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Review

Foraging behavior of egg parasitoids exploiting chemical information

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Female parasitic wasps seek hosts for their offspring often in a dynamic environment. Foraging egg parasitoids rely on a variety of chemical cues originating from the adult host, host products, or the host plant rather than from the attacked host stage—the insect egg itself. Besides pupae, insect eggs are the most inconspicuous host stage attacked by parasitic wasps. To overcome the problem of low detectability of host eggs, egg parasitoids have evolved several strategies such as exploiting long-range kairomones of the adult hosts, for example, host aggregation and sex pheromones, plant synomones induced by egg deposition or host feeding, or short-range contact cues derived from the adult host or the host plant. Moreover, egg parasitoids have evolved the ability to use chemical espionage in combination with hitchhiking on the adult host (phoresy) to compensate their limited flight capability and to gain access to freshly laid host eggs. Here, we provide a comprehensive overview on the variety of host-foraging strategies of egg parasitoids exploiting chemical signals. Furthermore, the use of such infochemicals is discussed with respect to the wasps' dietary breadth and their ability to learn. *Key words:* egg parasitoids, host-foraging behavior, infochemicals, kairomones, phoresy, plant synomones, sex pheromones. *[Behav Ecol 19:677–689 (2008)]*

Egg parasitoids are specialized to develop in the eggs of other insects. Insect eggs are nutrient-rich enlarged cells that do not feed and release feces and consequently lack intense long-range odors that can be exploited by their enemies. Additionally, many insect eggs develop rapidly, except when they enter diapause, from a nutrition source to a complex embryo and might therefore be present only for 2–3 days (Hinton 1981). Many eggs are well protected physically and/or chemically (Hilker and Meiners 2002a) because of their immobility and exposure to enemies and environmental influences. Some insects make their eggs less accessible by hiding them in plant tissue or by covering them with physical devices like hairs, feces, scales, or secretion (Hinton 1981; Hilker 1994; Blum and Hilker 2002). Maternally incorporated or applied toxins provide protection against enemies (Hilker and Meiners 1999; Blum and Hilker 2002; Bezzerides et al. 2004). Furthermore, insect host eggs are able to enhance transcription of some immune-related genes in response to parasitism (Abdel-latief and Hilker 2008). Consequently, egg parasitoids have to face many challenges when searching and finding their small and inconspicuous hosts.

Female parasitoids are forced to optimize their host-selection behavior because it is directly linked to their reproductive success: the host is the only food source for their offspring (Alphen van and Vet 1986). The parasitoids' searching behavior can be divided into several phases (i.e., host habitat location, host location, and host acceptance), which are completed with the oviposition in or on the host. This so-called host selection is mediated by numerous stimuli, of which chemicals are known to play a major role (Vinson 1976). Our review focuses on chemical cues used by egg parasitoids in the initial 2 stages of their host-selection behavior before host contact takes place, that is, long-range and short-range host location. Habitat location is generally mediated by long-range cues, such as plant volatiles or herbivore pheromones perceived by olfaction, whereas cues used in the closer vicinity are mostly short-range cues of herbivore products or of the plant surface often perceived by gustatory receptors.

Vet and Dicke (1992) stated that herbivore-foraging carnivores face a reliability-detectability problem: infochemicals (sensu Dicke and Sabelis 1988; see Glossary) provided by the herbivore itself are reliable indicators of the herbivore's presence, but their detectability is low due to 1) the small biomass of the herbivore relative to that of their host plant and 2) selection on the host to minimize the emission. On the other hand, plant-derived stimuli are supposed to be more detectable because they are available in larger quantities and emitted over larger distances although they are not necessarily reliable indicators of the presence of the host (Vet and Dicke 1992). It was assumed that the evolution of host location is restricted by this reliability-detectability problem of prey/host-derived infochemicals (Vet and Dicke 1992). The authors proposed 3 solutions to this problem, namely i) using infochemicals produced by the adult host stage, such as pheromones to locate eggs or larvae of the herbivore (termed infochemical detour), ii) using plant volatiles induced by host feeding (termed herbivore-induced synomones or herbivore-induced plant volatiles), or iii) linking detectable cues with reliable, host-derived cues through associative learning.

From an egg parasitoids' point of view, plant volatiles induced by host feeding are indicating the presence of the host but not

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necessarily the presence of host eggs (coined "infochemical detour" by Vet and Dicke 1992). However, a new example of solution (ii) is available: egg parasitoids were recently shown to use plant volatiles induced by egg deposition (Meiners and Hilker 1997, 2000; Hilker et al. 2002; for reviews, see Hilker and Meiners 2002b, 2006; Colazza, Fucarino, et al. 2004; Mumm and Hilker 2005, 2006). These oviposition-induced plant cues were shown in laboratory bioassays to attract egg parasitoids, whereas feeding-induced plant volatiles did not elicit any behavioral response by the parasitoids. Thus, oviposition-induced cues are expected to be a more reliable solution for these egg parasitoids than plant cues induced by host feeding.

This review covers the diverse foraging behavior of egg parasitoids with respect to the use of chemical signals and outlines adaptive strategies that egg parasitoids employ to find their hosts. We divided the signals roughly into either category long-range and short-range infochemicals. However, some cues might not fit into the 2 categories because they are intermediate or perceived both over short and long distances.

LONG-RANGE INFOCHEMICALS

Plant cues

When an adult egg parasitoid emerges from its host's egg, it may find itself in a habitat where in most cases the host population or the proper host stage is not present anymore. Consequently, egg parasitoids need to have an innate repertoire of responses to cues associated with the host habitat. Salt (1935) stated that most parasitoids are first attracted to a certain type of environment and then to a particular host. Vinson (1981) lists factors involved in habitat location such as sound, visual cues, forms of electromagnetic radiation, and volatile chemicals. Especially, plant volatiles may guide egg parasitoids to the habitat of their herbivorous hosts (Weseloh 1981; Vinson 1991; Steidle and van Loon 2002). In general, infochemicals used by egg parasitoids for host habitat location usually arise from sources associated with or connected to the host stage attacked rather than from the host egg itself.

