Review Article

Chemical Ecology of Egg Parasitoids Associated with True Bugs

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Parasitoids representing some 15 families of Hymenoptera develop in insect eggs; three of these families, Platygastridae (= Scelionidae), Mymaridae, and Encyrtidae, are associated with Heteroptera. Several species of heteropteran egg parasitoids are or may be important for biological pest control. Successful parasitism of insect herbivores by insect parasitoids arises through several phases of host searching, which lead female wasps to the vicinity of, or in contact with, their hosts. During the host location process, females encounter and explore a variety of stimuli, among which chemical cues (i.e., semiochemicals or infochemicals) play a pivotal role. Female parasitoids are under selection pressure to efficiently invest their limited time on the location and exploitation of host-derived stimuli. In general, the levels of reliability and detectability of a particular stimulus are inversely correlated. Female parasitic wasps adopt differing strategies to solve this dilemma. In this paper we focus on the various host selection strategies employed by heteropteran egg parasitoids and possible means whereby the chemically mediated behavior of these wasps may be exploited to enhance biological pest control.

1. Introduction

Egg parasitoids are the largest group of entomophagous insects associated with Heteroptera. Thus, considering that they attack the host before it develops and inflict feeding damage, egg parasitoids show remarkable potential as biological control agents of Heteroptera, as well as other pests [1]. These parasitoids, however, also attack predaceous bugs which, of course, is counterproductive for the efficacy of these important natural enemies [2, 3].

Of the approximately 15 hymenopteran families that include egg parasitoids, those most commonly associated with Heteroptera are Platygastridae, Mymaridae, and Encyrtidae [1]. Most studies of their chemical ecology concern species associated with herbivorous bugs and, to a much lesser extent, predacious Heteroptera. The majority of semiochemical research on egg parasitoids associated with true bugs has been limited to species belonging to the genera attacking economically important pentatomid, scutellerid, mirid, alydid, and coreid plant pests (Table 1): *Trissolcus*, *Telenomus*, *Gryon* (Platygastridae = Scelionidae; see Sharkey [4] and Murphy et al., 2007 [5]), *Anaphes* (Mymaridae), and *Ooencyrtus* (Encyrtidae).

Generally, in order to reproduce, a female parasitoid must find its host at a stage suitable for parasitization. The host selection process involves a sequence of phases mediated by physical and chemical stimuli from the host, the substrate, and/or associated organisms, eventually leading to successful parasitism [6–9]. Because parasitoid foraging time is limited and the potential cues available are numerous, the parasitoid faces the need to optimize exploitation of available cues and discriminate those most reliable in indicating the presence of a suitable host [8, 10]. However, the location and recognition of a suitable host is a complex process, especially for egg parasitoids, because of major constraints due to the small sizes of both the host and the parasitoid itself. Eggs are usually unapparent, especially when they are small, dispersed in the habitat, and concealed in plant tissue. As such, cues that are directly related to the presence of eggs may have low detectability, but high reliability [8, 11, 12]. Additionally, suitable host eggs are generally available for only a short time due to their rapid development [7]. Therefore, egg parasitoids have developed specialized strategies to overcome the reliability-detectability dilemma in order to efficiently parasitize host eggs. Successful parasitism is accomplished

TABLE 1: Host or host-associated semiochemicals exploited by egg parasitoids of Heteroptera for host location or recognition (modified and updated from Colazza et al. [14]).

