Bulletin of Entomological Research (2001) **91**, 411–417 DOI: 10.1079/BER2001117

Oviposition behaviour and host colony size discrimination in *Episyrphus balteatus* (Diptera: Syrphidae)

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Abstract

Three bioassays were used to examine the oviposition behaviour of the hoverfly, *Episyrphus balteatus* (Degeer) in which various stimuli purported to influence host assessment and choice were tested. *Episyrphus balteatus* failed to exhibit enhanced behavioural responses, in terms of approaches and landings, to artificial leaves with the highest numbers of aphids, suggesting that females are merely responding to the colour of the artificial leaves. A density-dependent oviposition response was reported in a second bioassay using whole bean plants, although there was an asymptotic relationship. Syrphid responses, which were measured by oviposition over a five-day period, were greatest towards those plants with the highest number of aphids. In a final series of trials, gravid female *E. balteatus* showed a behavioural preference for filter papers treated with the greatest honeydew concentrations (0.26 mg μl^{-1} honeydew). More time was spent in the treated areas and syrphids demonstrated more proboscis and ovipositor extensions in these treatments. These bioassays provided an opportunity to isolate some of the individual components of decision-making by female *E. balteatus* during egg-laying behaviour. A greater understanding of natural enemy behaviour is essential before enhanced control of pest populations in the field can be established.

Introduction

The larvae of aphidophagous species of syrphid such as *Episyrphus balteatus* (Degeer) (Diptera: Syrphidae) are important biological control agents of pest aphids (Ankersmit *et al*., 1986; Chambers & Adams, 1986). For the adult female syrphid, it is suggested that there are four phases of site selection for oviposition (Chandler, 1966), which involve the processing of a range of sensory cues (Guest, 1984). The first phase of searching behaviour involves the assessment of long-range optical cues, including the size, density and colour of the stand of vegetation (Chandler, 1966; Smith, 1969, 1976; Sanders, 1982; Sutherland *et al*., 1999). In the second stage, short-range optical cues are then thought to operate, which involve aphid colony recognition (Morley, 1910; Dixon, 1959; Sanders, 1979, 1983; Kan & Sasakawa, 1986). The decision to lay eggs is based not just on the density of aphids (Tamaki *et al*., 1967), but also on the quality of the aphid colony (Kan, 1988a,b). The penultimate stage involves the processing of olfactory stimuli. Amongst the aphidophagous syrphids, there is a dichotomy in behavioural responses to olfactory stimuli. Phytozetic syrphid species, such as *Melanostoma mellinum* (Linnaeus) (Diptera: Syrphidae), rely more on plant-derived stimuli than aphid-locating (aphidozetic) species such as *E. balteatus*, which use aphid-derived compounds (Chandler, 1968a). In the final stage, gustatory stimuli are utilized. A female will alight and use her labellum to monitor the substrate for the presence of honeydew (Dixon, 1959; Kan & Sasakawa, 1986; Budenberg

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https://doi.org/10.1079/BER2001117 Published online by Cambridge University Press

& Powell, 1992). Honeydew, the aphid-derived complex of sugars, amino acids and water, is known to serve as an important oviposition stimulus for syrphids (Bombosch & Volk, 1966; Budenberg & Powell, 1992).

There is good evidence, from laboratory experiments and field studies, to suggest that positive density-dependent oviposition occurs in *E. balteatus* (Chandler, 1968b; Itô & Iwao, 1977; Geusen-Pfister, 1987; Tenhumberg & Poehling, 1991; Bargen *et al*., 1998; Scholz & Poehling, 2000). However, field observations have also suggested that female syrphids avoid plants with large or ageing aphid colonies (Kan & Sasakawa, 1986; Kan, 1988a,b, 1989), which is termed the 'buy-futures' ovipositional tactic. In the decision-making process, there may be a trade-off point at which a female syrphid will no longer oviposit near an aphid colony. This paper, therefore, sets out to further our understanding of the decision-making processes which ultimately lead to oviposition by female *E. balteatus*. Three laboratory bioassays were used to investigate oviposition behaviour. The first looked at fly behaviour when presented with a choice of aphid colony sizes, the second examined the actual oviposition responses to those colony sizes and the final trial sought to assess behavioural responses to honeydew.