Volatiles from undamaged plants

A number of studies have shown *Trichogramma* spp. to respond to volatiles derived from undamaged plants or plant extracts (e.g., Bar et al. 1979; Altieri et al. 1982; Nordlund et al. 1985; Kaiser et al. 1989; Boo and Yang 1998; Reddy et al. 2002; Romeis et al. 2005) (Table 1). However, it seems that *Trichogramma* wasps and other egg parasitoids are generally arrested by plant volatiles after entering a habitat rather than attracted from a distance (Romeis et al. 1997). Due to their minute size, egg parasitoids like *Trichogramma* spp. are known to disperse passively by wind drifts rather than to fly directly to an odor source (Noldus, van Lenteren,

Table 1
Response to plant cues

Egg parasitoid	Host	Source	Response	Reference
Scelionidae				
Trissolcus basalis	*Nezara viridula*	Bean: infested with host adults and 3- to 4-d-old eggs	Attraction	Colazza, Fucarino, et al. (2004) and Colazza, McElfresh, and Millar (2004)
Telenomus podisi	*Euschistus heros*	Two legume species: infested with host adults and/or nymphs	Attraction	Moraes et al. (2005)
Eulophidae				
Chrysonotomyia ruforum	*Diprion pini*	Pine: infested with 3-d-old host egg masses	Arrestment	Hilker et al. (2002, 2005)
Oomyzus gallerucae	*Xanthogaleruca luteola*	Elm: infested with 3-h to 5-d-old host egg masses	Arrestment	Meiners and Hilker (1997, 2000)
Trichogrammatidae				
Trichogramma semifumatum	*Heliothis armigera*	Tomato: plants infested with host eggs	Increased parasitism in the field	Bar et al. (1979)
Trichogramma chilonis	*Helicoverpa armigera*	Sorghum and pigeon pea: uninfested plants	Arrestment	Romeis et al. (1997)
	Helicoverpa assulta	Hot pepper: uninfested plants	Arrestment	Boo and Yang (1998)
	Plutella xylostella	Cabbage: synthetic green leaf volatiles	Attraction	Reddy et al. (2002)
Trichogramma brassicae (or *Trichogramma maidis*)	*Pieris brassicae*	Brussels sprouts: leaves infested with 3-d-old egg clutches	Arrestment	Fatouros, Bukovinszkine'Kiss, et al. (2005)
	Ostrinia nubilalis	Maize: extracts in combination with the synthetic host pheromone and host eggs	Arrestment	Kaiser et al. (1989)
Trichogramma pretiosum	*Ephestia kuehniella*	Weed: extracts	Increased parasitism	Altieri et al. (1982)
	Spodoptera frugiperda	Cotton: leaves infested with host caterpillars	Attraction	Laumann et al. (2004)
	Heliothis zea	Tomato: plant extracts	Increased parasitism	Nordlund et al. (1985)
Myrmaridae				
Anagrus nilaparvatae	*Nilaparvata lugens*	Rice: host damaged plants	Attraction	Lou et al. (2005)
Anaphes iole	*Lygus Hesperus*	Various plants: host feeding (+/−egg deposition)	Attraction	Manrique et al. (2005)

and Lewis 1991). Wind speeds in the open field make directed upwind flight for *Trichogramma* impossible, which was also demonstrated in wind tunnel experiments (Keller et al. 1985; Noldus, van Lenteren, and Lewis 1991). Yet, within the vegetation either close to soil or within the canopy effects of wind might be different from those in open areas (reviewed by Murlis et al. 1992). Under low wind conditions, *Trichogramma* spp. were shown to disperse in all directions almost uniformly (see Fournier and Boivin 2000 and references therein). The eulophid egg parasitoid *Oomyzus gallerucae* can be attracted by a synthetic plant compound to freestanding sticky traps (Meiners T, unpublished data). This indicates the capability of egg parasitoids to actively orientate in the field toward an odor source.

Herbivore-induced plant volatiles

Various studies have demonstrated that plants respond to feeding herbivores by induction of volatiles that attract the enemies of the herbivores (reviewed by Dicke et al. 1990; Dicke and Vet 1999; Dicke and van Loon 2000; Turlings et al. 2002). However, plants can respond to insect oviposition by changing their release of volatiles prior to feeding damage by larvae. Meiners and Hilker (1997, 2000) were the first to demonstrate such "early alert": oviposition by the elm leaf beetle *Xanthogaleruca luteola* induces the field elm (*Ulmus minor*) to produce volatiles that attract the egg parasitoid *O. gallerucae*. At the site of egg deposition, the elm leaf beetle removes the epidermis of the leaf before laying eggs. However, the removal of plant epidermal tissue per se does not induce the volatiles attracting *O. gallerucae* nor do the eggs release attractants, nor does a combination of egg odor and plant volatiles attract the egg parasitoids. In fact, the egg deposition induces the release of volatiles from elm leaves. Nevertheless, the removal of plant tissue is required for the volatile induction, as no attractive volatiles are emitted when eggs are transferred to intact leaves.

Similar results were found in another tritrophic system where the eulophid egg parasitoid, *Chrysonotomyia ruforum*, is attracted by volatiles of Scots pine (*Pinus sylvestris*) induced by eggs of the sawfly *Diprion pini* (Hilker et al. 2002; Mumm and Hilker 2005). The sawfly does not only remove the plant epidermis when ovipositing but also slit the pine needle longitudinally to insert eggs in a row.

In both the elm and the pine system, a specific response by specialized egg parasitoids toward egg-infested plants was demonstrated: neither the eggs alone nor the artificially damaged plants mimicking the oviposition-associated wounding were arresting the egg parasitoids. The plant responses were both local and systemic: egg-laden plant parts as well as uninfested plant parts near parts with eggs emitted attractive volatiles (Meiners and Hilker 2000; Hilker et al. 2002, 2005).

Further studies showed that in some plant species not only egg deposition but also feeding of the adults is necessary to induce volatiles attracting egg parasitoids (Colazza, Fucarino, et al. 2004; Colazza, McElfresh, and Millar 2004) (Table 1). Colazza, Fucarino, et al. (2004) revealed that a generalist egg parasitoid, *Trissolcus basalis*, responds to plant synomones emitted by 2 different bean species (*Vicia faba* and *Phaeseolus vulgaris*) that are induced by the pentatomid bug *Nezara viridula*. Attraction took place only when egg deposition occurred together with plant damage, in this case feeding activity of *N. viridula*. However, the eggs were laid on the undamaged plant part. Thus, also annual plants can produce egg parasitoid–attracting synomones induced by insect egg depositions.

Also feeding damage of a plant alone (without egg deposition) can induce volatiles attracting egg parasitoids (Lou et al. 2005; Manrique et al. 2005; Moraes et al. 2005) (Table 1). Lou et al. (2005) suggested that the egg parasitoid's response to feeding-induced volatiles can be adaptive, for example, when all developmental stages co-occur on the same plant and an indirect association of feeding host adults or nymphs with egg presence provides a reliable cue.

