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## Host location in *Oomyzus gallerucae* (Hymenoptera: Eulophidae), an egg parasitoid of the elm leaf beetle *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae)

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**Abstract** Eggs of the elm leaf beetle *Xanthogaleruca luteola* are often heavily attacked by the chalcidoid wasp *Oomyzus gallerucae*. We studied the chemical signals mediating interactions between the egg parasitoid, its host, and the plant *Ulmus campestris*. Olfactometer bioassays with *O. gallerucae* showed that volatiles of the host-plant complex attract the parasitoid. In order to determine the source of attractive volatiles within this host-plant-complex, we tested separately the effect of odours of eggs, gravid elm leaf beetle females, faeces of the beetles and elm twigs (with undamaged leaves and leaves damaged either mechanically or by feeding of the beetles). Odours of faeces of the elm leaf beetle were attractive, whereas neither volatiles from eggs nor from gravid females acted as attractants. Volatiles from undamaged or damaged plants did not elicit a positive reaction in *O. gallerucae*, whereas volatiles from feeding-damaged plants onto which host eggs had been deposited were attractive. This latter result suggests that it is not feeding but deposition of host eggs onto elm leaves that induces the production of plant volatiles attractive to the egg parasitoid. Investigations of the search patterns of *O. gallerucae* within the habitat by laboratory bioassays revealed that the egg parasitoid encounters host eggs by chance. Contact kairomones from faeces were demonstrated to be important in microhabitat acceptance, while contact kairomones isolated from the host eggs are relevant for host recognition.

**Key words** Egg parasitoids · Microhabitat acceptance · Host finding · Kairomones · Induced defence

### Introduction

Parasitoids use numerous chemical and physical cues for host location. The task of host location facing a para-

sitoid includes processes of habitat location, microhabitat acceptance, host finding within the habitat and recognition of the host. The guiding signals may emanate from the host itself, but also from plants in case of phytophagous hosts and from other parts of the habitat (Vinson 1991). Our study focuses on the investigation of such signals in host location of the egg parasitoid *Oomyzus gallerucae* (Hymenoptera, Eulophidae). This palearctic species parasitizes eggs of the elm leaf beetle *Xanthogaleruca luteola* (Coleoptera, Chrysomelidae) which is known as a pest on elm. In Europe, *O. gallerucae* has been reported to be important for control of the elm leaf beetle (Hall and Johnson 1983). This wasp has been repeatedly introduced into the United States for biological control of the elm leaf beetle. Even though a high percentage of eggs of the elm leaf beetle were parasitized, successful establishment of *O. gallerucae* has been reported only once (Ehler et al. 1987; Hall and Johnson 1983).

### Habitat and microhabitat location

Chemicals that are used by female parasitoids to locate their (micro-) habitat may be emitted by different sources (for an overview see Vinson 1991). For example, *Gelis festinans*, an eggsac parasitoid of the linyphiid spider *Erigone atra* orientates towards the odours of wheat and grass leaves, main components of the habitat of its host (Van Baarlen et al. 1996). Many parasitoid species perform directed flights or walks towards volatiles of the plants their hosts are feeding upon (Vaughn et al. 1996; Whitman and Eller 1992; Wickremasinghe and Van Emden 1992). Kairomones emitted by the host itself or by products (e.g. faeces) of the host can also guide parasitoids into the right microhabitat. For example, the eulophid parasitoid *Aprostocetus hagenowii* locates its host *Periplaneta americana* with the help of (Z,Z)-6,9-heptacosadiene. This kairomone is released by oothecae and by frass of female American cockroaches (Suiter et al. 1996). Egg parasitoids face the problem

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that chemicals from eggs are the least detectable, but most reliable host-finding cues, whereas synomones from the plant are the most detectable, but least reliable ones. This reliability-detectability problem (Vet and Dicke 1992) could be solved in a tritrophic context. Turlings et al. (1991) have shown that host location of larval parasitoids may be guided by synomones emanating from plants damaged by the host's feeding activity. Egg parasitoids could parallel this solution by orientation towards synomones that were released by plants onto which eggs had been deposited. We tested whether *O. gallerucae* is attracted by odours of the habitat of the elm leaf beetle and tried to determine whether attractive habitat volatiles are emitted by the host itself or by the plant that is used by the host for feeding and egg deposition.