Materials and methods

Experimental insects

Adult *E. balteatus* required for experiments were taken from stock cultures of known age and kept in a culture room at 20 ± 2°C. Puparia were initially obtained from PK Nützlingszuchten, Welzheim, Germany. Adults were provided with mixed bee pollen (Sigma-Aldrich Chemicals), freeze-dried at −60°C, small droplets of honey placed on a Petri dish lid, sugar cubes and water absorbed in cotton wool. Care was taken to ensure experimental insects were fed from containers which would provide them with limited opportunity for associative learning. Thus, pollen and honey were provided on clear Petri dishes, as it was assumed that clear dishes would provide no colour stimulus.

Pea aphids, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), were reared on dwarf broad bean plants *Vicia faba* L. cv. Sutton Dwarf in a separate culture room at 20 ± 4°C. *Episyrphus balteatus* are known to preferentially oviposit near *A. pisum* colonies (see Sadeghi & Gilbert, 2000)

The influence of aphid number on syrphid behaviour

The first in the series of choice experiments was executed using model 'leaves', constructed as follows: White polystyrene oval balance boats (81 × 57 mm) (Cat. no. BAL1826, Scientific Laboratory Supplies Ltd, Nottingham, UK) served as model leaves. One ml plastic Pasteur pipettes were affixed to the underside of the weighing boats, using Scotch® Magitape™, cutting the pipette bulb so it could be attached easily. Model leaves were painted with phthalocyanine green acrylic paint (Liquitex® Basics™, Binney & Smith Inc., Pennsylvania, USA). The reflectance spectrum of the paint used was analysed in the laboratory using a Perkin Elmer Lambda 5 UV/visible spectrophotometer with an integrated sphere attachment, linked to a pen recorder, with an internal UV/Visible/IR light source. A fast scan was carried out from 280 nm to 800 nm to produce the spectral reflectance curve (fig. 1). The reference was a barium sulphate standard plate.

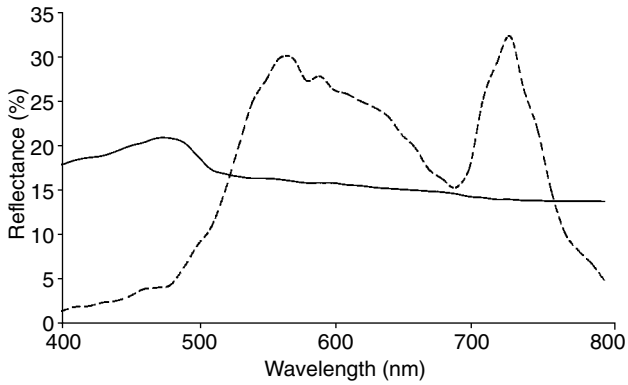


Fig. 1. Spectral reflectance curve for dark green artificial 'leaves' (—), showing the spectral reflectance of a broad bean leaf *Vicia faba* (– –) for comparison.

Five holes were drilled into a piece of fibre board (25 × 25 cm) in a 20 cm diameter circular pattern with equal spacing between each (11.8 cm apart) to serve as the experimental arena. Sticks (15 cm long) were inserted into each of the holes to support the leaves. Each position was assigned a number on the board, so that repetitions could be performed using a randomized block design. This arrangement was placed in an experimental cage (55 × 55 × 55 cm), similar to the cages used for rearing adult syrphids and had the advantage that the experimental array could be quickly changed. A small container of cotton wool soaked with water was also placed in the experimental arena so flies were permanently water-sated. Pollen, honey and sugar cubes were also provided in oviposition experiments, so flies were also sated. Five artificial leaves were placed in the arena. A cork borer was used to cut 2.5 cm diameter broad bean leaf discs, which were inserted into five hair-clip cages (mesh size 0.5 mm). Four of the clip-cages contained an increasing number of *A. pisum* and were marked B (1 aphid), C (5 aphids), D (10 aphids) and E (20 aphids); cage A contained no aphids and served as the control. Each cage was placed on one of the green artificial leaves in the numbered arena. The aphids were placed on the underside of the leaf discs inside the clip-cages. The numbers of aphids in the treatments were chosen to reflect a range of colony densities that occur naturally (Chandler, 1968b; although see Wnuk, 1977).

