- β -sesquiphellandrene	[139]
D			(E)-4-oxo-2-hexenal (M, F)	[99,140]
D			Unknown (5th instar)	[99]
SAg	M	M, F, n	<i>Piezodorus hybneri</i> β -Sesquiphellandrene*; (R)-15-hexadecanolide; methyl (Z)-8-hexadecenoate	[59,60]
D			<i>Piezodorus teretipes</i> (E)-2-Hexenal	[141]
SAg	M	M, F, n	Pentatominae: Rhynchocorini <i>Biprorulus bibax</i> Biprolure ((3R,4S',1'E)-3,4-bis(1'-buteny1)tetrahydro-2-furano; linalool; isomers of farnesol; nerolidol	[142–146]
D			Tridecane	[147]
D			<i>Vitellus insularis</i> Tridecane	[148]
Ag	M	M, F, n	Pentatominae: Strachiini <i>Bagrada hilaris</i> (E)-2-octenyl acetate	[149,150]
D			<i>Eurydema oleraceum</i> (E)-2-Octenal; (E)-2-hexenal	[102,151]
D		n	<i>Eurydema pulchrum</i> (E)-2-Hexenal (1st–3rd instar); tridecane	[133]
Ag	M	M, F, n	<i>Eurydema rugosa</i> (E)-2-Hexenal	[152]
D		n	(E)-2-Hexenal (2nd–3rd instar); tridecane	[133]
D			<i>Eurydema ventrale</i> (2E,6E)-Octadienedial; (E)-2-octenal	[102,151]
Ag	M	M, F, n	<i>Murgantia histrionica</i> Isomers of murgantiol ((3S,6S,7R,10S)-10,11-epoxy-1-bisabolen-3-ol; (3S,6S,7R,10R)-10,11-epoxy-1-bisabolen-3-ol)	[153–155]
D			(2E,6E)-Octadienedial	[151]

Table 1. Cont.

Pheromone ¹	Emitter	Responder	Compounds ²	References
			Podopinae: Graphosomatini	
			<i>Graphosoma lineatum</i>	
D			1-phenanthrenecarboxylic acid (M); tridecane (F); (E)-2-decenal (F)	[156,157]
			<i>Graphosoma rubrolineatum</i>	
D			(E)-2-Decenal (M, F)	[81]
			<i>Graphosoma semipunctatum</i>	
D			Tridecane (M, F)	[158]
			Podopinae: Podopini	
			<i>Scotinophara lurida</i>	
D			(E)-2-Decenal (M, F)	[81]

¹ For compounds where a pheromonal functionality has been assigned but no behavioural study has been conducted, the compounds were isolated from a specific structure where no other function has been observed.

² The most abundant compound of the alarm pheromone can vary among studies, and in these cases, each most abundant compound is listed. ³ Males attraction is unclear. Field tests were suggestive, and the data were limited to confirm the attraction. ? Indicates that it is a putative pheromone. No behavioural bioassays have been conducted to confirm the functionality. * Absolute configuration has not been determined.

In stink bug sex pheromones, the ratio of components appears to be important, with ratios that accurately reflect those produced by males being most attractive. In addition, they are species specific, and can vary with age, physiological status, or among populations [159–162]. For example, Endo et al. (2012) [159] showed that the ratios of the three components in pheromone emissions of *P. hybneri* are variable among individuals and over time. Variation in the pheromone blend has also been observed among *N. viridula* individuals from different geographic populations [116] and within a single population in Australia [162]. Thus, determining the ratio as well as the absolute configuration of the pheromones must be considered when optimizing attractants for monitoring and management purposes.

Field studies have shown that the number of stink bugs recovered in traps baited with sex pheromone does not always correlate with the density of the field population [163]. This is possibly because of sub-optimal trap design. Studies have shown that more pentatomids are observed in the vicinity of traps than inside the traps [97,143], a possible indication that stink bugs require vibrational signals to locate and enter the trap. A trap incorporating olfactory and acoustic stimuli was recently tested in the field for *Halyomorpha halys* (Stal) and demonstrated that the use of vibrations and pheromones can increase the efficacy of pheromone traps [164,165].