Host cues

Within a (micro)habitat, egg parasitoids are able to distinguish infested from uninfested areas. This phase of their foraging behavior can be mediated by cues originating from adult host insects. Spying on the host communication system seems a common strategy in predatory and parasitic arthropods (Vinson 1984; Stowe et al. 1995; Rutledge 1996; Zuk and Kolluru 1998). Several signaling modalities, including acoustic, visual, and olfactory information channels, are known to be exploited. Cues used for intraspecific communication are often host specific and thus provide reliable information for eavesdropping enemies. Furthermore, they are often volatile pheromonal signals and can therefore be detected over long distances. Eavesdropping on such pheromones is effective for parasitoids only when indicating the presence of the preferred host stage (e.g., Jones et al. 1973; Vinson 1976; Weseloh 1981; Godfray 1994; Nordlund 1994; Hilker and Meiners 1999; Steidle and van Loon 2002) (Table 2).

Exploitation of sex pheromones

The use of volatile host pheromones by egg parasitoids was shown for the first time by Lewis et al. (1982) in studies with *Trichogramma pretiosum*. Volatiles of the abdominal tips of female *Heliothis zea* moths as well as synthetic chemicals identified as the sex pheromone of *H. zea* females (hexadecanal, (*Z*)-7-hexadecenal, (*Z*)-9-hexadecenal, and (*Z*)-11-hexadecenal) increased parasitization rates by *T. pretiosum*. Later, follow-up studies verified that *T. pretiosum* responds to calling *H. zea* females (Noldus 1988). Since then, more and more studies demonstrate chemical espionage by egg parasitoids of sex pheromones of moths (e.g., Lewis et al. 1982; Nordlund et al. 1983; Noldus 1988; Noldus et al. 1990; Noldus, van Lenteren, and Lewis 1991; Frenoy et al. 1992; Arakaki et al. 1996, 1997; Colazza et al. 1997; Boo and Yang 2000; Reddy et al. 2002; Schöller and Prozell 2002; Fiaboe et al. 2003) or sawflies (Hilker et al. 2000) (Table 2). Powell (1999) gives a detailed overview on the responses of egg parasitoids to sex pheromones from lepidopteran hosts.

However, a response of egg parasitoids to calling virgin female moths does not necessarily mean a response to the host sex pheromone. In some cases, the sex pheromone blend or main compounds of the virgin moths elicited no response in the tested *Trichogramma* spp. (Noldus and van Lenteren 1985a; Noldus et al. 1990; Frenoy et al. 1992; Renou et al. 1992). Here, the kairomone seems to be a compound associated with pheromone production rather than the pheromone itself.

Some authors suggest that a synergism between host plant and host sex pheromone may act as a "bridge in time" for the chemical spies. Noldus, Potting, and Barendregt (1991) showed that the sex pheromone of the female moth *Mamestra brassicae* adsorbs onto the leaf surface of cabbage plants to such an extent that foliage exposed to the pheromone attracts conspecific male moths and simultaneously arrested *Trichogramma evanescens* females. This could be a common phenomenon because many hosts of which sex pheromones are exploited by a diurnal egg parasitoid are nocturnal moths and the pheromone compounds are all long-chain fatty acid derivatives with similar chemical properties that easily allow adsorbance to plant surfaces.

Arakaki et al. (1996) showed that *Telenomus euproctidis* is attracted to the sex pheromone [(*Z*)-16-methyl-9-heptadecenyl

Table 2
Response to volatile kairomones of adult hosts

Egg parasitoid	Host	Source	Response	Reference
Scelionidae				
Trissolcus brochymenae	*Murgantia histrionica*	Males and females	Attraction	Conti et al. (2003, 2004)
Trissolcus simoni	*Eurydema ventrale* *Nezara viridula*			
Trissolcus basalis	*N. viridula*	Mated females in a "preovipositional state" Virgin males Defensive metathoracic gland scent	Attraction	Mattiacci et al. (1993), Colazza et al. (1999), and Salerno et al. (2006)
Trissolcus utahensis	*Euschistus conspersus*	Synthetic aggregation pheromone	Attraction in the field	Krupke and Brunner (2003)
Telenomus remus	*Spodoptera frugiperda*	Virgin female abdominal tips	Attraction	Nordlund et al. (1983)
		Synthetic sex pheromone	Increased parasitism rates	
Telenomus euproctidis	*Euproctidis taiwana*	Virgin females	Attraction in the field Phoresy	Arakaki et al. (1996)
Telenomus calvus	*Podisus maculiventris*	Males	Attraction in the field	Bruni et al. (2000)
		Synthetic aggregation pheromone Mated females	Phoresy	Aldrich et al. (1984) and Aldrich (1995)
Telenomus isis	*Sesamia calamistis*	Calling virgin females	Arrestment	Fiaboe et al. (2003)
Telenomus busseolae	*Sesamia nonagrioides*	Calling virgin females	Attraction	Colazza et al. (1997)
	Sesamia calamistis	Calling virgin females	Arrestment	Fiaboe et al. (2003)
Gyron pennsylvanicum	*Leptoglosssus australis*	Males	Attraction in the field Increased parasitism	Yasuda and Tsurumachi (1995) and Yasuda (1998)
Eulophidae				
Chrysonotomyia ruforum	*Diprion pini* *Neodiprion sertifer*	Synthetic sex pheromone	Arrestment	Hilker et al. (2000)
Dipriocampe diprioni	*D. pini*			
Entodon leucogramma	*Scolytus multistriatus*	Synthetic aggregation pheromone	Attraction in the field	Kennedy (1984)
Encyrtidae				
Ooencyrtus nezarae	*Riptortus clavatus*	Synthetic aggregation pheromone of male bugs	Attraction in the field	Leal et al. (1995) and Mizutani (2006)
Ooencyrtus pityocampae	*Thaumetopoea pityocampa*	Virgin females	Attraction in the field	Battisti (1989)
Trichogrammatidae				
Lathromeris ovicida	*Sesamia calamistis*	Calling virgin females	Arrestment	Fiaboe et al. (2003)
Uscana lariophaga	*Callosobruchus maculates*	Virgin females	Attraction	van Huis et al. (1994)
Trichogramma evanescens	*Ephestia* spp. *Plodia interpunctella*	Synthetic sex pheromone	Arrestment	Schöller and Prozell (2002)
	Pectinophora gossypiella *Spodoptera littoralis* *Earias insulana*	Synthetic components of sex pheromone	Attraction	Zaki (1985)
Trichogramma brassicae (or *Trichogramma maidis*)	*Pieris brassicae*	Mated female butterflies Synthetic antisex pheromone	Arrestment Phoresy	Fatouros, Huigens et al. (2005)
	Ostrinia nubilalis	Calling virgin females	Attraction	Frenoy et al. (1992)
		No response to main sex pheromone component Eggs + pheromonal blend + maize extract		Kaiser et al. (1989)
	Lobesia botrana	Calling virgin females	Increase in movement Increased parasitism	Garnier-Geoffroy et al. (1999)
Trichogramma pretiosum	*Heliothis/Helicoverpa zea*	Abdominal tips	Increased parasitism	Lewis et al. (1982), Gross et al. (1984), and Noldus et al. (1990)
		Excretion and synthetic sex pheromone of virgin females	Arrestment	
		Calling virgin females	Arrestment	Noldus (1988)
	Plutella xylostella	Synthetic compound of sex pheromone	Increased parasitism	Klemm and Schmutterer (1993)
Trichogramma sibericum	*Rhodobota naevana*	Main component of sex pheromone	Increased searching time, arrestment	McGregor and Henderson (1998)
Trichogramma ostriniae	*Ostrinia furnacalis*	Mated female moths (before oviposition) Accessory glands of mated females	Attraction	Bai et al. (2004)
Trichogramma oleae	*Palpita unionalis*	Synthetic sex pheromone	Higher parasitization, attraction	Abdelgader and Mazomenos (2002)
	Prays pleae	Sex pheromone components	Attraction	Milonas et al. (2003)