Adult female syrphids used in experiments were aged between 18 and 25 days since emergence. Experimental insects were permitted free access to males for seven days prior to experiments. Two days prior to experiments, females were stimulated to oviposit on plants heavily contaminated with aphid honeydew, but with the aphids removed. It was necessary for the purpose of the experiment for flies to have had no visual experience of aphids.

The behaviour (approaches to and landings on each of the treatments) of groups of thirty female insects of known age was recorded using a Panasonic NV-M40B standard VHS camera (8:1 2 speed power zoom lens, focal length 5–40 mm) at an approximate distance of 50 cm from the arena. A

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total of five 60-min periods of observation was recorded for each replicate of the bioassay. This permitted 1 h for each treatment in each position of the arena. It was hoped that re-randomizing treatments each hour would eliminate choice by positional preference. Total numbers of approaches to and landings on each treatment were recorded. The definition of an 'approach' was any fly which came within 4 cm of the treatment, and a 'landing' was deemed any approach which terminated in contact with any part of the coloured area of the artificial leaf and/or clip cage. Clip cages were thoroughly cleaned with ethanol and distilled water after each trial to remove any traces of aphid honeydew.

The influence of aphid number on syrphid oviposition

The treatments for this trial were as for the first trial, except that the mesh size of the clip cages was decreased (0.1 mm) to exclude first instar hoverfly larvae from inside the cages containing the aphids. Each clip cage was positioned on the lowest leaves of five broad bean plants cv. Sutton, which were approximately one week old. The five plants and caged aphids were placed at random but with equal spacing between pots (15 cm), in an experimental cage ($55 \times 55 \times 55$ cm) similar to the cages used for rearing adult syrphids.

Thirty female hoverflies, aged between 27 and 45 days, were introduced into the cage and allowed to oviposit on bean plants for a period of five days (120 h). A small container of cotton wool soaked with water was also placed in the experimental arena, as were pollen, honey and sugar cubes. At the end of five days, eggs laid on all parts of each plant and clip cage were counted. In one of the five replicates performed, numbers of aphids remaining in the clip cages were also recorded. Clip cages were thoroughly cleaned with ethanol and distilled water after each trial to remove any traces of aphid honeydew.

The influence of honeydew on syrphid behaviour

Honeydew was collected on clean glass microscope slides placed underneath bean plants in an established pea aphid culture, for approximately one week. Honeydew residue was removed from the slides using a clean razor blade and the resulting solid placed in an evaporating dish with approximately 30 ml of distilled water. The crude honeydew solution was warmed gently to allow sugars and amino acids to dissolve and filtered through a Buchner funnel to remove dead aphids and exuviae. The filtered solution was cooled then flash-frozen in liquid nitrogen. The solution was freeze-dried under a vacuum at −60°C and yielded a brown crystalline solid. The solid (with a known mass) was re-dissolved in a known volume of distilled water to give a concentration of 0.26 mg μl^{-1} (as per Bouchard & Cloutier, 1984). This standard concentration of honeydew was kept in the deep-freeze until ready to use. This method of gentle heating was necessary to dissolve the high molecular weight sugars in *A. pisum* honeydew, but does not degrade the simple sugars and amino acids (Bouchard & Cloutier, 1984).