### Microhabitat acceptance

After the microhabitat has been located, the parasitoid has to decide whether and for how long it will spend time and energy in searching for hosts. This decision can be influenced by kairomones that are emitted during feeding or reproductive activity of the hosts. The egg parasitoid, *Trichogramma evanescens*, is stimulated to search within areas contaminated by scales from female moths left in the area of oviposition (Lewis et al. 1972). The duration of searching of the larval parasitoid *Cotesia glomerata* is influenced by contact cues from frass, silk, and herbivore-damaged leaf tissue of its host *Pieris brassicae* (Mattiacci and Dicke 1995). We investigated whether *O. gallerucae* stays longer searching for a host in a microhabitat with host cues than in one without any host signals.

### Host finding

For egg parasitoids, the predictability of host egg encounter depends on the oviposition behaviour of the host. If the host shows a preference for laying eggs on certain parts of the leaf (e.g. the leaf nerves), the parasitoid could exploit this information. We examined whether the elm leaf beetle displays distinctive features in oviposition behaviour that provide useful information for the egg parasitoid *O. gallerucae*.

### Host recognition

Host recognition and acceptance in egg parasitoids can be influenced by the shape, size or by physical and chemical cues of the egg surface. Detailed information on host recognition in egg parasitoids are scarce (Bin et al. 1993; Vinson 1985). For example, *Trissolcus basalidis*, a scelionid species, recognizes eggs of the southern green stinkbug, *Nezara viridula*, by the adhesive secretion that attaches the eggs to the substrate (Bin et al. 1993). The surface of the eggs of *X. luteola* may play a crucial role in host recognition by *O. gallerucae*. We studied the significance of chemical stimuli of the chorion of elm leaf beetle eggs for *O. gallerucae*.

## Materials and methods

### Insects and rearing conditions

Adults and eggs of *X. luteola* were collected from 1992 to 1995 in the environs of Méze (Southern France, Montpellier). For rearing beetles and parasitoid wasps, the egg masses collected in the field were placed in petri dishes. Emerging parasitoids and larvae of *X. luteola* were removed from these dishes and kept separately in different containers. *X. luteola* eggs, larvae and adult beetles were kept at 20°C and 16 h/8 h light:dark. Adults and larvae were fed with leaves of *Ulmus campestris*. *O. gallerucae* were kept at 10°C and 16 h/8 h light:dark and transferred to 20°C several days before testing. For reproduction, the parasitoids were offered freshly laid eggs of *X. luteola*. They were fed with diluted honey. Conditions were kept humid for beetles and parasitoids by frequently adding some water to the filterpaper that covered the bottom of the rearing containers.

### Bioassays

All observations and behavioural assays except the olfactometer tests were made by using a stereomicroscope. The events of all bioassays were recorded by the Noldus Observer programme 3.0 (Wageningen, The Netherlands). Only experienced female parasitoids with prior contact with host eggs were studied. These females had encountered host eggs 2 days prior to the experiments for a period of 24 h.

### Habitat and microhabitat location

The effect of odour of the habitat of *X. luteola* was studied in a four arm airflow olfactometer similar to the one described by Vet et al. (1983). Air was sucked into the olfactometer from outside the laboratory by a vacuum pump (capacity:  $2.458 \times 10^{-4} \text{ m}^3 \text{ s}^{-1}$ ). The incoming air was divided into four flows, which were conducted consecutively through a flow meter (Aalborg Instruments and Controls Inc., USA), a glass cylinder with water and the test (control) glass cylinder into the plexiglas olfactometer (volume of glass cylinders: 125 ml). The test glass cylinder contained parts of the habitat of *X. luteola* (an elm twig with 15–20 leaves, ten adults of *X. luteola* and eggs and faeces that were produced by these beetles during 48 h), while the control glass cylinders were left empty. Air could leave the olfactometer through a tube which was adjusted in the middle of the lower olfactometer plate and also served as entrance for the parasitoid females. The air was entering the exposure chamber of the olfactometer at each of the four arms with 156 ml/min. A female parasitoid was allowed to walk within the exposure chamber of the olfactometer for 600 s. Its duration of stay in each of the four odour fields was recorded. Data were statistically evaluated by a Friedman two-way analysis of variance by ranks and Wilcoxon-Wilcoxon tests.

