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Author: R.L. Day J.M. Hickman R.I. Sprague S.D. Wratten

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Title: Predatory hoverflies increase oviposition in response to colour stimuli offering no reward: implications for biological control

Author names and affiliations: R. L. Day[a], J.M. Hickman[a], R.I. Sprague[b] and S.D. Wratten[b*]

[a] Centre for Biological Sciences, Faculty of Natural & Environmental Sciences, Life Sciences Building 85/3007, University of Southampton, Highfield Campus, Southampton, SO17 1BJ, UK

[b] Bio-Protection Research Centre, PO Box 85084, Lincoln University, Lincoln, 7647, New Zealand

Abstract: There are increasing efforts worldwide to engineer agroecosystems to enhance ecosystem services such as carbon storage, minimisation of erosion, and biological control of pests. A key group of insect biological control agents is the hoverflies (Diptera: Syrphidae). While adult Syrphidae are pollen and nectar feeders, the larvae of many species are aphidophagous, thus demonstrating life-history omnivory and their potentially important role in the biological control of aphids and other pests. Several experiments have been conducted to assess whether the presence of flowers in or near crops has an effect on oviposition by syrphids, but the results have often been inconclusive. This paper describes a large-scale field experiment carried out over two years, in which standardised model flowers were placed in field margins and oviposition rates monitored near them. Statistically significantly more eggs were laid on broad bean (*Vicia faba*) infested with the pea aphid, *Acyrthosipon pisum*, near yellow model flowers with and without pollen and honey resources than at positions with no model flowers nearby. These results suggest strongly that the presence of model flowers increases hoverfly oviposition and that colour may be more important than food resources in enhancing this behaviour. This work indicates that biological control of pests by hoverflies can be enhanced by simple, non-floral agroecological interventions.

Zusammenfassung

Weltweit werden zunehmend Anstrengungen unternommen, Agrarsysteme so zu entwickeln, dass Ökosystemdienstleistungen wie Kohlenstoffspeicherung, Minimierung der Erosion und biologische Schädlungsbekämpfung gestärkt werden. Eine Schlüsselgruppe von biologischen Schädlingsantagonisten sind die Schwebfliegen (Diptera: Syrphidae). Während sich adulte

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* Corresponding author. Tel.: +64 3 423 0911; fax: +64 3 325 3864

Email address: steve.wratten@lincoln.ac.nz

Schwebfliegen von Pollen und Nektar ernähren, sind die Larven vieler Arten Blattlausräuber, womit sie ihre potentiell wichtige Rolle bei der biologischen Kontrolle von Blattläusen und anderen Schädlingen zeigen. Verschiedene Experimente wurden durchgeführt, um zu prüfen, ob das Vorhandensein von Blüten in der Nähe von Feldern einen Einfluss auf die Eiablage der Schwebfliegen ausübt, aber die Ergebnisse waren oft nicht beweisfähig. Diese Arbeit beschreibt ein zweijähriges, großräumiges Freilandexperiment, bei dem standardisierte Kunstblüten in Ackerrainen installiert und die Eiablageraten in ihrer Nähe registriert wurden. Signifikant mehr Eier wurden auf von der Erbsenlaus (Acyrthosipon pisum) befallenen Puffbohnen (Vicia faba) in der Nähe von gelben Kunstblüten (mit und ohne Pollen- oder Nektarressourcen) abgelegt als an Bohnen ohne Kunstblüten in der Nachbarschaft. Diese Ergebnisse legen nahe, dass die Anwesenheit von Kunstblumen die Eiablage durch Schwebfliegen steigert und dass die Farbe für diese Verhaltensbeeinflussung wichtiger als die Nahrungsressourcen sein könnte. Diese Arbeit zeigt, dass die biologische Schädlingsbekämpfung durch Schwebfliegen durch einfache, nicht-florale agroökologische Maßnahmen gestärkt werden kann.