Table 2, continued

Egg parasitoid	Host	Source	Response	Reference
Trichogramma evanescens	*Mamestra brassicae*	Calling virgin females	Arrestment	Noldus and van Lenteren (1985a), Noldus, Potting, and Barendregt (1991)
later		Host sex pheromone odor	Arrestment	
Trichogramma maidis (=*Trichogramma brassicae*)		No response to main sex pheromone component		
	P. brassicae	Virgin females in “mate-acceptance posture,” no sex pheromone known	Arrestment	Noldus and van Lenteren (1985a)
Trichogramma chilonis	*Helicoverpa assulta*	Sex pheromone of virgin moths	Arrestment	Boo and Yang (2000)
		Main component of sex pheromone		
	Plutella xylostella	Synthetic sex pheromone blend	Attraction	Reddy et al. (2002)
Trichogramma cordubensis	*Heliothis armigera* *Earias insulana*	Adult female moth	Attraction	Cited by Noldus (1989)
Trichogramma sp. *nr. buesi*	*Ephestia kuehniella*	Adult female moth	Attraction	Cited by Noldus (1989)

isobutyrate] of virgin tussock moths (*Euproctis taiwana*) before it mounts them, hiding in the anal tuft until the female moth starts laying her egg clutch. The phoretic wasps were still able to detect trace amounts of the host sex pheromone even 48 h after release, being retained on moth scale hairs at the anal tufts, thus employing another bridge-in-time strategy (Arakaki and Wakamura 2000).

Exploitation of antisex pheromones

For the first time, Fatouros, Huigens, et al. (2005) showed that an egg parasitoid (*Trichogramma brassicae*) exploits an antisex pheromone of its host, in this case the large cabbage white (*Pieris brassicae*). The antiaphrodisiac, benzyl cyanide, is transferred from *Pieris* males to females during mating to render the females less attractive to conspecific mates (Andersson et al. 2003). Mated host females were most attractive to the wasps; unlike in most other cases of chemical espionage where virgin females lured egg parasitoids. To examine the importance of the antiaphrodisiac for phoresy in *T. brassicae*, benzyl cyanide was applied onto virgin females. Indeed, the application of the antiaphrodisiac rendered the virgin females attractive to the wasps and stimulated them to mount their hosts. Flight chamber experiments demonstrated that the wasps were able to hitchhike on the butterflies until these landed on their host plant, then dismounted the host, and parasitized the freshly laid host eggs (Fatouros, Huigens, et al. 2005).

Other studies indicated an attraction of egg parasitoids to mated host females (Colazza et al. 1999; Conti et al. 2003; Bai et al. 2004). Bai et al. (2004) found that *Trichogramma ostriniae* responded positively to odor from gravid females of their host, the Asian corn borer (*Ostrinia furnacalis*). Virgin host females and mated host females after their first oviposition did not elicit any response. This specific response to gravid host females could indicate the presence of an antiaphrodisiac in the Asian corn borer. In *Pieris napi* butterflies, egg deposition is followed by a reduction in the titer of their antiaphrodisiac pheromone (Andersson et al. 2004). *Trichogramma ostriniae* might be attracted to just-mated but still oviposition naive host females because of their high pheromone titer. Host females that have already oviposited might have a lower antiaphrodisiac titer, which renders them less detectable to the parasitoids.

In sexually reproducing species, mated females might provide more reliable cues for host-searching egg parasitoids than virgin ones because mated ones are closer to egg deposition. The exploitation of antiaphrodisiacs or similar volatile pheromones of mated host females by egg parasitoids could be more widespread than so far assumed. Eavesdropping on the host’s sexual communication is supposed to be a stable strategy because the host is probably under strong selection pressure not to change the chemistry of its intraspecific signals. However, the detectability of sexual signals can be temporally restricted. Additionally, sexual host signals can be emitted far from oviposition sites, which limit the risk of host eggs to become exploited. Therefore, sexual host signals may be of limited reliability for egg parasitoids (Steidle and van Loon 2002). Unlike exploitation of antiaphrodisiacs of mated host females, exploiting the sex pheromone of virgin females does not ensure the egg parasitoid any access to host eggs because the host female still has to find a mate before it can oviposit. Except for phoretic egg parasitoids, many studies still show that the use of sexual signals can be beneficial for egg parasitoids: plants sprayed with synthetic pheromones arrest egg parasitoids, stimulate intensive searching behavior in these areas, and increase the probability to encounter host eggs resulting in high parasitism rates (Lewis et al. 1982; Nordlund et al. 1983).

Exploitation of aggregation pheromones

Insect pheromones that attract both sexes to a particular area are termed aggregation pheromones (Shorey 1973). They function as long-range signals and are known to be exploited by several parasitoids (Powell 1999). In Heteroptera, aggregation pheromones are emitted by male bugs (Aldrich 1995). Mating and oviposition often occur in the same area where these aggregation pheromones are emitted, which makes them a potential host location cue for egg parasitoids. Females and males of the leaf-footed plant bug (*Leptoglossus australis*), as well as their egg parasitoid *Gryon pennsylvanicum*, were captured by traps baited with male bugs but never in traps with females bugs, which indicates the presence of a male-derived pheromone acting as a kairomone for the wasps (Yasuda 1998). Additionally, parasitization was increased when cages with male bugs were placed next to host eggs (Yasuda and Tsurumachi 1995).