Parasitoid	Host	Plant	Function	Origin	Chemistry	Parasitoid response	References
Mymaridae							
Anaphes iole	Lygus hesperus	Gossypium hirsutum + other	Volatile induced synomone	Plants with feeding damage	Several HIPV, mostly α-farnesene, (Z)-3-hexenyl acetate, methyl salicylate	Attraction in olfactometer (effect of experience); response to EAG	[43, 44, 67]
			Short range synomones	Wounds in different substrates		Ovipositor probing	[52, 53]
			Short range kairomones	Host egg and adult		Ovipositor probing	[52–54]
Encyrtidae							
Ooencyrtus nezarae	Riptortus clavatus		Volatile kairomone	Host male attractant pheromone	(E)-2-Hexenyl	Attraction in field, increased parasitism	[34–36]
Ooencyrtus telenomicida	Nezara viridula		Volatile kairomone	Host male pheromone + ovipositing female	(Z)-3-Hexenoate	Attraction in Y-tube olfactometer	[38]
Platygastridae							
Gryon boselli	Gonocerus acuteangulatus		Contact kairomone	Host footprints		Arrestment and increased searching in open arena	Colazza et al., unpubl.
Gryon pennsylvanicum	Leptoglossus australis		Volatile kairomone	Host pheromone	Quantitative differences especially	Attraction in field	[56]
Telenomus podisi	Euschistus heros	Glycine max, Cajanus cajan	Volatile induced synomone	Plants with feeding damage; cis-jasmone treatments on resistant plants	(E,E)-α-farnesene, methyl salicylate, (Z)-3-hexenyl acetate, and (E)-2-octen-1-ol	Attraction in Y-tube olfactometer	[41, 42, 66]
			Volatile kairomone	Compounds from host defensive secretion	(E)-2-hexenal, 4-oxo-(E)-2-hexenal	Attraction and increased searching	[33]
			Kairomone	Host male sex pheromone	Methyl 2,6,10-trimethyltridecanoate	Choice in closed arena	[85]
			Contact kairomone	Host footprints		Arrestment and increased searching in open arena	[46]
	Euschistus conspersus		Contact kairomone	Acetone extract of host eggs	2,6,10-Trimethyltridecanoate		[51]
			Volatile kairomone	Host male attractant pheromone	Methyl(E,Z)-2,4-decadienoate	No parasitism increase in field	[86]
Telenomus calvus	Podisus neglectus		Volatile kairomone	Host pheromone		Attraction in field	[39]
	Podisus maculiventris		Volatile kairomones	Host male attractant pheromone; host female		Attraction in field allowing egg parasitism; phoresy	[2, 3, 87]
Trissolcus basalis	Nezara viridula	Vicia faba, Phaseolus vulgaris	Volatile induced synomone	Plants with oviposition + feeding	Increase of (E)-β-caryophyllene	Attraction in Y-tube olfactometer	[20, 21]

TABLE 1: Continued.

Parasitoid	Host	Plant	Function	Origin	Chemistry	Parasitoid response	References
Trissolcus brochymenae	Murgantia histrionica	Brassica oleracea	Volatile kairomone	Host defensive allomone	(E)-2-Decenal, 4-oxo-(E)-2-hexenal	Attraction in Y-tube olfactometer, increased searching	[30, 33]
			Volatile kairomone	Host attractant pheromone		Attraction in Y-tube olfactometer	[31]
			Contact kairomone (highly specific)	Host footprints (especially females)	Cuticular hydrocarbons	Arrestment and increased searching in open arena	[31, 71, 72]
			Contact kairomone	Follicular secretion and egg extracts	Mucopolysaccharide-protein complex	Host recognition	[50, 88, 89]
			Short-range induced synomone	Plants with feeding damage		Increased searching behavior	[22, 62, 63],
			Short-range induced synomone	Plants with feeding + oviposition (systemic induction)		Increased searching behavior	[22, 62, 63],
			Volatile kairomone	Pheromone from different host instars		Attraction in Y-tube olfactometer	[28]
			Contact kairomone (highly specific)	Host footprints (especially mated females)	Cuticular hydrocarbons	Arrestment and increased searching in open arena	[28, 32, 47]
			Volatile kairomone	Host egg masses		Attraction in Y-tube olfactometer	[28]
			Contact kairomone	Follicular secretion and egg extracts		Host recognition	[28]: Conti et al., unpubl.
Trissolcus euschisti	Euschistus conspersus		Volatile kairomone	Male attractant pheromone	Methyl(E,Z)-2,4-decadienoate	No parasitism increase in field	[86]
Trissolcus grandis	Eurygaster integriceps		Volatile kairomones	Host male attractant and female sex pheromones		Attraction in the field	[90]
	Eurygaster spp.		Contact kairomone	Host egg			[91]
Trissolcus simoni	Eurydema ventrale		Volatile kairomone	Host attractant pheromone		Attraction in Y-tube olfactometer	[92]
			Contact kairomone	Host footprints		Arrestment and increased searching in open arena	[32]
Trissolcus utahensis	Euschistus conspersus		Volatile kairomone	Host sex pheromone	Methyl(E,Z)-2,4-decadienoate	No parasitism increase in field	[86]