In order to elucidate whether the source of the attractive habitat odour is emitted by the host itself, the attractiveness of the following was tested by using the olfactometer: (a) 20 egg masses (48 h old) of *X. luteola* that had been cautiously removed from elm leaves by using a razor blade, (b) 10 gravid females of *X. luteola*, (c) faeces of 20 adult beetles that had been collected for 48 h, (d) 10 third instar larvae of *X. luteola*, (e) and faeces of 30 third instar larvae that had been collected for 48 h.

To determine the role of plant odours for habitat location in *O. gallerucae*, the effect of volatiles of an elm twig with 15–20 leaves was tested in the olfactometer. First, the effect of a twig with undamaged leaves was studied and compared to a twig with damaged leaves. We tested both leaves damaged artificially by cutting out five small disc (diameter 5 mm) per leaf and leaves damaged by feeding of 15–20 adult *X. luteola* for 48 h (their faeces was removed with a fine-haired brush). In addition to the effect of artificial and feeding damage, the effect of egg deposition on the attractiveness of plant volatiles was examined. Three alternatives were tested. First, the effect of an elm twig with 15–20 leaves, onto which 10–20 egg

masses were deposited in total, was bioassayed. Second, two test cylinders were connected in series, one of them with 20 egg masses and the other one with an elm twig with 15–20 leaves, onto which eggs had never been deposited. The leaves had been damaged by feeding of 15–20 adult *X. luteola* for 48 h. This test was conducted in order to examine whether a positive effect is due to either a change of plant volatiles caused by egg deposition or to a synergistic effect of egg and plant volatiles. Third, an elm twig with 15–20 leaves which had in total carried 15–20 egg masses that were carefully removed prior to testing was used as odour source. Since females of *X. luteola* always fed just before and after oviposition, all leaves of the elm twigs tested for the effect of egg deposition on the attractiveness of plant volatiles were damaged by feeding.

#### Microhabitat acceptance

To investigate whether contact with host derived cues elicits a positive response in *O. gallerucae*, elm leaves were offered for 48 h to ten gravid females of *X. luteola*. The beetles fed on and defaecated onto the leaves. After removal of the beetles, a test leaf was offered to a female parasitoid. Its duration of antennal drumming and time of stay was recorded for three minutes. For control, prior to exposure to the test leaf, the parasitoid female was observed on an untreated elm leaf. Data were statistically evaluated by Wilcoxon signed-rank test for matched pairs.

#### Host finding

In order to investigate whether *O. gallerucae* finds its host by chance or by certain stimuli, a three way choice experiment was conducted. An egg mass and a dummy made of yellow painted filter paper were offered in a petri dish (diameter 9 cm) to a parasitoid female. Egg mass and dummy were placed into the dish in a way that they formed an equilateral triangle with an imaginary point (*i*-point). The triangle sides were 5 cm long. After release of the parasitoid female in the middle of this triangle, it was recorded which of the three objects was contacted first: the egg mass, the dummy, or the *i*-point. The test was replicated 50 times with experienced females. Data were statistically evaluated by a one-dimensional chi-square test (Bortz 1993).

To investigate features of the oviposition behaviour of *X. luteola* that might be used by the egg parasitoid to find its host, we examined whether *X. luteola* prefers oviposition on leaf nerves. Twenty individuals of *X. luteola* were offered an elm twig with 15–20 leaves for a period of 48 h. The location of egg masses on the leaves was noted. This test was replicated six times and evaluated by a chi-square test for homogeneity. The importance of leaf structures for the host finding process of *O. gallerucae* was analysed by watching ten female parasitoids individually for ten minutes on an elm twig with 15 leaves. Each twig carried five egg masses, faeces of adult elm leaf beetles and leaves that were damaged by feeding. The position of the parasitoids on the leaves and their behaviour were noted. Data were statistically analysed by a Friedman two-way analysis of variance by ranks and Wilcoxon-Wilcoxon tests.

