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THE USE OF MODEL FLOWERS TO ENHANCE OVIPOSITION BY APHIDOPHAGOUS HOVERFLIES (DIPTERA: SYRPHIDAE) IN ARABLE CROPS

by

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ABSTRACT
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THE USE OF MODEL FLOWERS TO ENHANCE OVIPOSITION BY APHIDOPHAGOUS HOVERFLIES (DIPTERA: SYRPHIDAE) IN ARABLE CROPS

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This project examines the effect of using model flowers in the margins of cereal fields on oviposition by aphidophagous hoverflies. In 2002 there was significantly more syrphid oviposition on bait plants near standardised model flowers consisting of yellow painted flower pot trays mounted on stakes at three different heights, and containing pollen and nectar, than on bait plants at control positions. Further experiments carried out in 2002 and 2003 compared oviposition near yellow and unpainted (brown) model flowers with and without food resources. In both years, significantly more oviposition was found near the yellow model flowers than near the brown ones. However, the presence or absence of pollen, nectar or both had no effect on oviposition rates. In an attempt to explain these results, insectary based tests compared the numbers of eggs laid on bean plants infested with aphids, and the numbers of landings on yellow targets by starved and normally fed gravid females of *Episyrphus balteatus*, the commonest aphidophagous syrphid species in the U.K. The results indicated that hunger state had no effect on either response. This suggested that syrphids may be attracted towards an apparent source of food even if not in a state of hunger, and in the presence of aphids will lay eggs even if hungry rather than continuing to search for food.

Further work was aimed at improving the attractiveness of the flower models. The results of laboratory and field experiments comparing different shades of yellow indicated that fluorescent yellows with a UV component were the most attractive. When slow release nepetalactone lures were placed close to model flowers, significantly more syrphid eggs were laid at a distance of 25m from the model flowers than at 0m, suggesting that this volatile has a deterrent effect on syrphid oviposition. There were no significant differences between oviposition rates on bait plants (2004) or yellow water trap catches of gravid female syrphids (2005) in the presence or absence of *cis*-jasmone. The results may have been affected by rain water collecting in the lids of the vials which prevented dispersal of the volatile.

In separate experiments, yellow trap catches were used to compare their attractiveness to gravid syrphids using targets of different heights, of different sizes and with different patterns. Yellow water traps placed 30cms above the ground, the largest water traps (25cm diameter) and water traps without patterns were identified as the most attractive.

An experiment carried out in the grounds of the University of Southampton assessed the effect of a model flower with the ‘optimum’ attributes that had been identified, on syrphid oviposition. Overall, significantly more oviposition occurred near model flowers than at control positions.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. Aphids as pests of cereals

Aphids are the most important crop pests in the agriculture of the temperate climatic zones (Minks & Harrewijn, 1989), where one plant species in four is infested (Dixon, 1987). Aphids damage plants in several ways: by feeding on the phloem and draining nutrients from them, and by inoculating toxins through their saliva and thus transmitting virus diseases (Harrington *et al.,* 1989; Schepers, 1989). The production of honeydew that covers the leaves provides a rich medium for fungal growth. In turn, this leads to reduced photosynthetic efficiency, loss of plant vigour and a reduction in the potential yield (Fiebig *et al.*, 2004). The intricate lifestyle of aphids in close association with their host plants, their polymorphism, their ability to reproduce both sexually and asexually and the potential rate of population increase creates tremendous problems in agriculture. This telescoping of generations and parthenogenesis may lead to the development of 4,000 million alatae of the black bean aphid (*Aphis fabae*) on a hectare of field beans in the U.K. (Dixon, 1985).

In Britain, it has been estimated that in an average year, losses in crop yield due to direct feeding by aphids may exceed £100 million, with aphid transmitted viruses causing losses of a similar order (Tatchell, 1990). Aphids are also major pests in the United States (Brooks *et al.,* 1994), South Africa (Walters *et al.,* 1980), Ethiopia (Haile & Megenasa, 1987) and New Zealand (Kahl, 1996). In European orchard crops such as apple and pear, they frequently cause economic damage to flowers, fruitlets or fruits directly (Solomon *et al.,* 2000). The scale of the aphid problem is immense and therefore needs to be approached on an equally large geographical scale.

1.2. Aphid control

For some years, aphid control was achieved with the persistent organochlorines (Bartlett *et al.,* 1952). However, these chemicals had a serious effect on many non-target organisms and 'biological pest explosions' became so common (DeBach, 1973) that they were withdrawn from use in 1990. Some success was achieved with the organophosphate and hexachloro-hexane (HCH) compounds, although many of these have since been banned (Gange, 1996). Insecticides not only disrupt the ecological balance by enabling pests to increase in numbers sufficient to cause economic damage, they also eliminate or greatly reduce natural enemies. Overuse of chemical sprays can also lead to a rapid increase in the proportion of certain resistant variants within aphid species (Solomon *et al.*, 2000). Pesticide usage has not only had a negative environmental impact on water catchments, it has also been linked to the sudden declines of farmland birds and beneficial insects (Holland, 2004).

Adverse public attitudes to pesticides have intensified in recent years and wide-scale application of such chemicals is becoming increasingly unacceptable (Tatchell, 1990; Peterson & Coats, 2001). Their use needs to be optimised in an environmentally acceptable way so as to maintain farm incomes and an adequate food supply. Strategies that allow broad-spectrum pesticides to be applied at reduced rates to high-value crops (e.g. brassicas) with low pest 'damage' thresholds (White *et al.*, 1995) may help to maintain predator survival (Mann *et al.*, 1991). Insect repellents may also have a role in eliminating crop pests from agroecosystems (Peterson & Coats, 2001).