3. Alarm Pheromones

Stink bugs are well known for producing odoriferous compounds that play a role in chemical communication and defence [16,17,57,58,96,166]. These volatile compounds are produced and stored in specific glands (DAGs—dorsal abdominal scent glands and MTGs—metathoracic scent glands) according to their life stage (Figure 1) [58,122,127,132,135,166–169]. These glands secrete volatiles through the external efferent thoracic system when insects are disturbed [101,170] and can act as allomones and serve as a defence against natural enemies and microorganisms or mediate alarm or aggregation behaviours among conspecifics [16,96,100]. These compounds are highly conserved across species and are mostly represented by short-chain aliphatic aldehydes, alcohols, esters, alkanes, terpenes, and phenolics (Table 1) [16,57,58,96,99,166].

The use of semiochemicals for behavioural manipulation of natural enemies has been proposed as a tool to improve biological control [171,172]. Natural enemies can exploit the alarm compounds produced by pentatomids as kairomones to locate their hosts [91,173–175]. For example, the egg parasitoids *T. podisi*, *Trissolcus basalisi* (Wollaston) and *Trissolcus japonicus*

(Ashmead) are attracted to (*E*)-2-hexenal, (*E*)-2-decenal, and tridecane, defensive compounds released by their preferred hosts, *E. heros* [175], *N. viridula* [176], and *H. halys* [91], respectively. Each species seems to be able to recognise the compounds produced by their preferred hosts [174]. *Trissolcus basalis* responded preferentially to (*E*)-2-decenal and 4-oxo-(*E*)-2-hexenal, two compounds in *N. viridula* secretions, whereas *T. podisi* preferred (*E*)-2-hexenal and 4-oxo-(*E*)-2-hexenal compounds in the secretions of *E. heros*. Similarly, in field experiments, traps baited with alarm pheromone compounds such as (*E*)-2-hexenal + α -terpineol and 4-oxo-(*E*)-2-hexenal + linalool + tridecane captured the tachinid flies *Euclytia flava* (Townsend) and *Hemyda aurata* (Robineau-Desvoid) [166,177]. Other predators such as chloropid and milichiid flies, as well as spiders, have also been reported to be attracted to alarm pheromone compounds of Pentatomidae. Aldrich and Barros [178] showed the attraction of male crab spiders *Xysticus ferox* (Hentz) to (*E*)-2-octenal and (*E*)-2-decenal and Eisner et al. [179] demonstrated the attraction of chloropid and milichiid flies to chemicals released by crushed Pentatomidae. These flies are also attracted to defensive compounds such as (*E*)-2-hexenal, (*E*)-2-octenal, (*E*)-2-decenal, and hexanal [178,179]. These results suggest that stink bug natural enemies use scent gland secretions to locate their preferred hosts. However, to date, only one study has been conducted on Pentatomidae with the aim of attracting parasitoids with synthetic alarm pheromone to enhance parasitism of stink bug eggs [175]. Areas treated with (*E*)-2-hexenal showed an increase in the abundance of Telenominae with greater intensity of parasitism and an increase in egg predation. The utilisation of alarm pheromone compounds to improve the action of natural enemies has potential, but it needs further study to develop release devices that release effective doses. In addition, effects on natural enemy foraging and host location may be dose dependent, with some doses positively affecting associated behaviours and others negatively. Further research is needed to determine if release devices and dosages can be developed that enhance positive effects without negative effects. The combination with other semiochemicals or with trap crops could also help. In addition to the volatiles emitted from the scent glands, parasitoids of the Pentatomidae can use other cues when searching for eggs, such as volatiles from plants [180,181], volatiles from eggs [182], sex pheromones [177,183], chemicals left by stink bug footprints [184,185], vibratory signals [49], and visual cues [186]. Thus, specific knowledge about the stimuli that mediate interactions between natural enemies and stink bugs is required to improve the effectiveness of applications of semiochemicals in integrated pest control. Strategies such as attract and reward [187,188] or push–pull tactics [189–191], which combine alarm pheromone compounds with habitat manipulation, could improve the action of natural enemies of Pentatomidae.