#### Host recognition

The observations of the parasitoid's oviposition behaviour revealed that a parasitoid female always shows alternating contact of both antennae with the host egg for longer than 1 s and with a frequency  $\geq 5$  Hz. Thus, this antennal drumming may be used as an indicator for host recognition. In order to examine whether host recognition is elicited by chemicals of the chorion of host eggs, the eggs were extracted with solvents of different polarities (hexane, dichloromethane, and methanol). Twenty egg masses (c. 400 eggs) were extracted with 100  $\mu$ l solvent. A volume of 30  $\mu$ l of the extract was transferred onto a piece of filter paper (1 mm<sup>2</sup> = test paper). For control, only solvent was applied on another piece of paper. After 4 h, the solvent had evaporated. Then, control and test papers were offered subsequently to an experienced female parasitoid for 12 min. Duration of antennal drumming on the filter papers was

recorded for ten females. Data were statistically evaluated by the Wilcoxon signed-rank test for matched pairs.

## Results

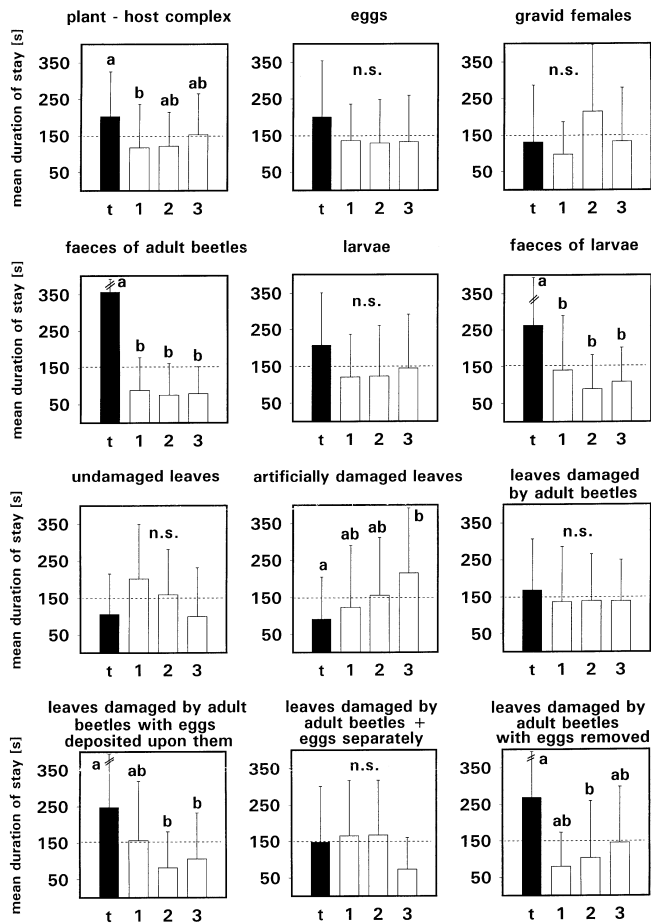
### Habitat and microhabitat location

Odours of the plant-host complex represented by elm leaves onto which eggs were deposited, by gravid females of *X. luteola*, and by their faeces and feeding damage elicited a positive response in *O. gallerucae*. In order to determine the exact source of the attractive volatiles of this plant-host complex, odours of the host and plant were tested separately. From the host, volatiles of faeces of both larvae and adults were attractive to *O. gallerucae*, whereas eggs, gravid females and larvae of *X. luteola* were not. From the plant, intact elm leaves had no effect on *O. gallerucae*, but feeding-damaged elm leaves onto which eggs had been deposited attracted the egg parasitoid. The attractiveness of these leaves carrying eggs was not due to a synergistic effect of volatiles emitted from eggs and leaves, since no effect was recorded when volatiles of eggs separated from leaves were offered together with volatiles from leaves that had never carried host eggs. Furthermore, elm leaves were still attractive when host eggs had been deposited on them but removed prior to the experiment. Odours of artificially damaged elm leaves elicited avoidance, whereas elm leaves damaged by feeding of adult *X. luteola* had no effect. (Table 1; Fig. 1). The attractiveness of odours of