Telenomus calvus is a specialized phoretic egg parasitoid of the spined soldier bug *Podisus maculiventris*. The wasps are known to utilize the aggregation pheromone of the male bugs, α-terpineol, to come in the host male’s vicinity and to wait for female bugs to arrive, whereupon they become phoretic after the female bug finishes mating (Buschman and Whitcomb 1980; Aldrich et al. 1984; Aldrich 1995). It is assumed that the wasps recognize the female bugs through female-specific volatiles that are produced by small glands underneath the wings. Besides spying on the 2 host pheromones, *Te. calvus* also possesses a number of behavioral and biological adaptations to facilitate phoresy, which makes it an efficient phoretic parasitoid (Orr et al. 1986). Some females of the nonphoretic, more generalistic *Telenomus podisi* were caught in male-pheromone–baited traps of *P. maculiventris* too (Aldrich 1985) but did not discriminate between host eggs placed in traps baited with the synthetic male pheromone and unbaited traps (Bruni et al. 2000). This implies that the synthetic pheromone does not affect the searching behavior of the nonphoretic *Te. podisi* females like it does in the phoretic *Te. calvus*. It was assumed that *Te. calvus* relies on other cues such as infochemicals of the eggs or the host substrate (Bruni et al. 2000).

CLOSE RANGE AND CONTACT INFOCHEMICALS

Plant cues

After landing on a host plant, egg parasitoids mainly use contact or short-range volatiles that indicate the presence of the host or more specifically its eggs. Studies by Fatouros, Bukovinszkine'Kiss, et al. (2005) indicate that phytochemical changes in the leaf surface of Brussels sprout plants induced by eggs of *P. brassicae* arrest *T. brassicae* (Table 1). However, no indication was found that egg deposition of *P. brassicae* induces volatiles that are used by the egg parasitoid for host location. Unlike in the other systems where egg deposition induces volatile plant cues (see above), the *Pieris* butterfly is not severely damaging the leaf of a Brussels sprout plant before or during oviposition. The response of the plant seems restricted to leaf surface modifications. Molecular evidence confirmed a locally restricted plant response to *P. brassicae* egg deposition in Arabidopsis (Little et al. 2007). It is assumed that chemical changes of the pattern of compounds in the wax layer are induced that guide the egg parasitoids to suitable host eggs after landing on the host plant. Also other short-range plant cues than cuticular waxes could play a role: egg deposition is able to reduce the plant's photosynthetic activity (Schröder et al. 2005), and thus, closure of stomata may affect the gaseous leaf boundary layer.

Host cues

Laing (1937) was the first to report arrestment of *T. evanescens* wasps by chemical traces left by the grain moth *Sitotroga cerealella*. Later, Lewis et al. (1971, 1972) found that wing scales left by ovipositing *H. zea* or *Plodia interpunctella* moths were used as kairomones by *T. evanescens*. Several follow-up studies showed a response of egg (larval) parasitoids to residues of the adult host, such as wing scales of butterflies or moths (e.g., Noldus and van Lenteren 1985b; Zaborski et al. 1987; Shu and Jones 1989; Thomson and Stinner 1990; Fatouros, Bukovinszkine'Kiss, et al. 2005; Yong et al. 2007), chemical traces of walking bugs (Colazza et al. 1999; Borges et al. 2003; Conti et al. 2003, 2004; Salerno et al. 2006), or a marking pheromone of a fruit fly (Roitberg and Lalonde 1991) (compare Table 3). Jones et al. (1973) found hydrocarbons like tricosane in wing scales of *H. zea* as biologically active cues, eliciting significant orientation and stimulation of parasitism by *T. evanescens*. Similar findings on other *Trichogramma* spp. using hydrocarbons were published by Lewis et al. (1975), Shu et al. (1990), Padmavathi and Paul (1998), and Paul et al. (2002). Colazza et al. (2007) revealed that *n*-nonadecane, a cuticular hydrocarbon released by the tarsi and scutella of female *N. viridula* bugs had a kairomonal activity on the egg parasitoid *Tr. basalis* acting as a "host-gender recognition" cue for the egg parasitoids. The significance of discriminating female host cues from male host cues is especially important with those host species in which oviposition occurs away from mating and feeding site like in the case of *N. viridula*. Chemical traces from adult hosts were also shown to be used by other scelionid wasps in finding bug eggs (Chabi-Olaye et al. 2001; Borges et al. 2003; Conti et al. 2004; Peri et al. 2006; Salerno et al. 2006). This emphasizes again the importance of the adult host stage for egg parasitoids.

Fecal volatiles of both larvae and adults of the elm leaf beetle (*X. luteola*) were attractive to its egg parasitoid *O. gallerucae* (Meiners and Hilker 1997). However, eggs, gravid females, or the larvae themselves were not attractive in the olfactometer. A substrate contaminated with feces of chrysomelids also arrested 2 eulophid egg parasitoid species when they had antennal contact with the contaminated site (Meiners and Hilker 1997; Meiners et al. 1997). Besides plant odors (see above), *O. gallerucae* uses cues from host feces for location of the elm leaf beetle's microhabitat. The beetle's feces also act as a contact kairomone for microhabitat acceptance. Kairomones isolated from the host eggs themselves were only used for host recognition (Meiners and Hilker 1997).

Yet, in some cases, airborne chemicals of the host eggs themselves were shown to stimulate an intensive search behavior in egg parasitoids (Frenoy et al. 1992; Renou et al. 1992; Hofstetter and Raffa 1998; DeLury et al. 1999; Bai et al. 2004; Yong et al. 2007). Analysis of the eggs of *Ostrinia nubilalis* and *M. brassicae* revealed the presence of various compounds on the egg surface such as hydrocarbons being responsible for the kairomonal activity on *T. brassicae* (Renou et al. 1989, 1992). However, other *Trichogramma* spp. did not react to host eggs from a short distance (Laing 1937; Kaiser et al. 1989). In many cases, kairomones present on the egg surface act at short range and thus play a role in host egg recognition (e.g., Strand and Vinson 1982; Leonard et al. 1987; Nordlund et al. 1987; Pak and De Jong 1987; Bin et al. 1993; Meiners and Hilker 1997; Meiners et al. 1997; Conti et al. 2003). In general, it is not expected that host eggs elicit chemical long-range attraction in egg parasitoids.

INFOCHEMICAL USE IN A TRITROPHIC CONTEXT

As outlined above, the foraging behavior of egg parasitoids is strongly affected by chemical cues from the first and the second trophic level. Vet and Dicke (1992) offered a conceptual framework by placing the ecology and evolution of infochemical use by herbivore-foraging carnivores in a tritrophic context. The central problem of foraging carnivores is the reliability-detectability problem of infochemicals. Vet and Dicke (1992) mentioned 3 solutions for this problem, which we will discuss with respect to egg parasitoids (see also in the Introduction). Furthermore, they proposed some general rules that predict how parasitoids solve the reliability-detectability problem. Parasitoids specialized at the host and host plant level are expected to use different foraging strategies and thus different infochemicals than those parasitizing numerous hosts, which are polyphagous herbivores themselves. Thus, the parasitoids' behavioral response to a cue depends not only on their degree of dietary specialization but also on the dietary specialization of their host species. The used infochemicals can be either specific for a certain host complex or generally present in various complexes, and responses to the cues can be either innate or learned.