Keywords: Aphidophagous Syrphidae, oviposition, visual, model flowers, yellow

Introduction

In response to the continued losses of ecosystem functions in intensive agriculture (Costanza et al. 1998; 2014), increasing attention is being paid to the restoration of farmland ecosystem services (ES) i.e., those ecological functions to which mankind attributes value (e.g., Wratten et al. 2013). Many agri-environment schemes have been implemented on farmland, in Europe particularly, but at a very high cost and with little evidence that biodiversity levels and ecosystem functions have actually improved (Kleijn et al. 2001; Blomqvist et al. 2009). These schemes, however, can sometimes lead to modest increases in populations of hoverflies and bees but whether these increases lead to improved ES (biological control of pests and pollination, respectively) has not been assessed. An important ES in agriculture worldwide is biological control of pests (Landis et al. 2000; Zehnder et al. 2007), and hoverflies (Diptura: Syrphidae) are an important component of the predatory insect communities in farmland (Leroy et al. 2010). The present work attempts to address the above gap by aiming to improve hoverfly egg-laying rates through simple within-field manipulations, as a key step towards enhancing pest biological control by this predatory insect group. These flies exhibit 'life-history omnivory' (Gurr & Wratten 2000); adults are pollen and nectar feeders and are attracted to flowers (e.g., Harwood et al. 1992; Cowgill et al. 1993;), but in many species the larvae are aphidophagous and have potential in limiting aphid population growth (e.g., Wnuk 1977; Hurej 1992; Hickman & Wratten 1996). In the case of such syrphid species the eggs are laid near aphids (Kan 1988a & 1998b; Gilbert 1993; Scholz & Poehling 2000) and it is essential to understand the cues involved in the selection of these sites, as well as in oviposition rates, if the efficacy of pest management is to be improved (Sutherland et al. 1999).

Adult hoverflies feed on pollen for the maturation of the ovarioles and eggs (e.g., Schneider 1948; Haslett 1989). Nectar, which provides amino acids, minerals and energy for locomotion and reproduction, is also a key resource (Kevan & Baker 1983). As many crops and field margins are deficient in floral resources, it is likely that where large areas of land are intensively cultivated, shortages of flowers may limit oviposition (Chandler 1968a). Therefore the introduction of flowers, as pollen and nectar resources, has obvious potential for the enhancement of biological control and other ecosystem services (Wratten et al. 2013) in the crop.

Although the mechanisms by which adult hoverflies are attracted to flowers are not fully understood, it is known that colour is an important cue (Mulligan & Kevan 1973; Kirk 1984; Haslett 1989). Evidence also suggests that aphidophagous hoverflies have a strong preference for yellow (e.g., Kevan & Baker 1983; Hoback et al. 1999; Sutherland 1998). However, neither the precise role of food resources as attractants nor the relationship between feeding and oviposition are well understood.

Flowers added to agro-ecosystems may attract hoverflies to the crop at a time when aphid numbers are beginning to increase. However, despite some evidence that the presence of flowers increases biological control by hoverfly larvae (White et al. 1995; Hickman & Wratten 1996), the experimental evidence for a direct link between hoverfly oviposition rates and the presence of flowers is still conflicting (Dean 1974). The investigations of Fluke (1937), for example, suggested that there was a direct relationship between the abundance of flowers and hoverfly oviposition rates in fields with or without flowers. In an unreplicated experiment, Van Emden (1965) noted that most aphid predation by hoverfly larvae occurred near flowers adjacent to the "edgegrowths" of fields and that aphid numbers here were significantly lower there than anywhere else. Hickman and Wratten (1996) reported higher oviposition in winter wheat fields bordered with *Phacelia tanacetifolia* (Benth.) than in control fields. Harwood et al. (1992) found yellow water-trap catches of gravid hoverflies to be significantly higher where wild flowers were found in field margins than in fields devoid of flowers. However, oviposition rates were not measured.

Dixon (1959) noted that maximum hoverfly oviposition coincided with the flowering of broom (*Sarothamnus scoparius* (L.)). However the important factor may have been peak aphid infestation, which occurred at the same time. In a large-scale experiment, Pollard (1971) compared two contrasting farmland areas, one with many more trees, shrubs and flowers than the other and found that oviposition rates were higher in the more diverse area. However, variables such as hoverfly distribution, aphid infestation and other confounding factors were not eliminated; Pollard (1971) concluded that the difference was the result of certain hoverfly species being restricted to woodland areas.

Contrary to these findings, Cowgill (1990) found no effect on oviposition rates at different distances from flowers in a 'conservation headland' (Haysom et al. 2004) while Chambers (1991) showed that field boundary type had no effect on hoverfly oviposition in the adjacent crop.