For bioassays the following series of solutions were made up: treatment A = distilled water, B = 5% (0.013 mg μl^{-1}) honeydew solution, C = 10% (0.026 mg μl^{-1}) honeydew solution, D = 20% (0.052 mg μl^{-1}) honeydew solution, E = 50% (0.13 mg μl^{-1}) honeydew solution and F = 100% (0.26 mg μl^{-1}) honeydew solution ('standard'). For each concentration in turn, 60 µl of solution was dispensed onto a small disc of filter paper (Whatman Grade 1, 3.5 cm diameter). The filter paper was allowed to dry, then placed on top of another disc of filter paper (Whatman Grade 1, 9 cm diameter) in the centre of a glass Petri dish (9 cm diameter). Gravid *E. balteatus* were released into the Petri dish and their behaviour observed for periods of 5 min each. Thirty replicates were performed for each honeydew concentration, recording the time taken to contact the treated area, the time spent within (or in contact with) the honeydew-treated area, whether the fly showed a gustatory response (proboscis extension) and whether it exhibited an abdominal protraction or oviposition.

Data analysis

Analysis of variance and regression were carried out on data from the experiments. For the first trial (the influence of aphid number on syrphid behaviour), the proportion (p) of visits to each treatment was calculated as $p = (r + 0.5)/(n + 1)$, where r was the number of visits to a treatment and n was the total number of visits to all treatments in each replicate of each experiment (0.5 and 1 were added to r and n respectively, to avoid zero values). The data were logit transformed ($\ln(p/(1 - p))$ to normalize the data set. An ANOVA was applied to the transformed data to determine whether there were significant differences between the means. For the second and third trials, ANOVAs were executed on untransformed data to determine whether there were significant differences between the means and, where the F-value was significant at the 5% level, a multiple pairwise comparison was performed manually using the Tukey HSD test (Zar, 1999). In examination of any trends in response to the aphid colonies, a variety of relationships may be predicted, including a linear relationship or an asymptotic (hump-shaped) relationship (possibly indicating a 'buy futures strategy'). Consequently, regression was used to estimate a variety of curves using the SPSS v10.0 curve estimation algorithm.

Results

The influence of aphid number on syrphid behaviour

There were no significant differences between the proportion of approaches by female *E. balteatus* to artificial leaves with increasing size of aphid colony (ANOVA; $F_{4,25} = 1.34$, n.s.) and a similar result was obtained with the proportion of landings on the leaves (ANOVA; $F_{4,25} = 1.50$, n.s.) The visits to each of the treatments are shown in fig. 2.

The influence of aphid number on syrphid oviposition

There were significant differences between the mean number of eggs laid per treatment (ANOVA; $F_{4,20} = 6.49$, $P = 0.0016$). Post-hoc comparisons (Tukey test; $P < 0.05$) show that there were significant differences between the numbers of eggs laid over the five day period on the control and the three bean plants with largest aphid 'colony' sizes (i.e. 5, 10 and 20 aphids, fig. 3). The differences between treatments with 1, 5, 10 and 20 aphids were not significant. It became apparent during this experiment that aphid propagation

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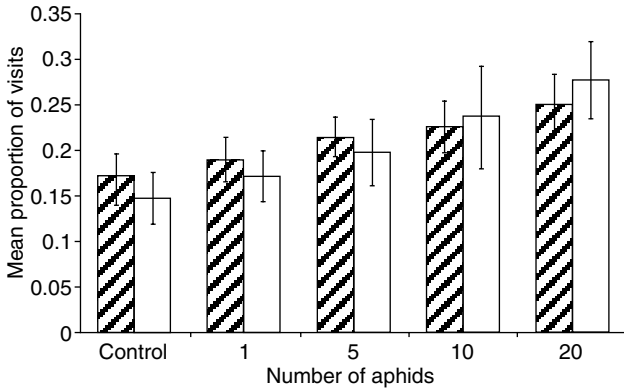


Fig. 2. Mean proportion of approaches (▨) to and landings (□) by female *Episyrphus balteatus* on green artificial leaves with increasing numbers of *Acyrthosiphon pisum*, showing standard error bars of means. All aphids were contained in clip-cages with a bean leaf disc. An ANOVA of logit transformed data revealed for both approaches and landings, that there were no significant differences between treatments ($P > 0.05$).