The literature on the biological control of aphids is extensive. Franz (1961), DeBach (1973), Dixon (1987) and Hemptinne *et al.,* (1994) provide a broad coverage of the subject. Biological control provides one of the best alternatives to chemicals: it causes no resistance and it does not taint or damage crops. Insects that contribute to the control of cereal aphid populations include ladybirds, parasitic wasps, spiders and aphidophagous hoverflies (Tenhumberg, 2005). In Western Germany, hoverfly larvae are by far the most important predators of cereal aphids (80% of all stenophagous predators) (Groeger, 1992; Tenhumberg, 1992; Winder, 1994). In the United States, hoverflies have substantially controlled several introduced aphid pests such as the spotted alfalfa aphid (*Therioaphis trifolii* (Monell)) and the walnut aphid (*Chromaphis juglandicola* (Kaltenbach)) in orchards and perennial crops (Laing & Hamai, 1976). In European orchards, hoverfly larvae are reported to be effective biological control agents in top fruit (Marboutie, 1976; Bonnemaison, 1972; Vogt & Weigel, 2000). The larvae of hoverflies from the genera *Melanostoma* have also been found to be effective predators of white butterfly (*Artogeia rapae* (L.)) and diamond-back moth (*Plutella xylostella* (L.)) larvae on a variety of plants (Valentine, 1967; Miller, 1971; Ashby and Pottinger, 1974).

In particular, the association of *Episyrphus balteatus* (Degeer) with aphids is clearly established and has been reviewed on several occasions (e.g. Wnuk, 1977; Carter *et al.,* 1980; Ankersmit *et al.,* 1986; Chambers, 1991). The larvae of *E. balteatus* are the most important predators of cereal aphids in the UK (Chambers & Adams, 1986; Pike *et al.,* 1991).They have the potential to prevent pest outbreaks if the adults arrive when aphid density is still low (Tenhumberg & Poehling, 1995). The larvae of *E. balteatus* have been known to consume over 416 aphids (*Aphis pomi*) (Stary, 1988; Gilbert, 1993). In Poland, Wnuk (1977) found that *E. Balteatus* could control aphid populations at predator: prey ratios of up to 1:200, if the rate of increase of the pest population was less than 16% per day. The larvae of *E. corollae* are also voracious predators of aphids. A single larva has been known to consume an average of 311 wheat aphids (*Diuraphis noxia*) (Rojo *et al.* 1996). The larvae of *Syrphus ribesii* (L.) are known to be efficient predators attacking aphids at a faster rate and searching more rapidly than species such as *Melanostoma.*

In aphidophagous hoverflies, oviposition preference is central to the biological control of aphids) resulting in a distribution of larvae on different hosts (Sadeghi & Gilbert, 2000a). However, the cues and behavioural mechanisms which enable females to locate and select an oviposition site are still unclear.

Hoverflies generally, and in particular what is known about their oviposition preferences, are reviewed below.

1.3. Hoverflies

1.3.1. Taxonomy

Hoverflies are one of the largest families of flies. Some 275 species of hoverfly have been recorded in the British Isles (e.g. Stubbs & Falk, 2000). Hoverflies are true flies from the Order Diptera, suborder Cyclorrhapha, class Insecta, phylum Arthropoda, family Syrphidae (Lee *et al.*, 1999). There are three subfamilies in the Syrphidae: Syrphinae, Eristalinae and Microdontinae (Stubbs & Falk, 2000). The Syrphinae (about 23 genera in Britain) are split into three tribes: the Syrphini (19 genera), the Bacchini (4 genera) and the Paragini (3 species) (Stubbs & Falk, 2000).

One third of the British hoverfly fauna belongs to the subfamily Syrphinae Stubbs & Falk, 2000). Syrphinae are distinct from Eristalinae and Microdontine in that the larvae are aphid predators (Gilbert, 1993; Stubbs & Falk, 2000). However, *Melanostoma* and *Platycheirus* species from the tribe Bacchini, may well be generalist predators in the leaf litter (Gilbert, 1993). *E. balteatus* constitutes 90% of the composition of syrphid species (Groeger, 1992). The larvae of *E. balteatus* have been reported from colonies of more than one hundred aphid species world-wide (Sadeghi & Gilbert, 1999).

1.3.2. Identification of the adult hoverfly

Hoverflies (Diptera: Syrphidae) can be distinguished from all other flies by the possession of a longitudinal ‘false vein’ between the radius and the media (Coe, 1953). The large eyes, which allow for acute vision, touch at the top in male hoverflies of most species, whereas the eyes of the female are separated by a gap (Stubbs & Falk, 2000). Male and female hoverflies are easily distinguished by looking at the underside of abdomen: males have curved asymmetrical genitalia, whereas females have pointed abdomens with unobtrusive genitalia. Mature eggs can often be seen (in the Syrphini) through the semi-transparent abdominal pleurites (Gilbert, 1993). Individual anatomies may look different because some specimens have full or empty crops and because some females may or may not have fully developed eggs. The biology of hoverflies has been reviewed in general by Gilbert (1993), Gilbert & Jervis (1998) and Stubbs & Falk (2000).

1.3.3. Hoverfly distribution

Due to their strong flight and high mobility, hoverflies (Diptera: Syrphidae) are widespread throughout the temperate regions of the world (Lee *et al.*, 1999). In the summer, large movements of aphidophagous hoverflies have been recorded flying over the Alps and the Pyrenees (Owen, 1956; Aubert *et al.*, 1976; Gatter & Schmid, 1990). North European populations have been known to migrate in huge numbers to the Mediterranean (Gatter & Schmid, 1990; Branquart, 1999). In the UK, *E. balteatus* and *Eupeodes corollae* (Fabricius) are the most dominant and economically important aphidophagous species on arable land (Sadeghi & Gilbert, 1999).

1.3.4. Larval development

Hoverflies pass through three larval stages before pupating as they develop from egg to adult. The number of eggs produced per female is species-specific and may depend on the nutritional condition and age of the female (Jervis & Kidd, 1986; Jervis & Copland, 1996). The females of most syrphid species are usually ready to lay eggs 7 or 14 days after emergence (Sadeghi & Gilbert 2000b; Dong *et al.,* 2004). In laboratory conditions, females of *E. balteatus* might lay between 2,000 and 4,500 eggs during their life-time at a rate of 1 to 2 eggs per ovariole per day (Branquarte & Hemptinne, 2000). However, Dong *et al.,* (2004) found the average found to be 488 eggs per female (maximum 701 eggs per female) with an egg-hatching rate of 88.4%. The average egg production of *E. corollae* has been reported to be 400 (Barlow, 1961; Wilkening, 1961) over its lifetime. Eggs may be elongated ovoids, soft and rather flattened and off-white in colour (Gilbert, 1993). The egg-stage is very brief in common species, typically lasting less than 5 days, although development may vary with conditions of temperature and humidity (Gilbert, 1993).