To minimise the variation associated with the use of naturally occurring flowers and aphid populations, the experiments below used standardised model flowers with or without pollen and nectar added and standardised aphid 'bait' plants. The aim was to assess the impact of the model flowers on hoverfly oviposition in their vicinity and to explore the relative importance of colour stimulus and food rewards.

Materials and methods

Model flowers. These consisted of brown plastic flowerpot saucers (diameter 19 cm). For yellow 'flowers', the inside of each tray was coated with a foundation base paint (Goo-Var Ltd., Ellenshaw Works, North Humberside, UK). A coating of yellow fluorescent paint (Goo-Var Ltd., high visibility: 1263) was applied 12 h later. Unpainted flowerpot saucers were used as controls. Four holes (diameters 4mm) were drilled in the base of each tray for drainage of rain water. Each tray was then screwed horizontally onto a wooden stake (2.5 x 2.5 cm cross section) which was then inserted into the soil. Model flowers were used in sets of three at different heights (125, 92 and 32 cm). Food resources (when used) consisted of a sprinkling of *Populus deltoides* Bartram pollen (Sigma Aldrich Co Ltd., Poole, Dorset, Cat. No. P-7395) and/or a sucrose cube soaked in a 25% solution of clover honey. All trays contained a central white cotton pad (diameter 5cm) on which the food resources, if used, were placed.

Reflectance spectrophotometry. The reflectance spectra of the yellow paint were analysed in the laboratory using an Ocean Optics B.V. S2000 dual channel fibre optic spectrometer with a DT-MINI Deuterium Tungsten halogen light source linked to a fibre optic reflectance probe. A fast scan carried out from 200 nm to 800 nm showed a sharp peak at approximately 520 nm (the yellow part of the light spectrum) but no peak within the ultraviolet part. Aphidophagous syrphids such as *Episyrphus balteatus* Degeer are sensitive to spectral curves within the 490-560 nm spectrum (e.g., Stavenger 1974; Horridge et al. 1975; Ortu & Floris 1990). The low ultra-violet reflectance of the paint was similar to that of *Ranunculus* flowers, which are frequently visited by hoverflies (Kevan et al. 2001). Unfortunately, yellow paint which mimicked the reflectance spectrum of high-ultra-violet reflecting flowers such as *Senecio jacobea* L. could not be found. Brown was chosen for controls because it reflects fairly evenly and dully across the insect visual spectrum (Kevan, 1978).

Oviposition bait plants. Broad bean (*Vica faba* (cv. Sutton Dwarf)) seeds were planted weekly in a peat based compost, in plastic plant pots (diameter 6 cm), with two seeds in each pot, and grown in a glasshouse. After two weeks (four leaf stage), each plant was infested with approximately 12 adult pea aphids (*Acyrthosiphon pisum* (Harris)) taken from a non-clonal laboratory stock. The plants were then left for one week, for the aphids to establish, before being taken to the field.

Experimental sites. In all experiments, the model flowers were placed in the field margins, approximately 1 m from the crop edge, of one side of each of five winter wheat fields on Uggford Farms at Wilton, in Wiltshire, UK. Fields 1 (2002/3) and 2 (2002) had well-established hedgerows situated approximately 2 m from the edge of the crop. Fields 3 (2002) and 4 (2003) were bordered by mature beech (*Fagus sylvatica* L.) and sycamore (*Acer pseudoplatanus* L.) trees and hedgerow shrubs. A grass strip (20 m width) separated the tree and hedgerow border from the crop in these two fields. Field 5 (2003) was open to a farm track. No insecticide was used on the experimental fields in either season. The winter wheat crops were harvested on 23 August (2002) and on 13 August (2003).

Experiment 1: oviposition near model flowers and at control sites (2002). Four sets of yellow model flowers were used in each experimental field (1, 2 and 3) and four sets of controls (stakes without flowerpot trays). Each set consisted of three model flowers or controls at different heights (125, 92 and 32 cm) arranged in an equilateral triangle with sides of 45 cm. These were positioned in the field margins, approximately 1 m from the crop edge at intervals of 50 m, with model flowers and control positions alternating (see Fig. 1). All model flowers contained pollen and honey on the cotton pad, renewed before oviposition bait plants were put out. Naturally-occurring flowers in the hedgerows on the experimental side of each field were removed weekly with a scythe.