through the combined exploitation of cues that are directly and indirectly related to host eggs [7, 8, 13, 14]. First, parasitoids may detect volatiles from nontarget instars of the host, that is, adults or juveniles, to reach the vicinity of the host eggs (infochemical detour *sensu* Vet & Dicke [8]), eventually enabling them to pin-point eggs using additional long- and/or short-range cues. A particular and interesting example of such detour behavior of egg parasitoids is phoresy on adult host females; via this strategy, not only are relevant cues more detectable, but the adult itself is also exploited by the parasitoid as a vehicle to arrive at host eggs [15–17]. Second, parasitoids may exploit plant volatiles induced as a consequence of herbivory, which are emitted in large quantities and are, therefore, easily detectable by foraging parasitoids but not necessarily highly reliable [13]. For example, recent investigations have shown that some egg parasitoids are capable of exploiting plant chemicals emitted as a result of egg deposition, thus rendering such highly detectable cues also highly reliable [18–24]. Third, egg parasitoids have been observed to associate, through learning, highly detectable but less reliable cues with the presence of suitable hosts, thus increasing reliability of such cues in experienced wasp females [25, 26].

The complex of stimuli that are used by parasitoids for host seeking and acceptance, originating from the host, the associated substrate and/or organisms, and their possible interactions, has been called the "host-egg unit" [27–29]. The host-egg unit is often quite complex and is related to the parasitoid strategies described above. Thus, the same host might represent different host units for different parasitoids, depending on whether they are specialist versus generalist parasitoids, or whether they have evolved capabilities to exploit adult kairomones or induced plant synomones, or whether they have developed phoretic strategies. In this paper we will focus on the behavioral steps of host selection strategies and the chemical cues exploited by egg parasitoids of emerging pest species of Heteroptera.

2. Exploitation of Indirect versus Direct Host-Related Chemical Cues

The most common indirect host-finding tactic known thus far for egg parasitoids is the infochemical detour strategy based on the parasitoid ability to detect chemical cues associated with stages other than the egg [7, 8]. Exploitation of pheromones and/or allomones from host adults has been demonstrated for both Platygastridae [28, 30–33] and Encyrtidae [34–38] (Table 1). These stimuli provide indirect information on the presence of the host community, leading the wasp female to the vicinity of host eggs. In spite of their low reliability, pheromones and allomones are produced in large amounts, and, therefore, these cues are relatively easy to detect by the female wasps from long to medium distances [39].

Phoresy is a different, but highly specialized bridge-in-time (and bridge-in-space) strategy exploited by egg parasitoids to reduce the spatial and temporal discontinuity between where host adults mate and where host females

oviposit [7, 40]. One well-documented case of phoresy by a heteropteran egg parasitoid is that of *Telenomus calvus* Johnson (Platygastridae) females that parasitize eggs of the predacious spined soldier bug, *Podisus maculiventris* (Say) (Pentatomidae). Female *T. calvus* wasps go to the male-produced *P. maculiventris* attractant pheromone, wait nearby for a conspecific soldier bug female to arrive and mate, and then become phoretic on the mated host female until she eventually oviposits [2, 3].

Another indirect means to locate host eggs is exhibited by *Trissolcus basalis* (Woll.) and *Telenomus podisi* Ash. (Platygastridae), which exploit plant synomones induced by oviposition and/or feeding of their hosts, *Nezara viridula* L. [20] and *Euschistus heros* (Fabr.) [41, 42] (Pentatomidae) (Table 1). In a hierarchical context, whether volatiles from host adults or from the host plants of host adults are exploited from the furthest distance has yet to be elucidated. In the case of *Tr. basalis*, because host oviposition is necessary for volatile induction in bean plants, such synomones appear more reliable compared to kairomones from nontarget instars or to feeding-induced synomones [20, 21]. Therefore, it can be hypothesized that kairomones from adults and feeding-induced plant synomones act as a long-distance, indirect cue used to localize the host community (or host habitat), whereas oviposition-induced plant synomones are shorter-range cues used to find plants that actually have host eggs.

Induced plant volatiles are also exploited by mymarids [43, 44] (Table 1). Feeding on cotton, and several other plants, by either sex of *Lygus hesperus* Knight (Miridae) results in the induction of volatiles that are behaviorally and physiologically active towards *Anaphes iole* Girault (Mymaridae). Oviposition appears unnecessary to induce active volatiles [44]; therefore, these synomones should also be considered as indirect cues, exploited to localize the host community.