Depending on temperature, humidity, food supply and day length and other factors, the larval stage may last only 10 days in some species and up to two years in others (Schneider, 1948 & Coe, 1953). Aphidophagous syrphid larvae are unique among fly larvae in that they are coloured. For example, the larva of *Sphaerophoria cylindrica* (Say) is greenish yellow, whereas the mature larva of *S. ribesii* varies in colour from yellow to pink on one part of the body. However, the larva of *E. balteatus* is white in colour (see Rotheray & Gilbert (1989) for detailed descriptions and keys to most genera).

The larvae of syrphid species such as *E. balteatus* and *S. ribesii* are normally sluggish during daylight hours, but voracious predators at night (Goeldin de Tiefenau, 1974). Larvae use sticky salivary secretions to immobilise prey and mouthhooks to pierce the aphid body and hold it aloft while the body contents are sucked out (Rotheray & Gilbert, 1993). Third-instar larvae can dispose of one aphid per minute and will often discard aphids half-eaten (Rotheray, 1989a). Aphid colonies are frequently obliterated resulting in periods of starvation for the larvae and third-instars have been seen crawling two metres/hr and living between three and six days without aphids (Rojo *et al.,* 1996). Starved larvae may also compensate for their nutritional deficiencies by searching harder, capturing prey more rapidly, and sucking 50% more of the contents of each aphid before discarding it (Leir & Barlow, 1982). In the absence of a host, the larvae of *Melanostoma* can subsist on plant materials such as pollen (Schneider, 1969). In the laboratory, Gilbert (1993) found aphid extracts, honeydew and sucrose to be suitable feeding stimulants for the larvae of many species of hoverfly.

The fully-grown larva, having attached itself to a suitable object, clears its digestive system by voiding a black oily liquid. In many species, the larval skin of the third-instar is not shed, but hardens to enclose the pupa (e.g. Rotheray, 1989a). Adult emergence may take place in the morning after a few days, depending on temperature and humidity. In some species, diapause may occur in the larval, pupal or adult stages when temperatures are low. The larvae of *S. ribesii* for example, over-winter in leaf litter at the foot of trees and shrubs, behind ivy leaves or in other sheltered places (Gilbert, 1993) and are known to be exceptionally cold-tolerant (Hart & Bale, 1997). Hoverfly species such as *E. corollae* and *Metasyrphus luniger* (Meigen) may overwinter as pupae. In *E. balteatus,* the bulk of the population migrates to southern Europe (Rotheray, 1989a; Gatter & Schmid, 1990; Branquart, 1999), although a few individuals may overwinter as adults (Gilbert, 1993). The limited cold tolerance of *E. balteatus* to temperatures below 5^{o}C indicates that individual overwintering success is highly dependent on UK winter conditions (Hart & Bale, 1997).

The number of generations produced per year varies between species. *Epistrophe eligans* (Harris) for example, has only one generation each year and the adults usually appear in the spring (Rotheray, 1989b). *E. balteatus* has a single generation (occasionally two) in the U.K. with adult activity in late summer (Gilbert, 1993). *Dasysyrphus albostriatus* (Fall) and *S. ribesii* are known to have two (sometimes three) generations per year (Rotheray, 1989a). In *E. balteatus*, longevity of 55.5 and 56.8 days for female and male adults, respectively, has been observed under favourable conditions (Dong *et al.,* 2004).

1.3.5. Mating behaviour

Males are generally smaller than the females, complete development slightly faster and usually emerge earlier in the season. This allows males to feed and mature their reproductive systems before females appear; thus ensuring that potential mates are not missed (Thornhill & Alcock, 1983). For many species, mating occurs 3-4 days after emergence and takes place in flight, lasting for a few minutes at most or less than a few seconds. In *E. corollae* and *Sphaerophoria scripta* (L.), mating may last several hours: the male resting on the back of the female as she flies about and rests on leaves (Gilbert, 1993).

If mating should occur while the eggs of the female are undeveloped, this may influence their final maturation (Gilbert, 1993).

1.3.6. Adult feeding-pollen

The requirement for adult hoverflies to feed on pollen for the maturation of the ovarioles and the eggs has long been recognised (Schneider, 1948, 1969; Haslett, 1989a, b) and reviewed on several occasions (e.g. van Emden, 1965; Haslett, 1983, 1989b; Gilbert & Jervis, 1998). Haslett (1983) found pollen from white, yellow and violet-blue/red flowers in the gut of *E. balteatus* at various times, although the pollens of white and yellow flowers were eaten most. Ankersmit *et al.* (1986) found that many different types of pollens were suitable for *E. balteatus* adults, although those fed on maize pollen did less well and produced fewer eggs. Schuhmacher & Hoffmann (1982) showed that the width of the food furrows overlying the pseudotracheal canals in a variety of Syrphidae, corresponded to the diameter of pollen grains taken by adults; flower species whose pollen grains were larger than this were not acceptable to the flies (Gilbert & Jervis, 1998).

Pollen contains about 25% (by weight) of energy-rich carbohydrates and various lipids rich in energy (Gilbert, 1993). Females of the genera *Melanostoma* may continue to feed mainly on pollen throughout their life span. However, *E. balteatus* females may take pollen and nectar in different ratios according to whether or not they are maturing a batch of eggs (Gilbert, 1993; Jervis *et al.,* 1993). Pollen feeding may be less important in males. Pollen may only be required for the maturation of the reproductive system and the maturation of sperm requires less investment than that of eggs (Godfray, 1994). Hickman *et al.* (1995) for example, showed that 71% of gravid *Melanostoma fasciatum* (Macquart) had maximum pollen content compared with 13% of males.

Differences in mouthpart morphology (e.g. McAlpine, 1981; Gilbert, 1981; Elzinga & Broce, 1986;) are strongly associated with pollen: nectar ratios; species with a short proboscis are those observed most often taking pollen from plants such as umbellifers (Gilbert, 1981, 1985). Long, narrow mouthparts (e.g. *Volucella, Rhingia* spp.) are used to obtain liquid nectar from flowers with narrow, tubular corollas (Gilbert & Jervis, 1998). Resources may be partitioned between insect species on the basis of tongue length (Inouye, 1978) and sugar requirements (Heinrich, 1978).