At weekly intervals, at each model flower and control position, two bait plants in their pots were selected at random and placed on the soil surface midway between the stakes and the edge of the crop. These plants were retrieved 48 h later and the number of hoverfly eggs were counted and where possible, identified to species by reference to photographs. As far as possible, eggs which could not be identified to species were kept and reared to the adult fly stage. The experiment was repeated four times at weekly intervals between 10 and 30 July 2002.

Winter wheat plants within a radius of 5 m of the bait plants were regularly checked for aphid populations each time bait plants were put out and collected.

Experiment 2: relative importance of colour, pollen and honey 2002 and 2003. This experiment was carried out at weekly intervals and repeated three times in 2002 (7- 20 August) and five times in 2003 (12 July –9 August). Four sets of three painted yellow model flowers and four sets of three unpainted brown ones were used in each experimental field (1, 4 and 5). Sets of model flowers were positioned at different heights (125, 92 and 32cm) and arranged in an equilateral triangle as above. For each ‘flower’ treatment in each field, one set of three ‘flowers’ (i.e., painted) contained pollen, one contained honey, one had honey on a sugar cube and pollen and one had no added food resources. In each of the three fields, sets of ‘flowers’ were randomly positioned approximately 1 m from the crop edge at intervals of 50 m. Prior to each repeat the positions were re-randomised. Pollen and honey resources were renewed immediately before bait plants were put out. The latter were positioned and removed as in Experiment 1.

In 2003, during the last three weeks of the experiment (26 July – 9 August), as well as the bait plants positioned as described above, two additional bait plants were placed on the ground in the wheat crop at 5 m from each set of model flowers and two more bait plants were placed at 10 m.

These plants were placed on a line running from the model flower stakes into the crop at right angles to the crop edge.

As in experiment 1, wheat plants within a radius of 5 m of the bait plants were regularly checked for aphids each time bait plants were installed and collected.

Analysis. Mann-Whitney U-tests were used to test the differences between the median numbers of hoverfly eggs found on bait plants near yellow model flowers and controls (Experiment 1), and also between the numbers of eggs found on bait plants at distances of 50 cm, 5 and 10 m from painted (yellow) flowers and unpainted (brown) controls (Experiment 2). For painted and unpainted treatments separately, Kruskal-Wallis tests were used to test the differences between the numbers of eggs laid on plants at different distances from model flowers with and without food resources. All statistical analyses were performed using SPSS11.

Results

Experiment 1 (2002): comparison of oviposition on bait plants near model flowers and at control sites. A total of 61 hoverfly eggs was found on bait plants near yellow model flowers and 15 near brown trays at control positions (Fig. 2). This difference was highly significant (Mann-Whitney U-test; U = 747; $n_1 = n_2 = 48$; $P < 0.001$). Over the whole experimental period, one or more eggs were found on the bait plants associated with 26 of the 48 yellow model flower sets and on 11 out of 48 in the brown controls. The highest number of eggs at any one position was 11 (yellow model flower, field 2). For sets of bait plants with one or more eggs, there was a trend for more to be laid on plants near the models ($x = 2.35$, S.E. 0.42) than at control positions ($x = 1.36$; S.E. 0.20), but this difference was not significant (Mann-Whitney U-test, U=98; $n_1= 11$, $n_2=26$; $P > 0.05$).

Approximately 80% of the eggs (60) were identified as *E. balteatus*; this was confirmed by allowing some to develop to adults. Eggs of other species included *Melanostoma scalare* (Fabr.), *Eupeodes corollae* (F.) and *Platycheirus peltatus* (Meigen). No aphids were found on wheat plants in any of the fields during the experiment.

Experiment 2 (2002 and 2003): relative importance of colour, pollen and honey. In both years a higher total number of eggs was found at all distances on bait plants near the yellow model flowers than near the unpainted ones (Table 1). These differences were highly significant at 50 cm (Mann-Whitney tests, 2002 U = 402; $n_1 = n_2 = 36$; $P < 0.001$; 2003 U = 1195.0; $n_1 = n_2 = 60$; $P < 0.001$). In 2003, significantly more eggs were found at 10 m from coloured than at 10 m from unpainted models ($U = 484.5$; $n_1 = n_2 = 36$; $P < 0.05$). Results were not significant at 5 m ($U = 549.0$; $n_1 = n_2 = 36$; $P > 0.05$), although the trend was similar to that at other distances.