Once close to a potential host, female parasitic wasps in flight preferably should alight on a plant that probably has host eggs and then commence searching on the substrate for suitable eggs. Different strategies, and cues, are used during this phase (Table 1). For example, *Trissolcus brochymenae* (Ashm.) exploits short-range chemicals that are induced in cabbage plants by *Murgantia histrionica* (Hahn) (Pentatomidae) during oviposition [22]. Such a directly host-related synomone that is systemically emitted by the plant provides reliable information on the presence of suitable host eggs, but not necessarily precise information on where the eggs have been laid [22].

While searching for the host eggs on the plant, different Platygastridae were shown to use chemical traces left behind from the adults and/or juveniles (Table 1). The typical response to such cues, which are perceived through gustatory sensilla [45], is arrestment behavior followed by increased searching intensity [28, 31, 32, 46]. These cues are not directly related to the host eggs, but because of finely tuned adaptations of the parasitoid, these cues may become quite reliable. In fact, although responding to the "footprints" of both males and females of the host species, *Tr. basalis* and *Tr. brochymenae* are able to discriminate host adult sex and

the physiological conditions of host adults (e.g., virgin versus mated females) [28, 31, 47, 48]. Interestingly, in addition to chemical footprints, *Te. podisi* also uses vibratory signals mediating sexual behavior of the host species, *E. heros* [49].

Short-range host location is the next and final step, and female wasps may use visual cues at this point or short-distance kairomones directly related to the host to finally reach the target egg. The presence of volatiles from *M. histrionica* eggs is detectable by *Tr. brochymenae* whereas, in this species, visual cues do not appear to play an important role [28] (Table 1). When a host egg mass is encountered, host recognition by *Trissolcus* species is elicited by contact kairomones present on the egg surface, although physical factors such as shape and size may also affect wasp behavior [28, 50, 51] (Table 1). Short-range physical and chemical stimuli from the plant and host egg are also exploited by *A. iole* to locate and recognize *L. hesperus* eggs embedded in plant tissue [52–54].

3. Long-Range Kairomones from Nontarget Instars of the Host

As mentioned above, a well-known solution for the egg parasitoids to overcome the low detectability of host egg cues is to eavesdrop on the pheromonal communication (sex and other attractant pheromones), or the allomonal defenses, of nontarget stages of their hosts. This strategy was initially studied for egg parasitoids of Lepidoptera (reviewed by Fatouros et al. [13]; Colazza et al. [14]), but several cases are also known under laboratory and field conditions for species associated with Heteroptera (Table 1).

In early laboratory experiments using Y-tube olfactometers, *Tr. basalis* was found to be attracted by volatiles from adults of *N. viridula* [55]. A subsequent study revealed that (*E*)-2-decenal, a component of the defensive secretion from the metathoracic scent gland of *N. viridula*, is responsible for this dose-dependent attraction [30]. More recently, both *Tr. basalis* and *Te. podisi* were found to be attracted to and increase their searching behavior in the presence of defensive compounds from metathoracic scent gland secretions of their hosts, *N. viridula* and *E. heros* [33]. *Trissolcus basalis* showed a significant preference for (*E*)-2-decenal and 4-oxo-(*E*)-2-hexenal, while *Te. podisi* responded positively to (*E*)-2-hexenal and 4-oxo-(*E*)-2-hexenal [33]. In addition to volatiles from metathoracic glands, those from the dorsal abdominal glands of nymphs also appear to be exploited as kairomones by *Tr. basalis*, but nymphal secretions may be attractive at intermediate range rather than long range [39].

Detailed investigations of *Tr. basalis* responses to volatiles from both sexes of *N. viridula* showed that the female egg parasitoid is attracted to the males and to preovipositional females, whereas it is not attracted to virgin females [31]. When males and preovipositional females were assayed in a two-choice test, the parasitoid preferred females [31]. Similar results were obtained in a Y-tube olfactometer with *Tr. brochymenae*, as this parasitoid was attracted by cues from differing stages (eggs, nymphs, and adults) and sexes but showed significant preference for gravid females when compared to males [28]. Therefore, volatile allomones and sex pheromones from host males can direct female wasps toward host aggregates, whereas volatiles from gravid females act hierarchically on a subsequent step, representing a more reliable indicator of the potential presence of host eggs [28, 31].