Dietary specialization in egg parasitoids

Egg parasitoids like *Trichogramma* species are known to be fairly polyphagous, parasitizing a broad range of hosts especially of the insect order Lepidoptera (Thomson and Stinner

Table 3
Responses to adult host residues

Egg parasitoid	Host	Source	Response	Reference
Scelionidae				
Trissolcus brochymenae *Trissolcus simoni*	*Murgantia histrionica* *Eurydema ventrale* *Nezara viridula*	Chemical traces from adult hosts	Arrestment	Conti et al. (2003, 2004)
Trissolcus basalis	*N. viridula*	Chemical traces of virgin males and mated females in a “preovipositional state”	Arrestment	Colazza et al. (1999), Peri et al. (2006), and Salerno et al. (2006)
		n-nonadecane, cuticular hydrocarbon of female hosts		Colazza et al. (2007)
Telenomus podisi	*Euschistus heros*	Chemical traces by walking female hosts	Arrestment	Borges et al. (2003)
Telenomus isis	*Sesamia calamistis*	Chemical traces by virgin and mated females	Arrestment	Chabi-Olaye et al. (2001)
Eulophidae				
Oomyzus galerucivorus	*Galeruca tanaceti*	Adult feces on substrate	Arrestment	Meiners et al. (1997)
Oomyzus gallerucae	*Xanthogaleruca luteola*	Adult feces on substrate Volatiles of feces of host adults and larvae	Arrestment	Meiners and Hilker (1997)
Trichogrammatidae				
Trichogramma evanescens (later *Trichogramma maidis* now *Trichogramma brassicae*)	*Pieris brassicae* *Pieris rapae* *Mamestra brassicae*	Cabbage leaves treated with wing scales from adult female hosts	Arrestment	Noldus and van Lenteren (1985b) and Gardner and van Lenteren (1986)
Trichogramma brassicae	*Ostrinia nubilali*	Chemical trail of moth females	Arrestment	Garnier-Geoffroy et al. (1996)
		Scale extracts and saturated hydrocarbons	Increased parasitism	Grenier et al. (1993)
Trichogramma brassicae	*Pieris brassicae*	Body scales and traces of adult hosts		Fatouros, Bukovinszkine’Kiss et al. (2005)
Trichogramma evanescens	*Heliothis zea*	Body scales and their hexane extracts	Arrestment and increased parasitism	Lewis et al. (1971, 1972) and Jones et al. (1973)
	Plodia interpunctella	Tricosane from scale extracts		
	Sitotroga cerealella *Mamestra brassicae*	Traces of adult hosts	Arrestment	Laing (1937)
	Choristoneura fumiferana	Hexane extracts from scales	Arrestment	Schmidt and Carter (1992)
Trichogramma pretiosum	*H. zea*	Hexane extracts from scales Acids in scale fractions	Increased parasitism	Gross et al. (1984) and Gueldner et al. (1984)
Trichogramma nubilale	*Ostrinia nubilalis*	Moth scale extracts Saturated hydrocarbon fraction	Increased parasitism and arrestment	Shu and Jones (1989) and Shu et al. (1990)
Trichogramma minutum	*Choristoneura fumiferana*	Hexane extracts of scales	Arrestment	Zaborski et al. (1987)
Trichogramma chilonis *Trichogramma brasiliensis*	*Corcyra cephalonica*	Saturated hydrocarbons, mainly tricosane	Increased parasitism	Padmavathi and Paul (1998) and Paul et al. (2002)
Trichogramma exiguum				
Trichogramma ostriniae	*Ostrinia furnacalis*	Volatiles of host scales	Attraction	Yong et al. (2007)
Braconidae				
Ascogaster quadridenata	*Cydia pomonella*	Volatiles of host scales	Attraction	DeLury et al. (1999)
Pteromalidae				
Halticoptera rosae	*Rhagoletis basiola*	Marking pheromone of female flies	Increased parasitism and arrestment	Roitberg and Lalonde (1991)

1990; Pinto and Stouthamer 1994). However, host ranges of *Trichogramma* spp. are mainly determined in the laboratory, where they tend to be broader than in the field (reviewed by Romeis et al. 2005). Still, there is growing evidence for *Trichogramma* spp. being more prevalent in certain habitats or on specific plants (reviewed by Romeis et al. 2005) probably due to their limited moving abilities. Plant structure, host density and distribution, and other (micro)habitat

Table 4
Response to kairomones associated with host eggs

Egg parasitoid	Host	Source	Response	Reference
Scelionidae				
Trissolcus brochymenae	*Murgantia histrionica*	Eggs Egg extracts	Arrestment Increase in encounters	Conti et al. (2003)
Eulophidae				
Ooencyrtus kuvanae	*Lymantria dispar*	Airborne chemicals of fresh egg masses	Arrestment	Hofstetter and Raffa (1998)
		Accessory gland secretion		
Edovum puttleri	*Leptinotarsa decemlineata*	Egg wash	Arrestment	Leonard et al. (1987)
Trichogrammatidae				
Trichogramma evanescens later *Trichogramma maidis* (=*Trichogramma brassicae*)	*Pieris brassicae*	Egg wash	Arrestment	Noldus and van Lenteren (1985b)
Trichogramma ostriniae	*Ostrinia furnacalis*	Airborne chemicals of egg masses	Arrestment and attraction	Bai et al. (2004) and Yong et al. (2007)
		Accessory gland secretion of mated host females		
Trichogramma brassicae (or Trichogramma maidis)	*Pieris brassicae*	Accessory gland secretion of mated host females	Arrestment	Fatouros (2006)
	Ostrinia mubilalis	Airborne chemicals of egg massesSurface extracts of egg masses	Increased mobility and arrestment	Frenoy et al. (1992), Renou et al. (1989, 1992)

specificities might vary and influence the host-foraging behavior of egg parasitoids (Gingras and Boivin 2002; Romeis et al. 2005). This habitat/plant loyalty could narrow their host range. Certainly, egg parasitoids in monocultures or habitats of low biodiversity will encounter only a small range of host species. The uncertainty of the host range in the field as well as wrong species determinations in the past make it difficult to put *Trichogramma* spp. into categories as generalists or specialists. This means that the dietary specialization aspects of Vet and Dicke (1992) are difficult to apply on *Trichogramma* spp. as long as their host specificity remains poorly known.