There were no significant differences in oviposition, in either year or at any distance between all three types of yellow model flowers compared with brown controls when yellow and unpainted treatments were analysed separately or together (Kruskal-Wallis tests, $P>0.05$ in all cases). As in experiment 1, the majority of eggs (145/162; 90%) were identified as *E. balteatus.*

Discussion

Although artificial flowers have previously been used to investigate the foraging behaviour of Diptera (Kugler 1956; Isle 1949; Lunau 1993; Sutherland 1998), they have not been used to assess their effect on oviposition. The model flowers in these investigations combined three of the attributes exhibited by real flowers, which are thought to be important in hoverfly foraging: colour, and pollen and nectar resources. The fact that significantly more eggs were laid in the vicinity of these models than in control positions strongly supports the findings of those workers who found an increase in oviposition associated with flowers (e.g., Fluke 1937; Dixon 1959; Van Emden 1965; Hickman & Wratten 1996). Of the three flower attributes used here, the results also suggest strongly that colour is of paramount importance in eliciting this response. The results are strengthened by the fact that significant differences were found in all experiments over two years and that the same trend was shown throughout the experimental period (Table 1).

The use of model flowers, and the removal of natural flora, enabled conditions to be standardised; this avoided problems associated with interpreting results when there are large numbers of different variables (e.g., Pollard 1971). The fact that no aphids were found in the crop during either year meant that this source of variation was also eliminated. However, thrips (Thysanoptera) may have occurred on the wheat but were not detected. No eggs were found on the wheat plants, however.

Ideally, as there is a positive correlation between hoverfly oviposition and prey density (Sanders 1979; Gilbert 1993; Van Emden 1990; Bargen et al. 1998) the bait plants should all have been infested to exactly the same extent when they were put out into the field. However, although the plants were of the same age, and all were initially infested with the same number of aphids, it was not possible to ensure this. However, the bait plants were allocated at random and with more than 1000 of these plants used in total, it is very unlikely that any such differences compromised the results. While not included in the scope of the experiment, the abundance of aphids on the bait plants when the syrphid larvae hatched would of course influence the biological control success of the hoverflies (Tenhumberg, B. & Poehling, H.M. 1995). A low oviposition threshold could facilitate larval reduction of aphid populations (Tenhumberg, B. 2004).

Pollen is required by immature adult hoverflies to mature their reproductive organs (Svensson & Janzon 1984; Cowgill et al. 1993) and by gravid females for ovigenesis (Schneider 1948). However, in this work, attraction of gravid syrphids into areas without floral resources could be achieved through the use of only yellow model flowers. Hoverflies rely on vision to select a feeding site (Sutherland 1998; Kan 1988a, 1988b) and this is supported in this experiment where there was no evidence of increased oviposition near coloured targets with food rewards compared with those without them. Indeed, in 2003, more eggs were laid near yellow targets with no food resources than in any other treatment. These results suggest that, even if gravid hoverflies respond to a colour cue primarily to obtain food, the presence of aphids near the target will elicit an oviposition response whether or not food for adults is available. Cues for hoverfly oviposition include aphid volatiles (Volk 1964; Budenberg & Powell 1992) and visual stimuli (Sanders 1979; Kan 1988a, 1988b). While plant green leaf volatiles and aphid attack pheromones encourage hoverfly oviposition (Verheggen et al. 2008), these volatiles come from the bait plants and are not related to the food resources, or lack thereof, on the model flowers.

Even though colour appeared to be the most important stimulus in attracting gravid females, it might have been expected that in its absence, olfactory cues from honey and pollen would result in more visits to unpainted targets with food resources and more oviposition near these targets. There was no evidence for this. In fact, the lowest numbers of eggs were found on bait plants near the unpainted model flowers which were provided with both pollen and honey (Table 1). This suggests that olfactory stimuli from pollen and nectar are much less important than is colour in orientating hoverflies towards flowers. This study did not investigate the potential of floral aromas as an attractant for hoverflies however. If an aroma that mimicked a flower had been added to the traps, they may have been more effective in stimulating oviposition.