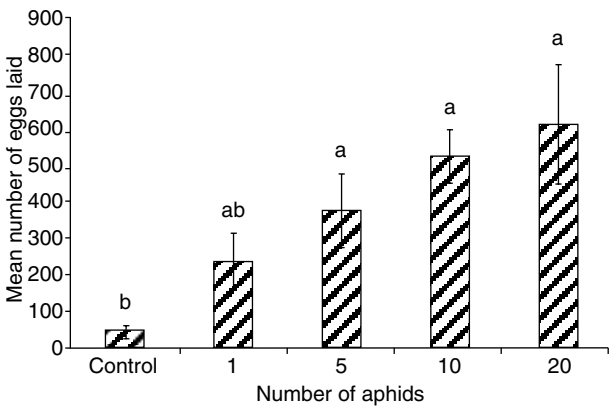


Fig. 3. Mean number of *Episyrphus balteatus* eggs laid on whole bean plants in response to increasing pea aphid colony sizes. An ANOVA revealed significant differences between the means ($P < 0.05$). Different letters above bars indicate significant differences between treatments according to the Tukey test. Bars indicate standard errors of the means.

rates varied across the colony sizes. This was duly recorded, but only for the final replicate (table 1). Regression analysis revealed trends in response to the aphid colonies. Both linear (df = 3, F = 13.80, $P = 0.03$, $R^2 = 0.82$) and quadratic (df = 2, F = 21.79, $P = 0.04$, $R^2 = 0.96$) relationships were significant, but the quadratic (asymptotic) relationship explained more of the variation in oviposition response.

The influence of honeydew on syrphid behaviour

Times taken to contact the different honeydew treatments were not significantly different between treatments (ANOVA; $F_{5,174} = 0.67$, n.s.) and nor were times spent within the different treatments (ANOVA; $F_{5,174} = 0.80$, n.s.) (table 2, fig. 4). As before, a variety of curves were estimated for the relationship between each of time spent in the honeydew-treated area and time to contact with the honeydew-treated area. Regression analysis revealed that there was no significant linear relationship for time for first contact with the honeydew (df = 4, F = 2.39, $P = 0.20$, $R^2 = 0.37$) but there was a significant linear relationship with time spent in the treated area (df = 4, F = 10.18, $P = 0.03$, $R^2 = 0.72$). Regression analysis of the gustatory responses (df = 4, F = 7.99, $P = 0.05$, $R^2 = 0.66$) and abdominal protraction responses (df = 4, F = 54.29, $P = 0.002$, $R^2 = 0.93$) revealed linear relationships in both instances.

Discussion

In these experiments, gravid female *E. balteatus* demonstrated a positive density-dependent response to aphid colony size in terms of oviposition behaviour, with a suggestion that a 'buy-futures' ovipositional tactic may be operating at higher colony sizes. Aphidophagous syrphids are know to demonstrate a positive relationship between aphid colony size and oviposition (Chandler, 1968b; Itô & Iwao, 1977; Geusen-Pfister, 1987; Tenhumberg & Poehling, 1991; Bargen *et al.*, 1998; Scholz & Poehling, 2000). Conversely, Kan & Sasakawa (1986) and Kan (1988a,b) observed in the field that female syrphids preferentially oviposit in young (apterous) aphid colonies and that they avoid plants heavily infested with aphids (Kan, 1989), thereby exhibiting an asymptotic relationship. This tactic ensures that eggs are not wasted on aphid colonies which are due to 'crash' in the near future. Furthermore, *Epistrophe nitidicollis* (Meigen) (Diptera: Syrphidae) also selected young aphid colonies (Hemptinne *et al.*, 1993, 1994).

In the first experiment there were only small increases in approaches and landings to an increase in aphid colony size,

Table 1. Numbers of each instar of *Acyrthosiphon pisum* remaining in clip-cages in experiment 2 after five days (120 h), showing the propagation rate per original number of 'founder' adult aphids in colony.