**Table 1** Habitat and host finding response of female *Oomyzus gallerucae* to odours of *Xanthogaleruca luteola* and elms (*Ulmus campestris*) offered in a four-arm olfactometer (*F-Chi*<sup>2</sup> Friedman chi-square; Friedman two-way analysis of variance by ranks)

Odour Source	n	F-chi <sup>2</sup>	P
Mixed volatiles of the plant-host complex			
Elm leaves onto which eggs were deposited + gravid females of leaf beetles + faeces of adult leaf beetles (leaves were damaged by feeding adults)	30	9.7	*
Host volatiles			
Eggs of leaf beetles	25	2.0	n.s.
Gravid females of leaf beetles	25	4.9	n.s.
Faeces of adult leaf beetles	20	20.6	***
Larvae	20	4.7	n.s.
Faeces of larvae	25	18.5	***
Plant volatiles			
Intact elm leaves	25	7.1	n.s.
Artificially damaged elm leaves	25	9.9	*
Elm leaves damaged by adult leaf beetles	20	0.9	n.s.
Plant volatiles depending on egg deposition			
Elm leaves damaged by adult leaf beetles onto which eggs were deposited	40	16.2	***
Elm leaves damaged by adult leaf beetles + eggs separately	25	1.2	n.s.
Elm leaves damaged by adult leaf beetles onto which eggs had been deposited and were removed afterwards	30	12.9	**

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ , n.s. not significant



**Fig. 1** Mean values and standard deviations of durations of stay recorded from females of *Oomyzus gallerucae* in test and control fields of a four-arm olfactometer (observation period per female parasitoid: 600 s, *t* field with test odours, 1, 2, 3 three fields with control air). Different letters indicate significant ( $P < 0.05$ ) differences, Wilcoxon-Wilcoxon test

the whole plant-host complex was not as high as that of odours of single habitat components (e.g. faeces). This result might have been caused by the different quantities of the tested substrates (see Materials and methods).

#### Microhabitat acceptance

Contact with substrate contaminated with faeces elicited a positive response in *O. gallerucae* (Table 2). Antennal drumming was significantly longer on leaves treated with faeces. However, the parasitoid did not stay significantly longer on treated leaves than on controls.

#### Host finding

Host eggs offered at close range to parasitoid females in a three-way choice experiment were not attractive (Fig. 2). Of 50 female parasitoids tested, 19 first contacted the dummy, 17 the imaginary point, and 14 the egg mass. None of the three aims was significantly pre-

**Table 2** Response of female *O. gallerucae* to leaf discs contaminated with host faeces. Mean values and standard deviations are given. (Wilcoxon signed-rank test for matched pairs)

Test parameter	n	Treatment (s)	Control (s)	P
Duration of antennal drumming	20	7.2 ± 9.0	0.8 ± 3.4	**
Duration of stay	20	81.4 ± 53.0	61.1 ± 60.2	n.s. <sup>a</sup>

\*\* ( $P < 0.01$ ), n.s. not significant

<sup>a</sup>  $0.07 > P > 0.05$

ferred. Even when the parasitoids passed the egg mass at 1 mm distance, no attraction was observed.

*X. luteola* significantly ( $P < 0.001$ , chi-square test) preferred leaf nerves for egg deposition: 60 (89.6%) of 67 egg masses deposited were located on the leaf nerves, 7 (10.4%) on the leaf surface. The egg parasitoid searching for a host did not spend most of its time on the leaf nerves. Most of the time spent searching for a host was spent on the edge of the leaf (43.6%) and the leaf surface (37.5%). They spent only 6.9% of their host-searching time on leaf nerves. Walking times on stems (3.6%) or near feeding holes (8.5%) were equally small (Fig. 3).