The fact remains that, although the pollen and/or honey provided in some model flowers may have dried out or been consumed by other insects, this possible unavailability did not lead to their being no significant difference between yellow and brown model flowers.

Although no comparison was made between the effects of natural and artificial flowers in this investigation, the model flowers were considerably larger and brighter than any of the flowering plant species that were removed during the experiment. There is a possibility that the highly significant results seen here were partly the result of these oversized models providing a ‘super stimulus’ (Kevan & Baker 1983) to gravid hoverflies. A large flower size generally means an increased ‘advertising’ area to potential pollinators (Mulligan & Kevan, 1973; Kevan, 1978; Schmid-Hempel & Speiser, 1988). Aphidophagous hoverflies may have difficulty in locating small flowers in large agricultural fields (Fægri & van der Pijl 1979). Therefore future studies could include a comparison of the yellow model flowers to natural flowers.

In both years of this study, most of the eggs laid on aphid-infested bait plants were identified as those of *E. balteatus*. While the number of eggs laid on the bait plants was significantly higher for those laid near the yellow model flowers compared to those laid near the unpainted control, the number of ovipositing females involved may have been low. Females of *E. balteatus* lay between 7-46 eggs per day depending on the nearby flower species (Laubertie et al. 2012).While these data were not recorded, it is important to recognise that the number of ovipositing females at the yellow and control model flowers may not have differed. However, the overall greater number of eggs near yellow model flowers still has large implications for biological control.

The larvae of this species can consume between 137-190 third-instars of the aphid *Sitobion avenae* (Fabr.) (Ankersmit et al. 1986) over their development time of 7-10 days (Rojo et al. 1996). In most years, *E. balteatus* is the predominant species on agricultural land in the U.K. (Dean 1982; Chambers et al. 1986; Cowgill et al. 1993). The species has also been implicated as the most important agent limiting aphid population growth on apple (Wnuk 1977) and on crops such as sugar beet (Hurej 1992), kale (Hughes 1963), Brussels sprouts (Pollard 1969) and winter wheat (Ankersmit et al. 1986). The possibility that yellow model flowers could be used to attract species such as *E. balteatus* to the crop would be of great practical importance in conservation biological control, assuming that aphid densities are above the predator's oviposition threshold.

For biological control in crops, artificial flowers have many advantages over natural ones. For example, they could be of particular benefit early in the season when flowering wild flowers are rare and aphid populations are still low and added or naturally-occurring flowering species (e.g., Hickman & Wratten 1996) have not yet produced inflorescences. The model flower placements in this study were selected empirically, Future studies are needed to determine the ideal model flower dispersion to minimise labour, materials, and crop damage.

These results are relevant to farmers and horticulturalists, especially in the context of ecosystem service-rich agriculture (Wratten et al. 2013), as it may be possible to enhance the biological control of aphids, using a novel and inexpensive method, based on at least a partial knowledge of adult hoverfly foraging ecology. The simple experimental protocols used here are ideal to be developed into a Service Providing Unit (SPU, Luck et al. 2003) so that growers can easily deploy this SPU with minimal negative impact on their usual agricultural practises. Although it is too early to determine the economic costs and benefits of this SPU, the results from this paper have laid the foundation for biological control methods of aphids using hoverflies to be made available to growers.

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Fluorescent yellow												
Food resources	**Pollen and honey**			**Pollen**			**Honey**			**None**		
Distance from flowers (m)	**0.5**	**5**	**10**	**0.5**	**5**	**10**	**0.5**	**5**	**10**	**0.5**	**5**	**10**
Total 2002	**24**	**-**	**-**	**10**	**-**	**-**	**13**	**-**	**-**	**15**	**-**	**-**
12-14.07.03	**0**	**-**	**-**	**5**	**-**	**-**	**2**	**-**	**-**	**2**	**-**	**-**
19-21.07.03	**5**	**-**	**-**	**10**	**-**	**-**	**3**	**-**	**-**	**9**	**-**	**-**
26-28.07.03	**2**	**0**	**1**	**2**	**5**	**0**	**6**	**0**	**7**	**7**	**3**	**4**
02-04.08.03	**3**	**0**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**3**	**2**	**2**
09-11.08.03	**3**	**2**	**4**	**0**	**2**	**4**	**2**	**4**	**2**	**4**	**6**	**3**
Total 2003	**13**	**2**	**6**	**18**	**7**	**4**	**14**	**4**	**10**	**26**	**11**	**9**