The generalist egg parasitoid, *Ooencyrtus telenomicida* (Vassiliev) (Encyrtidae), is attracted in Y-tube olfactometer to odors of virgin male and, less intensely, of mated *N. viridula* females in preovipositional state, suggesting that the parasitoid exploits the host male-produced attractant pheromone [38]. When exposed to tomato plants treated with *N. viridula* or untreated control plants, *O. telenomicida* females did not respond to healthy or damaged plants, but only to plants with adult bugs, indicating that active volatiles originate from the host rather than the plant [38]. Field experiments confirm parasitoid attraction towards host adults. Traps baited with the synthetic attractant pheromone of male *Riptortus clavatus* (Thunberg) (Alydidae) captured females of the encyrtid egg parasitoid *Ooencyrtus nezarae* Ishii [34]. Males of *R. clavatus* emit an aggregation pheromone, composed of a blend of three compounds that attract adults of both sexes and nymphs. One compound, (*E*)-2-hexenyl (*Z*)-3-hexenoate, attracts females of *O. nezarae* and resulted in higher parasitism in treated fields compared with untreated fields [35, 36]. This tiny parasitoid has the remarkable ability to fly just above the plant canopy in nonhost habitat, while exploiting the above cues to reach the host habitat [37], although the exact flight mechanisms are unknown. In a different system, the use of traps baited with live adult *Leptoglossus australis* F. (Coreidae) resulted in increased parasitism efficacy by *Gryon pennsylvanicum* (Ashmead) (Platygastridae) [56].

Field confirmation of egg parasitoid response to the attractant pheromone of *P. maculiventris* [2] was also achieved [3]. The phoretic females of *Te. calvus* Johnson parasitized significantly more host eggs in pheromone-baited versus nonbaited traps, whereas the generalist *Te. podisi* did not show any significant differences. As described earlier, *Te. calvus* females exploit the male attractant pheromone of *P. maculiventris* to locate females during mating and then become phoretic on mated female bugs [2, 3].

4. Plant Synomones Induced by Feeding or Oviposition

Host-induced plant synomones are reliable and readily available cues for foraging parasitoids that attack feeding stages of hosts [8, 57, 58]. Egg parasitoids may respond to plant synomones induced by feeding [22, 41, 43]. However, not only feeding but also oviposition by herbivores induces emission of plant compounds acting as synomones between the primary and tertiary trophic levels towards their respective egg parasitoids [18–22, 59–65] (Table 1).

Each of the above systems has unique characteristics *vis-à-vis* induced plant defenses. Important differences are the cause of induction (i.e., oviposition, feeding, or a combination of the two, i.e., direct versus indirect cues),

the type of oviposition (i.e., exposed or embedded), and the relationship between egg and plant (i.e., magnitude of synomone emission, local or systemic emission, and activity range of synomone). Other important differences involve timing of synomone release (often reliably related to host suitability), the elicitor source, and, if known, the chemistry of the induced synomone.

4.1. Egg Parasitoid Exploitation of Feeding-Induced Synomones.

Feeding likely induces higher synomone levels than does egg deposition. Regardless, exploitation of such indirect host-related cues seems to have evolved because it allows parasitoids to minimize the searching area, thus maximizing efficiency.

Tritrophic plant/bug/egg parasitoid systems involving Heteroptera have been described for *Glycine max* and *Cajanus cajan* (Leguminosae)/*E. heros*/*Te. Podisi*/[41, 42, 66]; *Brassica oleracea* (Cruciferae)/*M. histrionica*/*Tr. brochymenae* (including oviposition-induced synomones) [22, 62, 63]; *Gossypium hirsutum* (Malvaceae) and other plants/*L. hesperus*/*A. iole* [43].

In olfactometer tests, *Te. podisi* responded to volatiles from soybean and pigeon pea fed upon by adults and nymphs of *E. heros* [41]. Application of *cis*-jasmone elicited a similar volatile profile from soybean plants after 96 hours with quantitative, rather than qualitative, chemical differences and resulted in the concomitant attraction of egg parasitoids [66]. Remarkably, when resistant versus susceptible soybean cultivars were compared, parasitoids were only attracted to resistant cultivars; volatile profiles in damaged plants differed between cultivars. In addition, volatiles from oviposition-damaged plants did not attract *Te. podisi* females [42].