1.3.7. Adult feeding-nectar and honeydew

Nectar, an almost pure solution of sugars, provides energy to fuel motor activities such as flight and mate-seeking activity (Schneider, 1969). Males of many species can be seen taking nectar from flowers or feeding on honeydew, both of which are readier sources of energy than pollen (Gilbert & Jervis, 1998). Females given sugar-rich foods (natural or artificial) have generally been found to be more fecund and longer-lived than those deprived of such foods altogether (Harris & Miller, 1991; Gilbert & Jervis, 1998). Nectar contains only trace amounts of the essential nutrients and therefore adequate amounts of pollen are also essential for maturing successive batches of eggs (Schneider, 1948).

Honeydew appears to be a particularly 'cheap' food to exploit from an energy budget standpoint (Gilbert & Jervis, 1998). Compared with long-distance foraging for most other foods, exploitation of honeydew takes up a smaller proportion of foraging time and is metabolically very undemanding (Harwood *et al.,* 1994; Shonouda *et al.*, 1998). *E. balteatus* and *S. ribesii* can often be seen feeding from leaf surfaces where aphids have produced a film of honeydew (Gilbert, 1993). Hoverflies from the genus *Xylota* specialise almost exclusively on honeydew contaminated by pollen grains from anemophilous plants such as grasses (Gilbert, 1985; Ssymank & Gilbert, 1993). In laboratory studies on other insects (e.g. Leius, 1961; Avidov *et al.,* 1970; Idoine & Ferro, 1998), fecundity and life span may be reduced when honeydew has been given as an alternative source of energy (Gilbert & Jervis, 1998). Such effects have been attributed to the occurrence, in honeydew, of oligosaccharides such as melezitose (Zoebelien, 1955; Leius, 1961; Avidov *et al.,* 1970).

1.3.8. Flower choice by adult hoverflies

Floral resources are clearly valuable to hoverflies and likewise, constant foraging behaviour improves pollen transfer between the flowers of a species. Some of the nectar resources used by hoverflies include a variety of trees, shrubs and plants (Stubbs & Falk, 2000). Cover crops such as coriander (*Coriandrum sativum* (L.)) and buckwheat (*Fagopyrum esculentum*, Polygonaceae), which provide both pollen and nectar (Wratten *et al.,* 1995a) are heavily visited. Hoverflies may also be abundant on late season flowers such as yarrow (*Achillea millefolium* (L.)), and fennel (*Foeniculum vulgare* (Miller)) (Colley & Luna, 2000). Phacelia (*Phacelia tanacetifolia* (Benth)) flowers are especially attractive to adult syrphids (Ozols, 1964). Colley and Luna (2000) reported the relative attractiveness of phacelia, buckwheat, coriander and sweet alyssum (*Lobularia maritima*, Brassicaceae) flowers to hoverflies, showing preferential attraction of hoverfly adults to some flower species.

The colour of a flower may provide flower visitors with clues as to the age of the flowers and the presence of food rewards (Proctor & Yeo, 1973; Stavenga, 1974; Horridge *et al,* 1975; Menzel and Backhaus, 1991; Chittka & Menzel, 1992; Kevan *et al.,* 2001). For example, brown-centred, older inflorescences (e.g. ragwort (*Senecio jacobaea*)) may be ignored by hoverflies visiting younger, yellow-centred flowers (Kugler, 1950). Yellow flowers are often highly reflective and known to attract adult hoverflies (Kevan, 1983). Finch (1992) noted that yellow flowers from the family Compositae were highly attractive to syrphid species such as *E. balteatus*. Stavenga (1974) found that males of the species *E. balteatus* had a green-yellow sensitive pigment in the dorsal part of the eye which corresponded to the reflectance of yellow flowers within the 490 - 500nm action spectrum. Sensitivity to spectral curves near 350, 450 and 520nm has also been found in *Eristalis tenax* (L.) (Horridge *et al.,* 1975).

Within flowers, colour patterns may also function as pointers to assist foraging insects to find a food resource (Kugler, 1943; Manning, 1956). Other parameters such as floral structure, height and size, time of reward presentation during the day (Kevan & Baker, 1983), shape, plane of symmetry (Chittka & Menzel, 1992) and scent (Gilbert, 1993) may serve as additional identification cues. The range of flower species exploited may also depend on plant ecological factors such as abundance, species richness and nectar reward (Pyke, 1982). Physical environmental factors such as light, cloudiness, wind, temperature and humidity also influence flower visiting; syrphids are sun-lovers and tend to be inactive during cloudy periods (Kevan & Baker, 1983).

1.4. Oviposition

1.4.1. Oviposition preferences

Having fed on pollen and having mated, the females complete egg development and then seek out places to lay (Gilbert, 1993). The distribution of eggs is crucial; newly hatched larvae are relatively sessile and are unable to move any great distance to search for an appropriate host (Sadeghi & Gilbert, 2000a). Overall the evidence suggests that most syrphid larvae are able to develop successfully on a wider range of prey than those selected by ovipositing females (e.g. Wiklund, 1981; Smiley, 1978; Rausher, 1983). Although Rüžička (1975) reported that both elder (*Aphis sambuci* L.) and bean (*Aphis fabae* Scopoli) aphids were unsuitable food for the larvae of *E. corollae*, reducing early survival, Sadeghi & Gilbert (2000b) found no significant effect of aphid species on offspring survival. Rarer aphid-feeding larvae (e.g. *Parasyrphus* spp.) are often found on only a restricted range of hosts, or even on only one type (Gilbert, 1993).

In the laboratory, Sadeghi & Gilbert (2000b) found that *E. balteatus* and *S. ribesii* showed significant differences in selecting an aphid species for oviposition. Without exception, the females of both species ranked the sycamore aphid the highest, followed by the rose aphid and then the pea aphid. The lowest preference was for the nettle aphid. The distribution of eggs also changed with female age, with the most preferred declining in preference and the least increasing in preference. This supports the literature suggesting selectivity of oviposition (Reepmeyer, 1969; Milne, 1971; Phoon, 1973; Niemczyk & Pruska, 1986; Budenberg & Powell, 1992).