Brown (unpainted)												
Food resources	**Pollen and honey**			**Pollen**			**Honey**			**None**		
Distance from flowers (m)	**0.5**	**5**	**10**	**0.5**	**5**	**10**	**0.5**	**5**	**10**	**0.5**	**5**	**10**
Total 2002	**1**	**-**	**-**	**3**	**-**	**-**	**11**	**-**	**-**	**0**	**-**	**-**
12-14.07.03	**0**	**-**	**-**	**0**	**-**	**-**	**0**	**-**	**-**	**0**	**-**	**-**
19-21.07.03	**0**	**-**	**-**	**3**	**-**	**-**	**2**	**-**	**-**	**1**	**-**	**-**
26-28.07.03	**0**	**0**	**0**	**1**	**0**	**0**	**2**	**0**	**1**	**0**	**1**	**0**
02-04.08.03	**0**	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
09-11.08.03	**0**	**0**	**1**	**0**	**1**	**6**	**6**	**1**	**3**	**1**	**5**	**1**
Total 2003	**1**	**0**	**1**	**6**	**1**	**6**	**10**	**1**	**4**	**2**	**6**	**1**

Table 1. Experiment 2 (2002 and 2003) Number of syrphid eggs. Relative importance of colour, pollen and honey in hoverfly oviposition at all distances on bait plants near the fluorescent yellow model flowers and near the unpainted controls. The data collection dates for 2002 were 7-20 August. The observation data for 2003 were collected for 48 h at weekly intervals, and the total number of syrphid eggs was summed for 2003. *E. balteatus* eggs comprised 145/162, or 90%, of the total eggs laid.

Figure Captions

Fig. 1. Experiment 1 (2002). Diagram of setup for experiment 1. The model flowers were placed 1 m from the edge of the field, alternating between yellow model flowers and the control unpainted trays with 50 m between them. Two pots of bait plants (*Vica faba*) infested with aphids were placed halfway between the model flowers and the edge of the field.