Trissolcus brochymenae females' response to plant volatiles induced by host feeding is different than that of *Te. podisi* females. What is known for the former parasitoid indicates that females mainly exploit plant compounds systemically induced by a combination of oviposition, feeding punctures, and footprints of its host, *M. histrionica*, to elicit host searching. Nevertheless, failure to actually oviposit by the host still induces emission of leaf-surface volatiles but, in such cases, parasitoid response was observed only on the damaged leaves [22]. These types of cues appear less reliable compared with oviposition-induced cues, and would act hierarchically at a lower level than other semiochemical cues.

Olfactometer research with *Anaphes iole* Girault (Mymaridae) demonstrated that this species of egg parasitoid also employs volatiles from cotton and other herbaceous plants infested by adults of its host, *L. hesperus* [43]. Eggs of *Lygus* spp. are embedded through an incision made with the ovipositor in plant tissue, with only the operculum exposed, and compounds from these wounds elicit parasitoid behavioral responses even if no eggs have been laid [52, 53]. Both oviposition and feeding damage cause volatiles to be emitted from cotton plants although oviposition appears to induce release of constitutive terpenes from specific glands in cotton leaves adjacent to the oviposition incision, whereas feeding resulted in systemic induction of different volatiles

[67]. The volatile blend induced by *L. hesperus* salivary gland extracts is similar to that induced by volicitin, an elicitor isolated from the regurgitant of moth larvae [68], although chemical analyses of the salivary glands from *Lygus* spp. have shown no evidence of a volicitin-type of fatty acid-amino acid conjugate [67]. In electroantennogram (EAG) assays, *A. iole* responded to the majority of herbivore-induced plant volatiles tested, but most intensely to (Z)-3-hexenyl acetate, and methyl salicylate; females responded more than males [44]. Olfactometer and wind tunnel bioassays showed that the female wasps were positively stimulated by (Z)-3-hexenyl acetate, methyl salicylate and α-farnesene, although response to (Z)-3-hexenyl acetate was exhibited only after preconditioning females to blends of host-plant odors. In field trials, host eggs baited with α-farnesene and (Z)-3-hexenyl acetate were more heavily parasitized than were untreated eggs [44].

4.2. Egg Parasitoid Exploitation of Oviposition-Induced Synomones.

Oviposition-induced synomones, which are directly related to the target stage, are highly reliable and detectable for egg parasitoids. Herbivore oviposition induces emission of plant compounds that act as synomones towards a variety of egg parasitoids [18–22, 59–65]. This "early herbivore alert" [69] by the plant denotes a particular type of indirect induced defense, which, among parasitoids of Heteroptera, has been observed in two tritrophic systems: *Vicia faba* and *Phaseolus vulgaris* (Leguminosae)/*N. viridula*/*Tr. basalis* [20, 21] and, *Brassica oleracea* (Cruciferae)/*M. histrionica*/*Tr. brochymenae* [22, 62, 63] (Table 1).

In the Heteroptera, the first case of plant volatile induction by a bug gluing eggs on leaves without causing mechanical damage is that of *Nezara viridula* ovipositing on legumes [20]. *Trissolcus basalis* was attracted by oviposition-induced volatiles in an olfactometer, and the volatile emission was systemic (i.e., from damaged and adjacent undamaged leaves) [20]. By maximizing the release surface, the plant may have evolved to increase synomone volatilization, thereby increasing herbivores apparency to egg parasitoids. Over time, synomone activity seems to be finely tuned to parasitoid behavior and biology since the attraction fades when host eggs are near to eclosion. Oviposition by *N. viridula* females on *Vicia faba* L. and *Phaseolus vulgaris* L., combined with feeding punctures, induced release of (E)-β-caryophyllene, as well as two other sesquiterpenes. Only the fraction containing (E)-β-caryophyllene attracted *Tr. basalis* [21]. Whether the elicitor originates from the eggs, follicular tissue, or elsewhere is unknown; however, the combined presence of feeding punctures is necessary for synomone induction [21].