Chandler (1968d) divides aphidophagous syrphids into two categories, each differing in oviposition behaviour: one group primarily aphid-seeking (Aphidozetic) and the other primarily plant-seeking (phytozetic). The first group, comprising mostly *Syrphus* species, tend to lay single eggs nearly always close to aphid colonies (Chandler, 1968a, d) thereby providing an immediate food source for the emerging larvae. The second group, comprising certain *Melanostoma* and *Platycheirus* species, tend to lay eggs in small batches often on uninfested plants (Chandler, 1968a,b; Sanders, 1979). Chandler (1968d) suggests that such specific differences in preference would tend to decrease interspecific competition. However, the choice of an oviposition site may depend not only on the presence of aphids or aphid-associated stimuli, but also on aphid colony size (Kan, 1986, 1988a,b, 1989), the spatial position of the aphid colony (Chandler, 1968b; Sanders, 1983a,b) and host-plant characteristics (Dixon, 1959; Chandler, 1968a). Other factors such as previous experience, age, internal physiological state, changes in the environment (Fitt, 1986; Minkenberg *et al.*, 1992; Schoonhoven *et al.*, 1998) and the presence of other predators (Scholz & Poehling, 2000) may also be important.

1.4.2. Discrimination in oviposition

Young female *E. balteatus* are very discriminating about where they lay; laying eggs only in or near aphid colonies (Bombosch, 1962, 1963; Volk 1964; Chandler 1965; Schneider 1969). Sadeghi & Gilbert (2000b) found that host discrimination decreased in older flies and that fertile eggs were laid in the absence of aphids. Budenberg & Powell (1992) observed that given the choice of wheatears with and without aphid honeydew, *E. balteatus* were more likely to lay eggs on the latter as they became older. Over time, *E. balteatus* and *S. ribesii* also changed the height at which they laid their eggs (Chandler, 1968b). Chandler (1967, 1968c) found that oviposition distance from the nearest aphid also increased with age in *M. luniger* and in *Scaeva pyrastri* (L.). Chandler (1968a, b) suggested that in older flies, plant or visual features may be more important than olfactory (aphid) cues in stimulating oviposition.

There is some evidence that the presence of conspecific eggs and /or larvae may act as an oviposition deterrent. Scholz and Poehling (2000) found that female *E. balteatus* were able to perceive the presence of conspecific eggs and oviposited less often in aphid colonies in which eggs were present. The oviposition-deterring stimulus was also active when the eggs were removed, suggesting that olfactory cues were involved. Hemptinne *et al.* (1994) found that the presence of third instar syrphid larvae acted as a deterrent to syrphid oviposition on bean plants (*Vicia faba L.*) infested with *Aphis fabae* (Scop.). However, in contrast to these findings, Phoon (1973) and Chandler (1968c) could not detect a deterrent effect of syrphid eggs and larvae in many syrphid species.

1.4.3. Syrphid/prey dynamics

Chandler (1968d) found that syrphid oviposition varied with the size of aphid infestations and that different syrphid species had different optimum aphid population sizes for oviposition. Threshold densities of aphids required for oviposition can also be very low: Chambers (1991) recorded oviposition in winter wheat starting at an infestation level of only 0.2 aphids per shoot. However, in experimental studies, Sanders (1979) and Gilbert (1993) showed that larger colonies of aphids had a greater effect in stimulating females to lay. Bargen *et al.* (1998) and Chambers (1991) observed that *E. balteatus* and *M. corollae* evaluated aphid numbers and adjusted oviposition rates accordingly, with higher prey numbers eliciting increased oviposition. Van Emden (1990) also found that oviposition in *E. balteatus* increased when prey density was high (4000 aphids/m^2). Sanders (1979) found that aphid colonies 2 cm in diameter were most effective in stimulating oviposition by *E. corollae*, eliciting on average one egg per visit; a small colony of three aphids only elicited one egg every 10 visits. Because *E. corollae, S. ribesii* and *E. balteatus* lay the vast majority of their eggs singly (Chandler, 1968a, d; Guest. 1984) each egg laid can be considered to be an independent oviposition decision (Gilbert, 1990). Other workers (e.g. Banks, 1953; Dixon, 1959; Tamaki *et al.,* 1961; Reepmeyer, 1969; Ito & Iwao, 1977; Sanders, 1979; Sanderson *et al.*, 1992) have also found a positive correlation between the oviposition response of hoverflies and aphid density. *Melanostoma* species generally prefer low prey numbers per plant and show no response to aphid density (van Emden, 1990).

Banks (1953), Clark (1963) and Hickman and Wratten (1994) suggest that very high prey densities might deter syrphid oviposition. Ito & Iowa (1977), Wnuk (1979) and Chambers (1991) noted that as aphid densities increased, the ratio of eggs to aphids tended to be lower, possibly because of the limited egg complement of female hoverflies. Guest (1984) reported that in *E. balteatus*, response to aphid density reached a maximum at 200 aphids per plant, and then declined. Hickman (1996) suggests that the response of hoverflies to aphid density, coupled with the lessening of discrimination shown by old flies, would increase the efficacy of aphid control by distributing eggs more evenly through the crop.

1.4.4. The age of aphid colonies

The age of aphid colonies also appears to be important in determining whether or not eggs are laid. In a series of papers, Kan (1986, 1988a, 1989) investigated the oviposition behaviour of different syrphid species in relation to pea aphid colonies. Kan (1988a) found that several syrphid species discriminated against larger aphid colonies containing 4th instar nymphs and winged adults in favour of smaller "promising" colonies of nymphs and/or young winged adults. More than half the syrphid eggs, including *E. balteatus*, were found at small (less than 50) aphid colonies. Eggs of *Betasyrphus serarius* (Weidemann)*, Metasyrphus frequens* (Matsumura) *and* Syrphus *vitripennis* (Meigen) were found almost equally at the small or middle-sized (less than 300) aphid colonies. Pea plants heavily infested with older colonies of 4th-instar nymphs and/or winged adults were neglected. In spite of the danger of larval starvation, the female hoverflies appeared to assess the qualitative and quantitative value of aphid colonies in order to secure the successful development of their offspring (Kan, 1988a). Chandler (1968c) suggested that the avoidance of aphid colonies larger than the optimum size resulted from excessive olfactory stimulation and that this also accounted for the oviposition observed on neighbouring uninfested plants by species such as Platycheirus that show a preference for small aphid populations.