Here, we try to find a general concept for egg parasitoids, dealing with the major constraints of egg parasitoids concerning the host like: a small size, sessile and inconspicuous life stage, and usually limited temporal availability. Apart from a generally short longevity, egg parasitoids, like *Trichogramma* spp., are known to be restricted to passive downwind movements or walking and jumping. Which are the main infochemical strategies used in their long-distance search for hosts?

Infochemical detour: the importance of the adult host stage

Egg parasitoids seem to heavily rely on the adult host stage in all phases of their host-selection process. Pheromones and residues of host females and sometimes males have a large impact on indirectly locating eggs of moths, butterflies, bugs, beetles, flies, or sawflies: so far about 34 different egg parasitoid species were shown to use adult host cues (see Tables 2 and 3) compared with only about 6 species that were shown to use host cues from the host eggs themselves (Table 4). In most cases, egg-derived stimuli mediate host-recognition behavior (see above). Consequently, this infochemical detour by employing kairomones of the adult host seems an important strategy for many egg parasitoids. In contrast, only few larval or pupal parasitoids were shown to spy on adult sex, marking, or aggregation pheromones (Cortesero et al. 1993; Wiskerke et al. 1993; Zaki 1996; Hoffmeister and Gienapp 1999; Reddy et al. 2002).

Besides an arresting effect to areas likely to contain host eggs, adult host pheromones may have a much greater importance to phoretic egg parasitoids. Among parasitoids, phoresy is almost exclusively performed by egg parasitoids, which are smaller, compared with larval or pupal parasitoids and therefore often limited in their flight capabilities. So far, about 30 egg parasitoid species are known to be phoretic on their adult hosts (Fatouros 2006). Thus, we expect that chemical espionage on adult host pheromones sometimes in combination with phoresy to be a strategy commonly used by egg parasitoids to solve the reliability-detectability problem.

Plant volatiles induced by egg deposition and/or feeding

Egg parasitoids of herbivorous hosts developed to use a third so far underestimated solution, mentioned by Vet and Dicke (1992): plant volatiles induced by herbivore infestation. This could solve the detectability problem that egg parasitoids face. Here, they are known to follow 2 different strategies: plant volatiles induced by herbivore feeding or by egg deposition. Both types of plant cues can be specific in indicating the presence of host eggs and thus play important roles for the host location process in egg parasitoids: so far about 10 species were shown to rely on such plant synomones (see Table 1).

From the plant's point of view, an attraction of parasitoids/predators to eggs deposited on the plant might have a great advantage because herbivore larvae are killed before they can start feeding. Especially, annual plants (with a smaller biomass and shorter life time) are expected to benefit from such an indirect defense mechanism (Hilker and Meiners 2002b). From the egg parasitoid's perspective, it remains unclear when it is beneficial to use oviposition-induced plant cues to locate their hosts and when the use of feeding-induced plant volatiles becomes adaptive. Generally, plant volatiles induced by feeding damage should be more abundant due to the greater plant damage than plant volatiles induced after egg deposition by herbivores. However, a response to feeding-induced plant volatiles should be only adaptive to egg parasitoids when they provide reliable information, for example, when host generations overlap and different developmental stages co-occur on the plant. On the other hand, a response of egg parasitoids to oviposition-induced plant volatiles requires fine-tuned sensory abilities, especially when the induction by feeding induces a stronger response in the plant than eggs do. Such perceptive abilities are likely present mainly in systems where the first and third trophic levels specialized on each other over evolutionary time.

We expect such an indirect plant response to egg deposition by release of plant volatiles attractive to the egg parasitoids in those systems where 1) wounding is involved during oviposition and 2) the egg parasitoid has the capability to actively orient to an odor source by walking, jumping, or flying. If no simultaneous wounding occurs (either by egg deposition or by adult or larval feeding), we expect no induction of volatiles by the plant but short-range cues, likely to be restricted to the plant surface and perceived by the egg parasitoid only in close vicinity (see Fatouros, Bukovinszkine'Kiss, et al. 2005).

The influence of experience and associative learning

According to Vet et al. (1990), a response to infochemicals was considered as learned when it was observed in only experienced insects after having encountered host/prey or host plant/feeding substrates. Associative learning by connecting an unconditioned stimulus, always host derived, with a conditioned stimulus is frequently observed in parasitoids. Generally, responses of carnivores to host-derived kairomones are fixed, whereas responses to plant volatiles are more variable and are learned mostly during adult foraging (Vet and Dicke 1992). Immature parasitoids can also gain experience with certain stimuli through development inside the host (Corbet 1985).

Several studies show that learning of plant cues during foraging in egg parasitoids does occur frequently. For example, experience during emergence modified the searching behavior of 1 of the 2 tested *T.* nr *brassicae* strains toward plant stimuli: females that emerged from their host on a tomato plant subsequently searched a tomato leaf longer than females emerging in a vial without plant stimuli. When comparing a preadult experience with the effect of adult learning through an oviposition experience on host preference in 2 strains of *T.* nr *ivelae*, it was shown that adult experience had a stronger effect than learning through development inside the host (Bjorksten and Hoffmann 1998).

Responding to oviposition-induced plant cues requires experience with the plant–host complex by some egg parasitoids studied so far (e.g., Fatouros, Bukovinszkine'Kiss, et al. 2005; Mumm et al. 2005), whereas others respond innately (e.g., Meiners and Hilker 2000; Colazza, Fucarino et al. 2004; Meiners T, unpublished data). The necessity of experience to respond to oviposition-induced pine odor might be an adaptation to the high intraindividual and intraspecific variability of pine volatile blends (Mumm and Hilker 2006).

Egg parasitoids often exploit host cues innately, for example, *T. brassicae* a butterfly antisex pheromone (Fatouros, Huigens, et al. 2005) or *C. ruforum* the sex pheromones of sawflies (Hilker et al. 2000). But even such specific host cues like sex and antisex pheromones need to be learned by some egg parasitoid species, as was shown for *Trichogramma* species (e.g., Kaiser et al. 1989; Schöller and Prozell 2002; Fatouros et al. 2007; Fatouros and Huigens, unpublished data). Besides *Trichogramma* spp., also a scelionid wasp was shown to use associative learning that enhanced its arrestment response to host female residues after an oviposition experience (Peri et al. 2006). In conclusion, the host range of egg parasitoids seems not to affect the ability to learn certain cues. However, complex and variable cues often need to be experienced first before being used.