The other known case of an oviposition-induced synomone for an egg parasitoid of true bugs is quite different from the one just described because the induced compounds act at a very short distance. *Tr. brochymenae* perceives the induced synomone only when it alights on a damaged plant [22, 62]. Compared to healthy plants, females of this parasitoid intensely antennated and searched on leaves having a host egg mass, plus nearby feeding punctures and

chemical footprints (treated surface). Parasitoid response was tested on the upper (adaxial) leaf surface, opposite to the treated (abaxial) surface. Female wasps also responded in a static olfactometer at near contact range to volatiles perceived through olfaction, but host-damaged plants in a Y-tube olfactometer were not attractive to wasps. As with *N. viridula* on leguminous plants, the induction is both local and systemic, but the origin of the elicitor and the mechanisms involved remain unknown. However, in the case of *M. histrionica* on cabbage, egg mass deposition is sufficient, as are feeding punctures, to elicit parasitoid response, although the combination of oviposition, feeding, and footprints increases parasitoid response [22]. Parasitoid reaction to compounds emitted as a consequence of host feeding appears to be a response to damaged host plants [22]; leaves with feeding punctures exhibit alteration of tissues and photosynthesis [70].

5. Short-Range Kairomones from Nontarget Host Stages

Indirect host-related cues originate from adults or juveniles of the host and, in general, elicit arrestment and searching behavior in the parasitoid. Trichogrammatidae and Platygastridae species responses to lepidopteran moth scales were studied earlier (reviewed by Colazza et al. [14]). However, a comparable strategy was also discovered for the heteropteran egg parasitoids, *Trissolcus* spp. [28, 31, 32, 71] *Te. podisi* [46], and *Gryon boselli* Mineo & Szabo (Colazza, Lo Bue, and Cusimano, personal observation), which respond to chemical footprints of pentatomid bugs (Table 1). Both *Tr. basalis* and *Tr. brochymenae* females are able to discriminate chemical footprints left by host females, to which they respond more strongly than to chemical traces left by walking males or nymphs [28, 31, 47, 72]. In addition, *Tr. brochymenae* is able to detect cues from mated females in the preovipositional state, which are preferred to virgin females and parous females (i.e., those that have already produced offspring), thus finely tuning their searching to the host stage most likely to lead to host eggs [47]. This preference was strictly related to the transfer of sperm and associated substances from the conspecific male bug to the female during copulation. The compounds mediating arrestment of *Tr. brochymenae* females are from host cuticle, and those that play a role as gender-specific cues are most abundant on the legs of the host adult [47].

Associative learning plays an important role in host footprint recognition behavior. Oviposition experience increased the arrestment response of *Tr. basalis* females to footprints of *N. viridula* females, whereas prior experience not followed by oviposition led to the gradual fading of the learned behavior [25]. In contrast, previous experience with the footprints of host males did not result in a change of parasitoid response, indicating that residues from males only provide general information for the parasitoid, which is not directly associated with host eggs [25]. There is significant variation in the learning ability of *Tr. basalis* females as a function

of environment and spatial distribution, but learning always helps make foraging more successful [26].

Footprint chemistry was investigated in the *Tr. Basalis-N. viridula* relationship. Analysis of extracts of cuticular lipids from *N. viridula* revealed the presence of normal alkanes, with quantitative and qualitative differences between the sexes. One compound, *n*-nonadecane, was recovered only from the cuticle and footprints of males. When added to cuticular extracts of *N. viridula* females, *n*-nonadecane caused *Tr. basalis* females to significantly reduce their residence time in the arena, similar to the behavior of female wasps in the presence of hexane extracts of male hosts [72]. Parasitoid response to host footprints is mediated by adsorption of the contact kairomone in the epicuticular wax layer of plants walked upon by host bugs [48, 73].

6. Short-Range and Contact Kairomones from Host Eggs

Semiochemicals from or on host eggs are likely present in faint amounts and, thus, are probably exploited by egg parasitoids only at close range or upon contact. Short-range and contact kairomones are best known for egg parasitoids of Lepidoptera [14]. Among the Heteroptera, this semiochemical level has been investigated for the egg parasitoid of the harlequin bug (*M. histrionica*), *T. brochymenae*, in both a Y-tube olfactometer and an open arena. In the olfactometer the *T. brochymenae* females were attracted to volatiles from host egg masses, whereas, in the open arena, the female parasitoids oriented towards egg clusters or dummies treated with chemical extract of host eggs. When the egg extract was applied without dummies, it elicited the same response, whereas dummies without extract did not influence parasitoid behavior, indicating that visual factors are unnecessary for this last step in host location [28] (Table 1).