1.4.5. Olfactory stimuli

Responses to olfactory cues (semiochemicals) increase the probability of an insect selecting an oviposition site (Paynter & Brady, 1993; Wall & Warnes, 1994; Schofield & Brady, 1997). Hagen *et al.* (1971) suggested that olfactory receptors in syrphids are able to detect the volatile components of honeydew. Hood Henderson (1982) investigated the contact chemosensillae on the ovipositors of two *Metasyrphus* species and recorded responses to water, honeydew, sucrose, alanine, tryptophan and to indolacetaldehyde, an oxidation product of tryptophan. Stimulation by these compounds was considered important in the selection of an oviposition site.

In *E. corollae*, Bombosch (1962) found that the volatile components of honeydew, in the presence of aphids, were the main stimuli for oviposition, perceived mainly via the antennae, but also via the tarsi and/or mouthparts. Similarly, Volk (1964) found that aphid honeydew and/or cornicle secretions were the main stimulus for oviposition, supplemented by the visual and tactile cues of aphids. Although visual response to aphids does occur (Chandler, 1968d), Dixon (1959) and Volk (1964) demonstrated the importance of aphid odour over other oviposition stimuli for *M.luniger* and also for *E. corollae.* For example, *M. luniger* females responded mainly to olfactory stimuli and laid more eggs in denser aphid colonies (Dixon, 1959).

Hagen *et al.* (1971) found that although several species of syrphid were attracted to plants sprayed with artificial honeydews, this did not result in an increase in the number of syrphid eggs laid on the plants. In the laboratory, Budenberg & Powell (1992) found that in the absence of aphids, honeydew from the rose-grain aphid and pea aphid, but not from the nettle aphid elicited oviposition by *E. balteatus* but not *Platycheirus albimanus* (Fabricius). Buddenberg & Powell (1992) also reported that when honeydew concentrations were high, the addition of aphids had little effect on oviposition. However, when honeydew concentrations were low, the presence of aphids increased oviposition. Scholz & Poehling (2000) found that although honeydew attracted the females via olfaction and elicited oviposition, hardly any eggs were laid in the absence of aphids.

Apart from volatiles in honeydew which attract adult hoverflies and enable the larvae to locate their prey, many aphid species also communicate using pheromones (Zhu *et al.,* 2005). Pheromones play an important part in reproduction and defence against predation and parasitism (Wadhams *et al.,* 1999). The sex pheromone nepetalactone (Powell et al., 1991) and the alarm pheromone (E)-beta farnescene attract predatory parasitoids and the seven-spot ladybird (*Chrysopereria carnea*), and there is some evidence to suggest that hoverflies show good electroantennograph responses to them (Sutherland, 1998).

As well as aphid volatiles other research has found evidence that plant volatiles cause neural activity in some insects and influence where they deposit their eggs. Mozuraitis *et al.*, (2002) showed that Germacrene-D activated a major type of olfactory receptor neuron on the antennae of the tobacco moth (*Heliothis vitrescens*) and increased attraction and oviposition. *Cis*-jasmone shows potential for enhancing parasitisation of aphid populations by predatory parasitoids (Bruce *et al.*, 2003) and in inducing plant defence that deters colonising aphids (Powell & Pickett, 2003). However, little is known about the effect of these compounds on hoverflies. Flower volatiles are known to be a mixture of several or even scores of compounds that provide potential insects with information about the location and identify of flowers, however the synergistic interactions of visual (colour, shape) and olfactory signals are far from understood (Pichersky & Dudareva, 2007). Harris & Miller (1983) suggest combinations of sensory inputs may reinforce weak stimuli during host selection in the field. For example, the turnip root fly (*Delia floralis*) accepts the host plant more readily following the addition of an oviposition stimulant such as *n*-dipropyl disulphide (Harris & Miller, 1991).

1.4.6. Plant-related factors

Different species have different oviposition preferences for colour, height, surface texture and ground cover. Chandler (1968a) found that when offered a choice of beans in pots at different heights, *E. balteatus* laid most eggs at 30 cm, while *E. corollae* oviposited at 123 cm above the ground. Sanders (1979) observed that *E. corollae* showed a preference for vertical rather than horizontal surfaces, and dark rather than light or striped areas. Volk (1964) found that rugose surfaces and the presence of chemical stimuli played a role in the choice of an oviposition site. Dixon (1959) reported that *M. luniger* laid more eggs on green poles with a crushed aphid stimulus than on black or white ones. Humphrey *et al.* (1999) found that stands with high field layer cover supported greater syrphid diversity, while Lewis (1965) showed that syrphids (and aphids) concentrated in areas sheltered by artificial windbreaks. There are a number of examples in the literature which illustrate that the prey searches of syrphid larvae may be hampered by leaf shape and structure and/or by dense hairs (e.g. Rabb and Bradley, 1968; Obrychi *et al.* 1983; Rotheray, 1986). Rotheray (1986) found that the aphid capture rates of three different syrphid species varied greatly on the same host plant as a result of a differential ability to grasp the host plant stem or leaf. Differences in the nutrition plants provide for aphids may also have deleterious effects on natural enemies (see van Emden, 1987, 1990).

1.4.7. Habitat manipulation

Agrosystems with flowers have been associated with significantly higher numbers of pollen and nectar feeding natural enemies in and around farm fields (Cowgill, 1989). Many farmscapes however are florally impoverished and cultural activities such as tillage, weeding, intercropping, and harvesting, can have serious effects on insect populations (Colley & Luna, 2000). Janzen

(1967) reported that large-scale habitat destruction left many farmscapes florally impoverished so that populations of beneficial insects declined to inefficient levels. Similarly, the removal of weeds from apple orchards reduced floral resources for biocontrol organisms, which were then ineffective in protecting the crop from certain pests (Leius, 1967). Kevan and Baker (1983) noted that reductions in pollinator populations were largely due to the cultivation of fallow or neglected land and to the removal of hedgerows to create larger fields. In agrosystems where detritus was cleared and hedgerow boundaries were substituted by wire fences, breeding places and refuge sites for many predatory insects were likewise reduced. For polyphagous predators such as carabid beetles, grass ridges and weedy strips in the field boundaries are important overwintering sites (Coombes & Sotherton, 1986).