#### Host recognition

All chorion extracts tested elicited host recognition behaviour. The duration of antennal drumming was always longer on the extract-treated paper than on the control. The longest duration of drumming was obtained by the dichloromethane extract (Table 3).

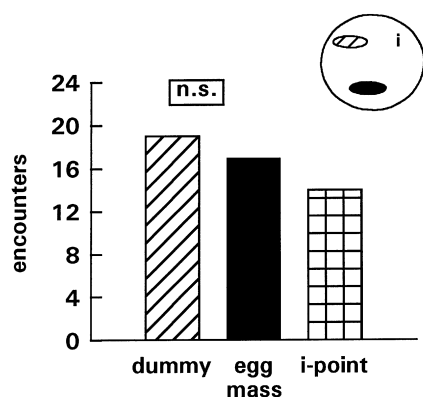
## Discussion

#### Habitat and microhabitat location

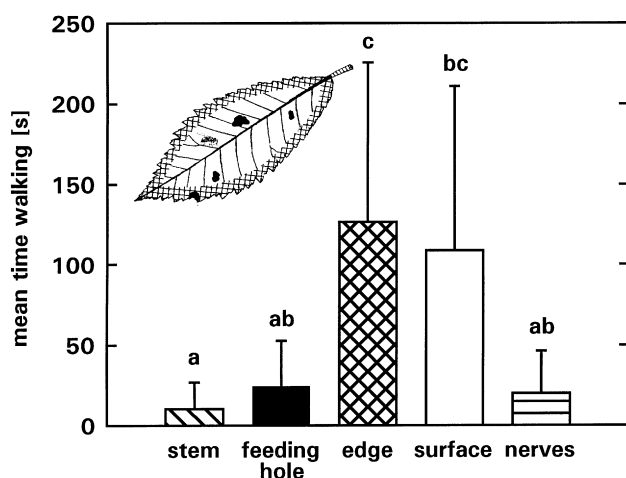
Our bioassays showed that *O. gallerucae* clearly responds positively to odour of the habitat. In order to determine the exact source of the attractive volatiles, we test both odours from the host and from the plant, the host is feeding and laying eggs upon.

#### Plant volatiles

The significance of plant odours for parasitoids of phytophagous insects is known for numerous species (review in Tumlinson et al. 1992). Parasitoid females can be guided into the habitat of their hosts by orientation to odours of undamaged host plants. A more directed response would be a flight or walk towards plants damaged by host feeding, because these indicate the presence of a potential host. For example, *Aphidius ervi* shows a stronger response to plants of *Vicia faba* that had been damaged by the feeding activity of its host *Acyrtosiphon pisum* than to undamaged, artificially damaged or non-host damaged plants (Du et al. 1996). The eulophid



**Fig. 2** Number of first contacts of *O. gallerucae* females with each of three objects offered in a three way choice test (see text for detailed explanation of the objects). Fifty females were tested individually; we recorded which of the three objects was contacted first. (n.s. not significant). One-dimensional chi-square test



**Fig. 3** Time spent by *O. gallerucae* walking on different structures of elm leaves during search for a host with an observation period for 10 min. Mean values and standard deviations for 10 female *O. gallerucae* are given. Values indicated by different letters above columns differ significantly ( $P < 0.05$ ), Wilcoxon-Wilcoxon test

**Table 3** Host recognition response of female *Oomyzus gallerucae* to extracts of egg masses of *Xanthogaleruca luteola*. Mean values and standard deviations are given. Duration of antennal drumming was at first recorded on a control filter paper treated with solvent only and subsequently on an extract treated paper. The observation period for each female on each paper was 12 minutes. (Wilcoxon signed-rank test for matched pairs)

Solvent	Duration of antennal drumming		
	Extract (s)	Control (s)	<i>P</i>
Methanol	5.0 ± 8.1	0.2 ± 0.4	*
Hexane	8.1 ± 7.8	0.5 ± 1.0	*
Dichloromethane	10.8 ± 6.3	0.7 ± 1.2	**