Treatment	1st instar	2nd instar	3rd instar	4th instar	5th instar	Total after 120 h	Propagation rate (aphids per day)
Control	0	0	0	0	0	0	0.0
1 aphid	7	13	4	11	1	36	7.2
5 aphids	31	21	29	31	3	105	4.2
10 aphids	19	18	22	31	1	91	1.8
20 aphids	20	24	16	18	5	83	0.8

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Table 2. Effect of pea aphid honeydew on the behaviour of female *Episyrphus balteatus* walking across filter paper treated with extracts of various concentrations.

Honeydew concentration mg µl^{-1}	*N*	Time to contact treated area (s)[a]	Time spent within treated area (s)[a]	% syrphids showing gustatory response	% syrphids showing abdominal protraction
0.0	30	1.94 ± 0.15 n.s.	0.81 ± 0.15 n.s.	23.3	0.0
0.013	30	2.09 ± 0.18 n.s.	0.92 ± 0.19 n.s.	40.0	0.0
0.026	30	2.12 ± 0.18 n.s.	0.98 ± 0.18 n.s.	40.0	0.0
0.052	30	2.00 ± 0.18 n.s.	1.19 ± 0.19 n.s.	46.7	3.3
0.13	30	2.01 ± 0.20 n.s.	1.02 ± 0.20 n.s.	50.0	3.3
0.26	30	1.88 ± 0.20 n.s.	1.24 ± 0.20 n.s.	56.7	10.0

An ANOVA on $\log_{10}(n + 1)$ transformed means revealed no significant differences between the means ($P > 0.05$). a $\log_{10}(n + 1)$ transformed means ± standard error.

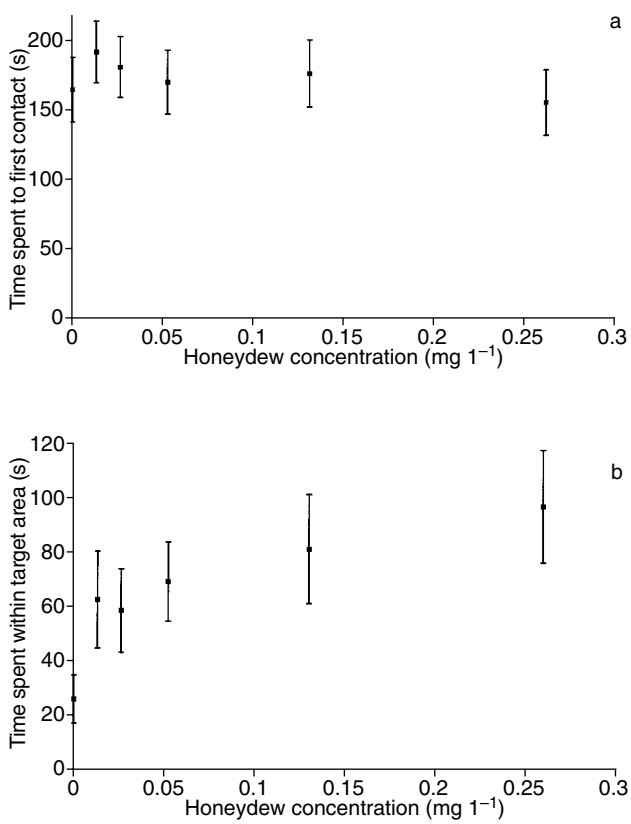


Fig. 4. Mean times of female *Episyrphus balteatus* a) to contact honeydew-treated areas and b) spent in honeydew-treated areas, when presented on filter paper discs in a glass Petri dish. Bars indicate standard errors of the means. An ANOVA indicated no significant difference between the means ($P > 0.05$).

and these increases were non-significant. In this trial the influence of visual, olfactory and gustatory cues from the aphids were minimized by presenting the aphids on the underside of leaf discs within the perspex clip cages, with each cage placed on one of the artificial leaves. It is likely that the females would only be able to see the colony after landing on and searching the leaf disc. This suggests that in this trial, *E. balteatus* is using vision as a means to identify suitable sites for oviposition, i.e. responding to the colour of the leaf (Chandler, 1966; Smith, 1969, 1976; Sanders, 1982) even though the reflectance of the artificial leaf disc did not necessarily correspond to the reflectance of a natural bean leaf (fig. 1).