With increasing problems of insecticide resistance and public concerns regarding pesticide safety, it has become increasing practice among organic growers to encourage naturally occurring predators and parasitoids by enhancing their growing environment (Peterson & Coats, 2001). In Hampshire, the Game Conservancy Trust has launched a large-scale study, which aims to boost the numbers of beneficial insects in crops by habitat manipulation. The trust was the first organisation to firmly establish the link between the intensification of agriculture and the sudden declines of bird and insect populations (Holland, 2004). Part of the study involves the development of conservation headlands and beetle banks to restore plants and beneficial insects (*Ibid.*). Other workers (e.g. Thomas *et al.*, 1991, 1992) have shown the creation of 'island' habitats to be a major factor in encouraging recolonisation of the field centre by predators. Wyss (1995) also found that weedy strips left across fields increased predator numbers and reduced pest populations. Similarly, Horn (1981) and van Emden (1990) found that weeds within a crop appeared to increase the number of *Melanostoma* species, although Frank (1999) found that syrphid numbers declined slightly with increasing distance from the weed strips.

Insectary plantings to enhance populations of predatory insects have been demonstrated by a number of workers. Weems (1953) and Telenga (1958), for example, recommended the planting of pollen and nectar crops in fields devoid of nectar resources in order to foster beneficial insects. Huffaker (1959) grew *Phacelia* as a cover crop in orchards and found that parasite-host synchrony increased as a result. In France, Mackauer & Way (1976) found that flowers planted along the margins of fields attracted hoverflies to lay more eggs on aphid colonies within the crop. In New Zealand, Lövei *et al.* (1992) found that local densities of adult syrphids increased when *Phacelia* strips were planted across fields. *Phacelia* was also a good biological marker when determining how far flower-feeding adults had penetrated the crop (Lövei *et al.*, 1992). In Switzerland, Wyss (1995) recorded lower numbers of aphids in apple orchards under-sown with wild flower mixtures. In New Zealand, Kahl (1996) demonstrated that border strip planting could achieve significant increases in biological control of some pests by aphidophagous hoverflies. Wratten and van Emden (1995) also promoted the use of beneficial insectary plantings in agricultural systems as a strategy to enhance the effectiveness of hoverflies for biological pest control (Wratten & van Emden, 1995). Colley and Luna (2000) planted insectary flowers adjacent to broccoli fields, but were unable to measure a reduction in cabbage aphid (*Brevicoryne brassicae*) population densities. Hoverflies appeared very late in the phenology of the aphid and the crop, which reduced their effectiveness as biological control agents.

In the UK, flowers, in particular *Phacelia,* have been used as a pollen resource in an attempt to enhance hoverfly populations in cereal fields. Harwood *et al.* (1994) and Hickman & Wratten (1996), for example, found that fields with *Phacelia* border strips had higher numbers of adult hoverflies, a higher level of oviposition by syrphids and fewer aphids in the crop than control fields without *Phacelia* border strips. In New Zealand, White *et al*, (1995) also found that the provision of *Phacelia* strips in and around farmland attracted hoverfly adults resulting in increased oviposition, and a decrease in pest numbers. Border strips of *Phacelia* around a paddock of cabbages and captured approximately seven times as many *Melanostoma fascitatum* in *Phacelia* bordered plots than in controls. Aphid numbers were also significantly lower.

1.5. Aims and content of the thesis

The first aim in this work was to carry out experiments on as large a scale as possible, to attempt to answer the question of whether the presence of model flowers, near arable crops might be associated with increased oviposition by aphidophagous syrphids in their vicinity. A secondary aim was to establish the relative importance of the different components of the model flower in any response that was seen (Chapter Three).

From the results of the main experiment, work was undertaken to produce an optimum design for a model flower by using field experiments to assess colour, size, height and pattern preferences and to test the effects of an aphid-derived and plant derived volatile in relation to their attractiveness to gravid hoverflies (Chapters Four, Five and Six). This was done by comparing numbers of gravid females caught in yellow water traps and by comparing numbers of eggs laid on bait plants within the vicinity of the model flowers. Chapter Six incorporated the 'optimum' features (colour, height, and size) into one model and compared the oviposition responses of gravid hoverflies on bait plants near to and distant from this model.

In Chapter Seven the results of the previous six chapters are discussed and suggestions are made for future work that could be carried out.

Data from yellow trap catches of aphidophagous syrphids throughout the project (2001 – 2005) was collated and analysed and is presented in an appendix at the end of the work. This work was undertaken to show the phenology, abundance and diversity of aphidophagous syrphids, and in particular of gravid females, in an attempt to explain some of the results of the main project.

CHAPTER 2

THE USE OF YELLOW MODEL FLOWERS TO ENHANCE OVIPOSITION BY APHIDOPHAGOUS SYRPHIDS IN THE FIELD.

This Chapter describes a large-scale field experiment carried out over two years, which compared hoverfly oviposition on bait plants in the vicinity of yellow model flowers and at control positions. Model yellow flowers and standardised bait plants were used in order to minimise the variations associated with real flowers and aphid populations. Preliminary laboratory experiments were carried out to establish the form that the standardised bait plant should take. After the field experiment, further laboratory tests were conducted in an attempt to explain the results of the fieldwork.

2.1 General introduction

Habitat manipulation approaches, such as the provision of floral resources for adult aphidophagous syrphids, are sometimes used to maximise the biocontrol potential of the larvae (Landis *et al.*, 2000). The larvae may have potential in slowing aphid multiplication and in limiting population size (e.g. Wnuk 1977; Chambers *et al.,* 1986; Hurej 1992; Winder *et al.,* 1994) if they arrive when aphid density is still small (Tenhumberg, 2005). However, if flowers are to be used as food resources, it is essential to understand the cues involved in their selection by adult syrphids, and the effect of such cues on subsequent oviposition.

Hoverflies are clearly attracted to some flowers over others, probably because of the availability and accessibility of specific food resources (Colley & Luna, 2000). Adult hoverflies feed on pollen for the maturation of the ovarioles and eggs (Schneider 1948, 1969; Haslett 1989b), while nectar provides energy for locomotion and reproduction (Kevan & Baker 1983). Flower colour may also advertise floral reward and influence choice (Mulligan & Kevan 1973; Kirk 1984; Haslett 1989a; Colley & Luna, 2000). Evidence suggests that hoverflies have a strong preference for yellow (e.g. Finch 1992: Sutherland 1998;

Hoback *et al.*, 1999; Lunau & Wacht, 1994). *Episyrphus balteatus* is frequently seen feeding from yellow flowers (Stubbs & Falk, 2000) Yellow traps are often used in field work to attract hoverflies. Presumably these are seen as a source of food by flower-feeding adults (Hickman *et al.*, 2001). Although flower choice may be partially dependent on the colour of the flower (Haslett, 1989a), the precise role of pollen and honey as an attractant to gravid hoverflies requires further investigation.