4. Aggregation Behaviour and Pheromones in Pentatomidae

Aggregation behaviour is a common phenomenon in Heteroptera [192]. In Pentatomidae, aggregations are first observed when stink bug eggs hatch, but also later by adults (Figure 1). These two separate phenomena are likely mediated by entirely different cues and signals. The maintenance of aggregations of first instar pentatomids is mediated by a combination of tactile cues and chemical compounds, which are normally considered as defensive compounds in later instars [79,84,152]. It has been shown that these defensive compounds can also mediate heterospecific aggregation behaviour of first instars [152], suggesting that compounds which mediate aggregation of first instar stink bugs may be conserved among species. In adults, aggregations can be observed at different times of the year. For example, *H. halys* forms aggregations in both summer and winter during diapause. In the summer, aggregations are mediated by aggregation pheromones which attract both sexes and nymphs [87]. The identity of the stimuli that mediate adult overwintering aggregations remains unknown. Tomaya et al. [193] suggested that tactile and olfactory stimuli might be involved, whereas Bedoya et al. [194] demonstrated that the overwintering aggregations are not mediated via vibration signals.

Aggregation pheromones produced by stink bugs are complex and include saturated hydrocarbons, methyl esters, terpenes, and terpenoids [16,17,57,195]. Although these pheromones

are species specific, some similarities among Pentatomidae occur (Table 1) [16,17]. For example, within the Carpocorini tribe, methyl (*E,Z*)-2,4-decadienoate (MDD) has been identified as an aggregation pheromone in five *Euschistus* species including *E. servus*, *Euschistus tristigmus* (Say), *Euschistus politus* (Uhler), *Euschistus conspersus* (Uhler), and *Euschistus ictericus* (L.) [97]. Other methyl esters have also been reported as aggregation pheromones, such as methyl (*E,E,Z*)-2,4,6-decatrienoate (MDT), methyl (*E*)-5-2,6,10-trimethyl-5,9-undecadienoate, and methyl (8*Z*)-8-hexadecenoate produced by *Plautia stali* Scott [82], *Chlorochroa* sp. [121] and *P. hybneri* [59], respectively. Another example is the presence of sesquiterpenoids such as murgantiol (10,11-Epoxy-1-bisabolene-3-ol), where isomers have been identified in *Murgantia histrionica* (Hahn) [153,154], *Halyomorpha halys* (Say) [87], and *Mormidea v-luteum* (Lichtenstein) [107]. Other similar sesquiterpenes and sesquiterpenoids (α -bisabolol, *trans*- α -bergamotene, β -bisabolene and zingiberenol) have also been detected as sex and aggregation pheromones in various Pentatomidae species [68,69,71,104,124]. A recent study revealed that these similarities of sesquiterpene compounds observed in Pentatomidae are linked to a conserved gene function in terpene biosynthesis [196]. Furthermore, attraction to heterospecific pheromones has been observed in Pentatomidae [16]. For example, the pheromone of the Asian species *P. stali* (MDT) attracts other pentatomids such as *Glaucias subpunctatus* (Walker), *H. halys*, and the North American species *C. hilaris*, despite the fact that *H. halys* and *C. hilaris* do not produce this compound. In fact, trap captures of *H. halys* can be synergised by the addition of MDT [197] and this has been observed in different populations globally [198]. Other examples of cross attraction can, however, be attributed to some overlap in pheromone chemistry, as is the case between *Nezara antennata* (Scott) and *N. viridula*, which share their two compounds [116].

Aggregation pheromones have been used in stink bug management to monitor the phenology and abundance of populations. For *H. halys*, the discovery of its aggregation pheromone has facilitated the development of an extensive monitoring program across the United States to define its infestation range and damage to crops [199]. Pyramid traps baited with MDD lures have been used to monitor populations of *E. servus* and *E. tristigmus* in apple and peach orchards [200,201] and for *E. conspersus* on tomatoes [202]. Nevertheless, studies have shown that although pheromone-baited traps can attract stink bugs to their vicinity, the number of captures often does not correlate with populations in the field [159]. For example, in apple and peach orchards, only 50% of *E. servus* attracted within 10 m of traps were captured [201], whereas traps placed on the border of tomato plantations attracted only *E. conspersus* females [159].