In the second trial, females were permitted to oviposit freely on plants with a range of aphid colony sizes. All oviposition cues, namely visual, olfactory and gustatory stimuli (i.e. aphid-, and leaf-produced volatiles and honeydew) could be accessed by the syrphid, as the aphid colonies were visible to an approaching syrphid. Regression analyses tended to indicate an asymptotic relationship between colony size and numbers of eggs laid. This would support the 'buy-futures' findings of Kan & Sasakawa (1986) and Kan (1988a,b, 1989). Confounding factors which may have masked the effect of initial colony size, were that colonies with the lowest number of founding aphids have higher rates of increase, meaning that colonies with the least aphids did not necessarily remain the smallest throughout the experiment. In addition, overcrowding in the largest colonies may have led to increased mortality and therefore a decrease in density over the period of the experiment. This may have caused fewer eggs to be laid in these treatments towards the end of the experiment. This problem could be alleviated in the future, by simply decreasing the length of the experiment.

Results from the final bioassay indicate that female *E. balteatus* uses honeydew as a contact kairomone to initiate oviposition. The experiments using filter paper discs indicate that syrphids spend longer in honeydew treated areas, as was found by Budenberg & Powell (1992). It has been suggested that syrphids detect sugars using either the labellum or tarsal receptors and then confirm their presence using sensilla on the ovipositor. Hood-Henderson (1982), using single sensillum recording found significant responses by aphidophagous syrphids to honeydew, tryptophan, indoleacetaldehyde, alanine and water. Therefore, the penultimate factor in ovipositional selection by female syrphids appears to be based on the presence of amino acids and sugars in honeydew.

In the current study, a concentration of 0.052 mg µl^{-1} honeydew solution (equivalent in this trial to 0.324 mg honeydew cm^{-2}) provoked a 50% gustatory response in female *E. balteatus*, whereby 50% of test animals respond with proboscis extension. Further experiments would be necessary to determine the colony size at which this level of

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honeydew deposition would occur in the field. As discussed by Hood-Henderson (1982), short-range olfaction probably does not play a part in the detection of honeydew and results here would tend to support this, as the variation in the time taken to contact the honeydew was non-significant. This would serve to support those findings of Hood-Henderson & Wellington (1982), who reported poor electroantennogram responses to honeydew's breakdown products tryptophan, indolealdehyde and indoleacetaldehyde. Moreover, it has been suggested that other volatile compounds from the aphid's cuticle, such as *n*-pentane (Shonouda, 1996; Bargen *et al*., 1998) may also play a minor role in oviposition site selection, although this was not under investigation in the present study.

The implications of this research are that artificial honeydews, which have been used to enhance the numbers of predators and parasitoids in field situations (Hagen *et al*., 1971, 1976; Ben Saad & Bishop, 1976; Evans & Swallow, 1993; McEwen *et al*., 1994), could potentially be used to augment aphidophagous syrphid numbers. Syrphids may be encouraged to remain in an area with elevated honeydew levels (such as from an artificial spray) and lay more eggs even when aphid numbers are low. It has been demonstrated that in parasitoids, success-motivated retention time (Vinson, 1984) is altered after learning/excitement, so that they search more and for an increased time when in this state. This can have a significant effect even when there are low aphid densities. If artificial honeydews can be used in conjunction with extensive aphid monitoring, then greater aphid control via the augmentation of natural enemies could be achieved, i.e. using an artificial honeydew spray during the initial colonization phase of aphids.

In this study, some of the visual and gustatory stimuli of importance to an ovipositing female syrphid have been identified. By understanding the mechanisms of the response to aphid colonies of different sizes, we may be better able to utilize aphidophagous syrphids within an integrated pest management strategy.

Acknowledgements

The authors wish to thank Peter Katz in Welzheim, Germany for initially providing the insects for culturing and Paula Byron for the culturing facilities. This work was supported by a BBSRC CASE Studentship with IACR-Rothamsted. IACR-Rothamsted receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom.

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(Accepted 8 June 2001)
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