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$

parasitoid *Diglyphus isaea* is strongly attracted by odours arising from bean plants that were inflicted by the American serpentine leaf miner *Liriomyza trifolii*, but not to undamaged plants (Finidori-Logli et al. 1996). *X. luteola*, the host of the egg parasitoid investigated in this study, oviposits on elm species (see Introduction). In the olfactometer experiments, *O. gallerucae* was not attracted by odours of undamaged or damaged elm leaves. Chemicals from damaged or undamaged leaves indicate the presence of its host with low reliability, since the presence of intact or damaged elm leaves does not guarantee the presence of host eggs. The risk of losing time and energy by host searching in the wrong habitat (undamaged elms, elms damaged by other herbivores) might be too high. By avoiding odours of artificially damaged leaves (see Fig. 1), females of *O. gallerucae* may avoid searching in inappropriate habitats.

### Plant volatiles depending on egg deposition

Females of *O. gallerucae* responded positively to odours of elm leaves that carried host eggs (Table 1). This is not a synergistic effect, because a combination of odours of eggs and damaged leaves (without eggs) was not attractive to the parasitoids. When eggs had been carefully removed from elm leaves, the odour of these leaves was still attractive to *O. gallerucae*. We suggest that egg deposition onto an elm leaf induces a release of synomones that attract *O. gallerucae*. While numerous studies clearly showed that feeding by herbivores induces the release of plant synomones attracting predators and parasitoids (Dicke 1994; Mattiacci et al. 1994; Takabayashi and Dicke 1996; Tallamy and Raupp 1991; Turlings et al. 1990, 1995), knowledge about induced changes in plants by egg deposition of herbivores is scarce. Blaakmeer et al. (1994) provided evidence that egg deposition by *Pieris brassicae* onto cabbage induces a change in the chemistry of cabbage leaves that inhibits further egg depositions on these leaves. Our results provide for the first time evidence that host egg deposition induces plant synomones attractive to an egg parasitoid. Such plant synomones are both detectable and reliable for an egg parasitoid.

### Microhabitat acceptance

Several products of a host, like oral discharges, faeces, scales, and marking pheromones have been shown to release host-seeking cues for several parasitoids (Lewis et al. 1972; Nordlund and Lewis 1985; Prokopy and et al. 1978; Vinson and Lewis 1965). Females of *O. gallerucae* might recognize their host habitat with the help of contact kairomones emitted by faeces of its host. Contact with substrate contaminated with faeces of adult *X. luteola* elicited antennal drumming (Table 2), a behaviour that is also shown with host recognition. Even though the female parasitoids did not stay significantly longer in the contaminated area, there seemed to be a

tendency to forage longer after they had contacted faeces of a host. Thus, signals derived from faeces may lead the parasitoid into the vicinity of host eggs.

### Host recognition

The bioassays revealed that antennal drumming of *O. gallerucae* is elicited by kairomones of the egg surface. Host recognition behaviour could be induced by extracts of host eggs without any addition of physical cues from the eggs. When comparing the results obtained with egg mass extracts of different polarities (Table 3), the high activity of the dichloromethane extract suggests that the compounds for host recognition are of intermediate polarity.

In contrast to the results obtained with *O. gallerucae*, the significance of physical cues for host recognition has been demonstrated in several parasitoid species. For example, Pak and De Jong (1987) found that besides a kairomone from the host egg surface, also the size, colour and texture play a role in host recognition for different strains of *Trichogramma buesi* and *T. maidis*. The shape of eggs is important for the egg parasitoids *Tetrastichus hagenowii* (Vinson and Piper 1986) and *Telenomus heliothidis* (Strand and Vinson 1983).

In conclusion, habitat location in *O. gallerucae* is mediated by odours both of the host (faeces) and of the plant onto which host eggs had been deposited, whereas finding of the host within the habitat is by chance. Contact kairomones from the faeces are important for microhabitat acceptance, while kairomones isolated from the host eggs are relevant for host recognition. Further studies are needed to identify the kairomones demonstrated in this study for habitat finding, microhabitat acceptance and host recognition.

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