The use of stink bug aggregation pheromones in combination with host plants as trap crops has also been examined. A study with *E. conspersus* has shown that if MDD lures are deployed directly on a host plant, such as mullein plants, higher numbers of bugs are attracted and retained on these baited plants [203], demonstrating the potential of using trap crops for stink bug control. This concept of combining aggregation pheromone with host plants was later used on *P. stali*, where eggplants were baited with pheromones and treated with a high rate of systemic insecticide to kill attracted bugs [204]. However, in this study, significant damage to adjacent trees of the main persimmon crop was observed due to a spillover of attracted stink bugs. More recently, this concept was also applied in commercial apple orchards to control *H. halys* [205–207]. Morrison et al. [206] observed better retention of attracted bugs in the area surrounding lures when they were deployed in host plants, suggesting that deployment protocol can limit spillover and damage to untreated plants. Although this approach looks promising for managing *H. halys* and may be a viable option for other stink bug species [207], important economic considerations still exist. In fact, Morrison et al. [207] compared the cost of the attract and kill strategy and grower standard treatment for insect management. Although yield generated by the attract and kill treatments were higher than the standard treatments, the cost of the attract and kill treatments was seven to ten times higher, and as such remains the biggest limitation of this type of management approach.

5. Symbiotic Relationships and Vertical Transmission of Bacteria in Pentatomidae

Symbiotic interactions between bacteria and insects are ubiquitous [208,209] and can be crucial to insect fitness [210,211]. They play an important role in the digestion and detoxification of food, and provide essential nutrients for development, such as amino acids and vitamins often lacking in xylem/phloem sap [210–212]. Gut symbionts also provide protective functions to their host against pathogens and parasites [210,211].

Various bacterial taxa have been identified as Heteroptera symbionts, including Actinobacteria, Alphaproteobacteria, Bacteroidetes, Betaproteobacteria, Firmicutes and Gammaproteobacteria [213], with Gammaproteobacteria representing the most dominant taxa within the Heteroptera suborder [20,214,215]. These symbionts are essential to the growth, development, and survival of the host [215]. The bacteria *Wolbachia* has also been recorded in several pentatomid species; nevertheless, its role in host biology and, as such, its symbiotic impact has been poorly investigated [216]. The microbial gut symbionts among the Pentatomidae have been well described [10,15,19]. The Pentatomidae primarily harbour bacteria related to the *Pantoea* genus (Enterobacteriaceae family) in their midgut [217]. Pentatomidae are sap feeders and have a stylet (i.e., mouthparts modified from mandibles and maxillae) which allows them to pierce into plant tissue to suck xylem/phloem, and these symbionts provide their hosts with nutrients missing in their diets [218,219] and help to detoxify and deactivate plant chemical defences [220]. Reduced genome size (<1 Mb), high AT content and a fast evolutionary rate have been generally observed in bacterial symbionts of stink bugs [218,219,221,222].

Symbionts in the Pentatomidae are vertically transmitted by females to offspring during or after oviposition via physical deposition upon egg masses (e.g., egg smearing) [9,11,223,224]. After hatching, the first instars aggregate on the egg surface and ingest the bacteria by probing the egg chorions [224–226]. The symbionts of Pentatomidae are located extracellularly in tubular outgrowths called crypts or caeca in the posterior region of the midgut (e.g., M4 or V4 section) [11,15,20,224,227]. The establishment of gut bacteria in these crypts occurs directly from the first instar after ingestion of the symbiont [214,224]. Although these crypts can be found in both males and females, they are morphologically enlarged in females, suggesting that these enlarged crypt structures represent a female-specific specialised morphological trait for vertical symbiont transmission in Pentatomidae [227].

Symbiont acquisition failure can impact nymph survival [20,23,224]. Disruption of symbiont acquisition may thus offer pest control opportunities. Methods for disruption of vertical symbiont transmission in the Pentatomidae have been reviewed recently [19]. Different approaches to egg sterilisation have been tested in the laboratory, such as the utilisation of bleach [12,23] or bleach combined with ethanol [10,20,21], or with ethanol and formaldehyde [22,228,229]. Increased mortality, development time and sterility, reduced fecundity, and morphological abnormalities have been observed in pentatomid adults and nymphs, where symbiont acquisition was disrupted by these sterilisation methods [19]. More recently, egg sterilisation has also been successfully used under laboratory and in field conditions to control *H. halys* populations via the suppression of its primary symbiont *Pantoea carbekii* using antimicrobial treatments [24,230,231]. Since some of these products (i.e., Dentamet[®], Keos[®] and Bio-D[®]) are commercially available in Europe for organic farming as micronutrient fertilisers [230], this demonstrates the potential of targeting eggs to reduce population levels in the field.