Parasitoid host recognition to egg contact kairomones is much more obvious than are responses to egg volatiles (Table 1). When in contact with the heteropteran host egg mass, *Trissolcus* spp. use both physical and chemical cues; egg size and the shape are important cues, but chemicals on the egg surface are fundamental for host acceptance [50]. The recognition kairomones are contained in the adhesive secretion from the follicular cells of heteropteran hosts [28, 50, 51], composed of mucopolysaccharide-protein conjugants [50], but their chemical nature has not been defined yet. Surprisingly, (*E*)-2-decenal, a component of the defensive secretion from the metathoracic scent gland of *N. viridula* that was attractive to *Tr. basalis* in an olfactometer, also elicited parasitoid antennation and ovipositor probing of egg-sized glass beads [30].

When host eggs are embedded in plant tissue, semiochemicals may originate from the egg, the damaged plant, or from their interaction. Females of the mymarid, *Anaphes iole*, respond to *Lygus* eggs inserted into plant tissue with arrestment, increased antennation, and ovipositor probing even if oviposition wounds do not contain eggs, although probing is much more intense if the incision contains a host

egg. Artificial wounds are also probed by the parasitoid, and so are eggs removed from the substrate and placed on a surface [52, 53]. Although chemical cues appear to play a major role, physical cues are also important in this phase; *A. iole* females adopt a probing posture when chemicals from host or plants are combined with appropriate shapes [52–54]. Electroantennogram assays showed that the parasitoid antennae sense several plant volatiles, including green leaf volatiles, confirming the importance of plant chemicals during host searching in this species [44]. Ovipositor probing behavior is the final step of host searching by *A. iole*, rather than merely host recognition; perhaps this explains why these mymarid females insert their ovipositor, although less frequently, even in artificial wounds made in a parafilm substrate containing neither host eggs nor contaminated by host material [52]. Moreover, learning host and plant cues increases *A. iole* oviposition efficiency [53]; indeed, a preference for (*Z*)-3-hexenyl acetate occurs only after preconditioning with host-induced plant volatiles [44].

7. Conclusions

The importance of egg parasitoids as biological control agents for herbivorous insect pests is widely recognized. Nevertheless, their success in classical biological control programs is slightly lower than that for other kinds of introduced parasitoid species [74]. Several Mymaridae and Platygastridae species have been used for augmentative biological control of Heteroptera [74], the most successful of which involved releases of *Tr. basalis* against *N. viridula* on soybean in Brazil [75, 76].

While several egg parasitoids of Heteroptera are potentially effective biological control agents, there are still constraints preventing the realization of this goal. Incomplete behavioral and ecological knowledge for most parasitoid species remains problematic and, perhaps most importantly, mass production of egg parasitoids remains inefficient [77–79]. Understanding the host selection strategies of egg parasitoids and the chemical stimuli involved could lead to improved biological control efficacy through behavioral manipulation of egg parasitoids in the field and to development of better *in vivo* and *in vitro* rearing methods. An estimated 16 million ha of cropland worldwide currently receives inundative releases of egg parasitoids, primarily involving species in the genus *Trichogramma* [77]. Efficient mass rearing of *Trichogramma* spp., as well as intensive, focused research preceded this achievement, including elucidation of the chemicals necessary for acceptance of artificial host media and the parasitoid development [79]. The success of *Trichogramma* biocontrol programs is a model of what may be achieved with other parasitoids given the required research investment.

Successful implementation of egg parasitoids against true bugs will depend on judicious applications of synthetic semiochemicals, particularly synomones and kairomones, and appropriate strategies to overcome existing constraints, including treatments facilitating parasitoid rearing, conditioning, and manipulation [61, 74, 80, 81]. Other interesting possibilities include the development of plants with elevated expression of indirect induced resistance factors (i.e., the induction of plant synomones exploited by the herbivores' parasitoids) or spraying fields with resistance elicitors [61]. Accurate knowledge of parasitoid chemical ecology will be important in all phases of biocontrol and integrated pest management [82]; important elements toward implementation include procedures for selection of egg parasitoids, evaluation of their specificity [27, 32, 71], risk assessment of new introductions [83], release methods [80], and quality control [80, 84]. Implementation of knowledge gleaned from laboratory studies must finally be scaled up and transferred to growers.

Acknowledgments

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