Vet et al. (1995) stated that learning of foraging cues by egg parasitoids is not expected. The more foraging decisions a wasp makes the more likely infochemical learning becomes adaptive. The high availability of eggs (compared with other stages such as larvae or pupae) and the short longevity of egg parasitoids in combination with their limited ability to search may restrain the number of foraging decisions that lead to host encounters. However, the low detectability of mostly inconspicuous eggs might require numerous foraging decisions, which could be optimized by the ability to learn. Vet et al. (1995) further hypothesized that if learning occurs, then this is most likely to occur in the more polyphagous egg parasitoid species that attack hosts that lay spatially separated single eggs. Yet, also specialist egg parasitoid species searching for hosts in a variable chemical environment may benefit from the ability to associate host-indicating chemicals with positive experience, as is suggested by the studies on the specialist egg parasitoid *C. ruforum* that needs to learn oviposition-induced plant synomones (see above).

General patterns in egg parasitoid–foraging strategies

To reach (new) habitats, egg parasitoids have to move over larger distances. They can achieve this by spreading passively by wind or by using larger hosts for transportation (phoresy) (see Figure 1). Both ways implicate a momentum of chance either by coming down at the right spot in the landscape or by sitting at the right place to catch a suitable host for transportation. However, egg parasitoids might use general abiotic or biotic habitat cues or cues of host encounter places (like flower heads) to enhance the chance to reach a suitable habitat. On the other hand, we expect directed orientation of egg parasitoids to hosts over a smaller distance. In closer vicinity to host eggs, both host cues (if available in sufficient quantities) and plant cues might play equally important roles for the

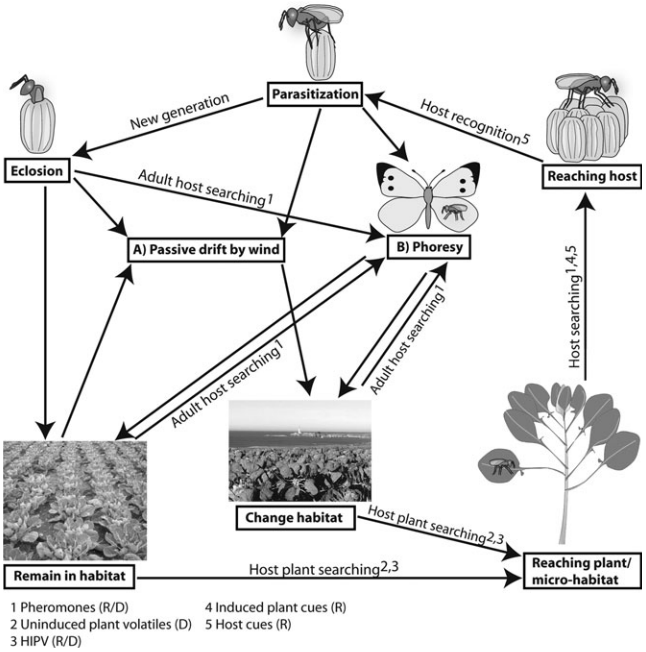

Figure 1

The general host location behavior of egg parasitoids and the possible infochemicals involved are shown on the basis of a virtual system. After eclosion, an egg parasitoid can choose to remain in the same habitat and search for a host plant or to change to a new habitat. To reach habitats, the wasp has 2 possibilities: A) by chance and drift passively with the wind or B) by searching adult hosts for transportation (phoresy). By using cues of the adult host, either to directly find the host plant and deposited herbivorous eggs or to achieve phoresy, egg parasitoids are shown to rely on the adult host stage more than other parasitoids do. Besides host pheromones, herbivore-induced plant volatiles (induced by egg deposition or feeding) seem to have a so far underestimated impact on the host-foraging behavior of egg parasitoids. The parasitoids' response to all types of infochemicals shown may be innate or learned (see text for more details). R = reliable cue, D = detectable cue, HIPV = herbivore-induced plant volatiles.

host location process depending on factors such as learning capabilities or the dietary specialization of the egg parasitoid and its host.

To fully understand infochemical-exploiting strategies used by foraging egg parasitoids, it is necessary to study plant–host–parasitoid interactions at different scales in the field. Hereafter, the mechanism of infochemically mediated host searching should be investigated experimentally. Furthermore, behavioral and electrophysiological investigations should provide information on the identity of the chemicals that egg parasitoids use.

CONCLUSIONS

This paper summarizes the extensive research conducted so far on the role of infochemical use by egg parasitoids during host foraging. Egg parasitoids play an important role in biological control programs of pest insects. Understanding their host location behavior is a crucial step for a targeted application of parasitoids in crop fields and greenhouses. A general pattern of strategies has been highlighted here: due to the inconspicuousness of host eggs, egg parasitoids have developed various so-called infochemical detour strategies to locate their hidden hosts. This infochemical detour via specific cues from the adult host stage, sometimes in combination with phoresy, or via cues from plants induced by larval or adult feeding implies a widespread exploitation of host-specific infochemicals by egg parasitoids. The use of oviposition-induced plant cues indicating the presence of the host eggs is another elegant solution to the reliability-detectability problem. A previous experience with the plant stimuli in association with a host cue seems to play a role in the exploitation of induced plant cues especially in variable environments. The innate response by polyphagous parasitoids to specific host cues is considered to be unlikely because of physiological constraints caused by the diversity of specific cues expected from several hosts (Vet and Dicke 1992). Yet, it cannot be excluded that these constraints are less severe than expected and that generalists with a smaller host range are indeed able to innately respond to the specific information from different hosts (Steidle and van Loon 2002). However, an uncertainty of the host range in the field makes it difficult to categorize some egg parasitoids, for example, *Trichogramma* spp., as generalists or specialists.

GLOSSARY

Parasitoid: Insects that lay their eggs on or in other insects (or sometimes other invertebrates). The hatching larvae then live parasitic on the host and eventually kill it, whereas the adults are free living.

Infochemical: A chemical that conveys information in an interaction between 2 individuals, evoking in the receiver a behavioral or physiological response that is adaptive to one of the interactants or both.

Pheromone: An infochemical emitted by one organism evoking a response in a receiving organism of the same species.

Sex pheromone: A pheromone that is produced by a member of one sex specifically to attract members of the other sex for the purpose of sexual reproduction.

Antiaphrodisiac: An antisex pheromone transferred during mating to reduce the females' receptivity and reinforce monogamy.

Aggregation pheromone: A pheromone that causes aggregative behavior in conspecifics of both sexes or in the same sex as the emitter.

Kairomone: An infochemical of an organism that on emission evokes in the receiver, an individual of a different species, a behavioral or physiological response adaptively favorable to the receiver but not the emitter.

Synomone: An infochemical of an organism that on emission evokes in the receiver, an individual of a different species, a behavioral or physiological response adaptively favorable to both receiver and emitter.

Chemical espionage: Exploiting intraspecific communication through infochemicals by a third organism for its own benefit, which is detrimental for the organisms that communicate intraspecifically.

Phoresy: The transport of one organism (phoront) on the body of another for a limited time period and for purposes other than direct parasitism.

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