6. Other Important Traits to Consider for Pest Management

Compared with olfactory stimuli, considerably less is known about the visual ecology of Pentatomidae. A few studies have looked at the effect of trap colour and demonstrated that trap colour influences the number of bugs captured, and this increase might result in better management and improved pest control. It has been shown that large numbers of phytophagous insects respond to yellow [232]. A study in the US observed that unbaited yellow traps captured more native stink bug species than traps painted light and dark green, black, or covered with aluminium foil [233]. However, intermediate results for

Euschistus spp. with yellow traps have been observed in comparison to white and green pyramid traps [200]. For *H. halys*, adults and nymphs seem to be more attracted to black pyramid traps than to yellow, white, green, and clear ones [234], for both plastic and wood traps [205]. Similar results have been obtained with black traps for *Bagrada hilaris* (Burmeister) [235]. Other coloured traps such as purple, white, or red also captured more adult *B. hilaris* than yellow traps, while no effect of trap colour was observed for nymphs. Laboratory and field work on the harlequin bug showed that this species is more attracted to green and black than white, yellow, red, or purple [236].

Artificial light can influence insect phototaxis, with both attraction [237] or repellence [238] being observed. Various studies have been conducted on the incorporation of lights into trapping devices or pest management programs [239,240]. The monitoring of Pentatomidae can often be difficult, but the incorporation of UV light traps can improve the performance of surveillance traps significantly [241]. Additional factors that can influence insect behavioural responses to light include light intensity and wavelengths [239,240,242–244]. In this regard, laboratory and field trials on *H. halys* have been conducted in order to determine optimal wavelengths and light intensities for the use of surveillance [245,246]. Leskey et al. [246] observed that this species was attracted to white (full spectrum of the visible light, 400–700 nm wavelength), blue (approximately 410 nm wavelength), and black (ultraviolet, <400 nm wavelength) fluorescent bulbs. However, in the field, blue and “white” sources were more attractive. Cambridge et al. [245] demonstrated recently that *H. halys* was attracted to “white” light (400–700 nm wavelength) at 75 lx of intensity.

Understanding the dispersal of stink bugs is crucial to the improvement of integrated pest management strategies targeting Pentatomidae pests. Although the Pentatomidae are regarded as heavy insects that have a small wing area in relation to their body weight in comparison to other insects [247], studies on *H. halys* suggest they are active fliers with good flight performance [248,249]. The establishment of stink bug flight potential could inform the development of management strategies which are influenced by stink bug movement, such as the attract and kill strategy [207]. A few laboratory studies have examined stink bug flight capacity using flight mills. A recent study assessed the baseline flight potential of *Euschistus servus* collected over 2 years from different host plants with the longest distance flown of 16 km [248]. Previous work with *H. halys* demonstrated that 85% of individuals could fly up to 5 km in 24 h, with the longest distance of 117 km flown by an individual [248,249]. The effects of starvation, age, mating status, sex and pre-flight weight on flight parameters have been examined on laboratory-reared *H. halys* [249]. This work suggested that only starvation impacted the number of flight bouts and velocity, suggesting that this species has a robust dispersal capacity which may contribute to its success as an invasive species. Multiple parameters can impact flight mill results, such as handling of insects, lack of natural stimuli, increased weight load, and reduced energy expenditure [250,251]; thus, caution needs to be taken when interpreting flight mill data. For example, distances flown by laboratory-reared stink bugs in a study by Aita et al. [252] were lower than the distances flown by stink bugs collected from the field [248,249]. Furthermore, flight response can vary among stink bug species and over the season. For example, *H. halys* exhibits a high flight potential toward the end of the season and before entering diapause, compared to the mid-season [249], whereas *E. servus* has a lower mean flight potential during the mid-season and toward the end of the season [253]. Determining when and how long-distance and short-distance movements of stink bugs occur throughout the growing season could help growers to predict the area of infestation and to implement time- and location-appropriate control strategies.

7. Conclusions

Current management programs for stink bug pests rely on the use of chemical insecticides, which often have hidden costs associated with environmental impacts, effects on human health [254,255], and the selection of resistant pest populations [6]. Additionally, the intensive use of chemicals is often incompatible with biological control and establishment

of natural enemies [256]. Pesticide exposure can negatively impact natural enemies and reduce their biological control services, which can lead to pest resurgence and secondary pest outbreaks [257,258]. Alternative management options are needed [259], but the successful development and implementation of these alternatives usually requires considerable knowledge of pest biology. The development of alternative tactics is particularly difficult for new pests or invasive species due to the limited knowledge we often have of the pest life cycle in these situations.