Fig. 1

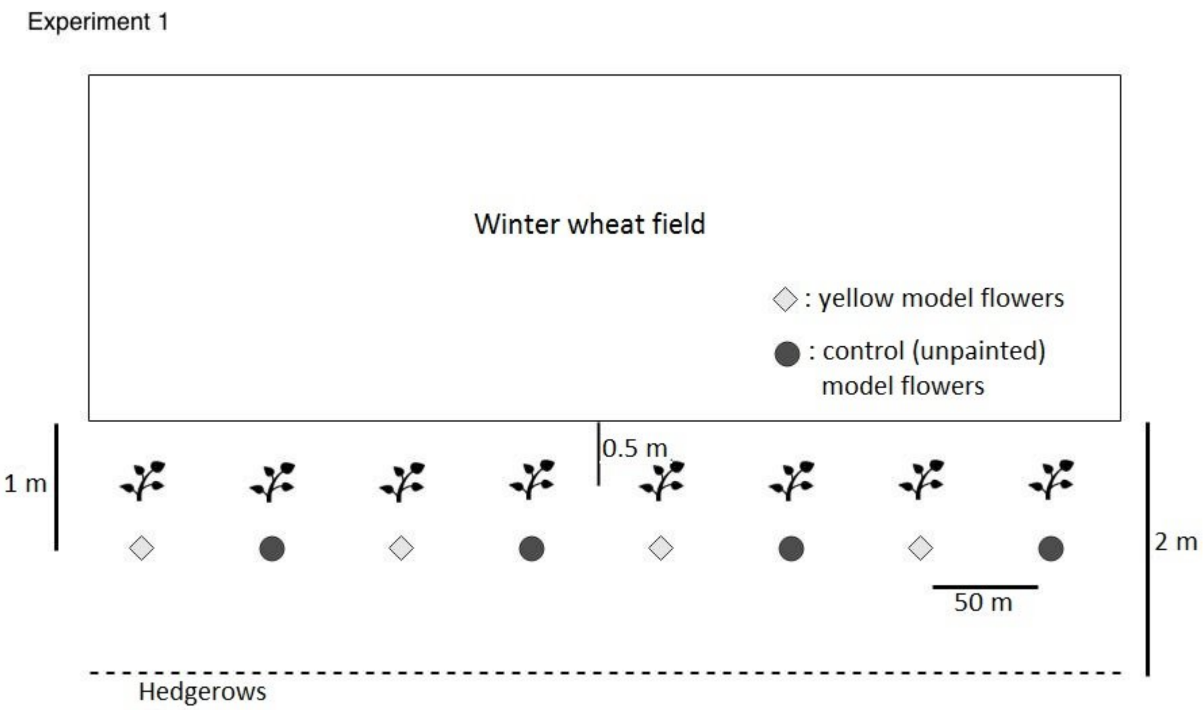
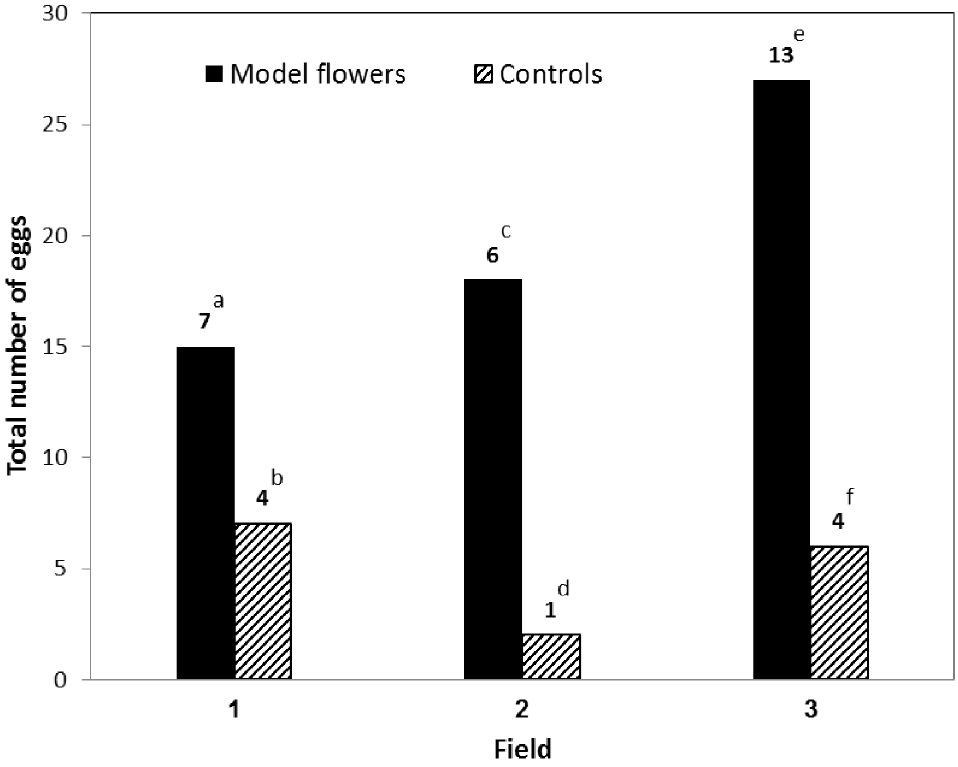

Experiment 1
Winter wheat field
◇ : yellow model flowers
● : control (unpainted) model flowers
0.5 m
1 m
2 m
50 m
Hedgerows

Fig. 2. Experiment 1 (2002). Comparison of oviposition on bait plants near model flowers and at control sites. Numbers are eggs of the hoverflies *E. balteatus* (90% of the total), *Melanostoma scalare* (Fabr.), *Eupeodes corollae* (F.) and *Platycheirus peltatus* (Meigen) found near model flowers and at control sites. The letters indicate statistical significance between sets of bait plants with one or more eggs in each of the three fields.

Fig. 2


■ Model flowers
▨ Controls
Total number of eggs
0
5
10
15
20
25
30
7 a
4 b
6 c
1 d
13 e
4 f
1
2
3
Field