Pentatomidae have specific traits which are promising targets for pest management. The presence of sex and aggregation pheromones is one example. Despite the fact that these pheromones have been identified for several species, their use in pest management is still restricted to monitoring the phenology and abundance of a few major stink bug species. Nevertheless, management tactics such as mass trapping and trap cropping have been improved with the commercialisation of various aggregation pheromone lures. Preliminary results suggest that the attract and kill tactic has potential and warrants additional research [206,207]. Although this tactic is promising, the costs linked with the synthesis and production of compounds, along with the deployment of pheromone devices, are still an obstacle limiting the commercial implementation of this method.

Recent advances in genomics and transcriptomics of stink bugs [260–263], along with new technologies such as reverse chemical ecology [264] or CRISPR-Cas9 [265,266], should facilitate the identification and functional characterisation of semiochemicals and their biosynthetic pathways. This could, in turn, lead to alternative options for synthesis of pheromone compounds in the future. CRISPR-Cas9, as a tool for genome editing, targeting for example pheromone and odour-related genes, genes involved in sexual reproduction or insecticide resistance, could also become a viable option for pest management in the future. In terms of this, research should focus on the development of these gene knockout systems in non-model organisms, similar to Cagliari et al. 2020 [266] who developed this for *E. heros*. Biosafety concerns in terms of the release of genetically transformed insects, which range from the risk of non-target effects if hybridisation (gene flow) can occur between target and non-target species, to the ecological impact on a niche if the target is removed from the environment [267], also exist and represent major challenges to the use of these technologies.

In parallel, precision agriculture methods for detection of pests or crop injury have also evolved, and electronic nose (E-nose) technology using semiochemicals has been developed. Various E-noses have been tested to detect stink bug damage on cotton [56,268,269], and more recently to detect *E. heros* sex pheromone [270]. This new technology may well offer a cheaper and new alternative method for stink bug detection in the future. Finally, it is important to also underline the potential of plant volatiles in combination with pheromones to improve trapping and trap cropping methods in pest management [271]. The use of aggregation pheromones in Pentatomidae offers this opportunity, and this has been recently investigated with *H. halys* [207] and *M. histrionica* [272]. Further research should therefore focus on this underexplored topic for stink bug pest management.

Disruption of symbiont acquisition is another interesting target. Some active substances are already commercially available as antimicrobials or fertilisers, and their utilisation is allowed in organic farming as a sustainable option [230,231]. This method therefore seems promising, although practical aspects still need to be addressed in terms of application, rate, and cost. In addition, questions regarding its applicability to other cropping systems as well as other stink bug species, and the long-term effects of these fertilisers on the cropping system, also need further attention before commercial implementation.

Other traits of the Pentatomidae that can be targeted for pest management are the utilisation of alarm pheromones for enhancing natural enemies [175], and the use of substrate-borne vibration for mating disruption [45,47] and surveillance [164,165]. To date, there is no study which shows that the utilisation of alarm pheromone for enhancing natural enemies can suppress the utilisation of insecticides, but these volatiles might be valuable as complementary tools to minimise insecticide spraying. Precautions may also need to be taken, as some of these volatiles have antifungal effects and their utilisation

might interfere with the use of entomopathogenic fungi as biological control agents [100]. Novel methods such as attract and reward [186] have not been tested in Pentatomidae, and future studies should focus on this aspect, whereas the use of vibrational signals and pheromones in a bimodal trap can increase trap captures and might have utility for mass trapping of stink bugs. Finally, the visual ecology and flight behaviour of Pentatomidae are still poorly studied. Colour preferences may improve the accuracy of mass-trapping and surveillance activities. In addition, advances in stink bug genomics and transcriptomics can help to determine which visual genes occur among Pentatomidae and which colours stink bugs can see. Currently, opsin genes have only been described in one Pentatomidae species [273,274], illustrating that we are far from truly understanding their visual ecology. Finally, knowledge regarding dispersal capacity is another important component for pest monitoring, especially for control tactics such as attract and kill or push and pull methods which rely on pest movement.

While many of these tools are still in the early stages of development, they offer valuable targets for improved and more sustainable Integrated Pest Management systems that should receive more focused attention.

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