Despite increasing evidence to suggest that the presence of flowers may enhance biological control of aphids by hoverfly larvae (Fluke, 1937; van Emden, 1965; White *et al.*, 1995; Hickman & Wratten, 1996; Salveter, 1998), the link between hoverfly oviposition and the presence of flowers is still controversial. However, van Emden (1965) noted that most aphid predation by hoverfly larvae occurred near flowers in the edge of a Brussels sprout field than anywhere else in the field, and that aphid numbers there were significantly lower here than anywhere else. More recent examples have been demonstrated in California by Kloen and Altieri (1990), in New Zealand by White *et al.* (1995), in the UK by Hickman & Wratten (1996). 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.

Contrary to these findings, Chandler (1968b) did not find that buckets of yellow ragwort (*Senecio jacobea* (L.)) influenced nearby hoverfly oviposition in replicated Brussels sprouts (*Brassica oleracea gemmifera*) plots with and without flowers. However, in this small-scale experiment, it is possible that both plant nectar content and production altered as a result of changes in the physiological condition of the excised flowers (Wade & Wratten, 2007). Goulson *et al.* (2007) also found nectar volume to be markedly lower in flowers with damaged petals, which were also likely to be older. Brown-centred older inflorescences of *S. jacobaea* may be ignored by hoverflies, which are known to prefer younger, yellow-centred flowers (Kugler, 1950).

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) found that adult syrphids were more abundant in areas with flowers, but that oviposition was depressed in unsheltered areas, regardless of whether flowers occurred nearby. Chambers (1991) showed that field boundaries with flowers had no effect on hoverfly oviposition in the crop, while Cowgill (1990) found no effect on oviposition rates at different distances from flowers in a conservation headland. Salveter (1998) found that oviposition rates decreased with increasing distance from herb strips in the field margins. Similarly, Colley and Luna (2000) were unable to measure any reduction in cabbage aphid (*Brevicoryne brassicae*) populations by hoverflies in broccoli fields adjacent to blocks of insectary flowers. However, the late appearance of hoverflies relative to the phenology of the cabbage aphid presumably reduced their effectiveness as a biological control agent.

The effects of flowers on oviposition have proven difficult to demonstrate, perhaps because of the difficulties of spatial scale encountered with the high mobility of the adults (Bugg, 1992). However, shortages of flowers in large areas of intensively cultivated land might limit oviposition (Chandler, 1968a; Colley & Luna, 2000). Therefore the introduction of flowers, as both a pollen and nectar resource, has obvious potential for the enhancement of biological control in the crop (Gurr *et al.*, 1999; Landis *et al.,* 2000; Colley & Luna, 2000). Flowers added to ecosystems may also serve to attract hoverflies to the crop at a time when aphid numbers are beginning to increase.

In the experiments described below, the model flowers and aphid infested bait plants used were standardised as far as possible to eliminate the variation associated with naturally occurring flowers and aphid populations. The aims were firstly, to establish whether the presence of the model flowers in the field margins of crop fields enhanced oviposition on nearby bait plants and secondly to explore the relative importance of colour stimulus and food rewards in any response that was observed.

2.2. Preliminary laboratory experiment

The main experiment described in this chapter used standardised bait plants so that oviposition levels near different treatments could be compared. The oviposition responses of *E. balteatus* and other syrphid species to aphids have been much discussed in the literature (e.g. Kan, 1988a, b: Kan, 1989; Chambers, 1991; Sadeghi & Gilbert, 2000a). However, using live aphids on bait plants makes it impossible to completely standardise the oviposition stimulus. Live aphids move, and even if plants are infested with the same number of adult aphids, reproduction rates vary. To determine the best oviposition stimulant to be used on bait plants in the field, a preliminary laboratory experiment was carried out to compare oviposition on plants treated with aphids or aphid derived compounds.

2.3. Methods and materials

2.3.1. The treatments

For each bioassay, 12 singly potted broad bean plants (*Vicia faba* (L.)) (cv. Sutton Dwarf) at the 6-leaf stage (10 cm high) were treated with the vetch aphid, *Megoura viciae* (Buckton) (taken from stock cultures). Almohamad *et al.* (2007) found *M. viciae* to be a suitable oviposition stimulant for *E. balteatus.* Plants were labelled and treated as follows: Treatment A = control. Treatment B = 50 winged and non-winged undamaged whole *M. viciae* applied with to the underside of the leaves with a paintbrush. It was thought that 50 *M. viciae* would be sufficient to stimulate oviposition in *E. balteatus* (see Kan, 1986; 1988a, b; 1989; Chamber, 1991). Treatment C = 50 *M. viciae* squashed on the lower leaf surfaces with a spatula. Treatment D = 0.25mg of crude *M. viciae* honeydew residue applied to the lower leaf surfaces. For treatment D, honeydew was collected from *M. viciae* by placing strips of Parafilm (5 x 5cm) (Sigma-Aldrich Co Ltd., Poole, Dorset, UK.) on acetate sheets under heavily infested broad bean plants (after Bouchard & Cloutier, 1984). Honeydew residue was scraped from the Parafilm using a spatula, and weighed. Honeydew alone has been found to elicit oviposition responses in *E. balteatus* (Budenberg & Powell, 1992).

2.3.2. Experimental arena

Twelve gravid 3 week old (second generation) *E. balteatus* (from laboratory stock) were placed in each of three perspex cages (40 x 60 x 40cms) in the Insectory at Southampton University. Individuals had not been previously exposed to aphids. *E. balteatus* were given *ad libitum* access to tap water, sieved pollen from *Populus deltiodes* (Marsh) (Sigma-Aldrich Co Ltd., Poole, U.K. Cat N^{o}.P-7395) and a 10% solution of blended honey (Gales Original Clear, UK). Methods for rearing *E. balteatus* were adapted from Frazer (1972). Pollen and honey were supplied on Petri dish lids on upturned plant pots at the back of the cage. To maintain the numbers of *E. balteatus* used throughout the experimental period, gravid females from stock were used to replace any dead flies.

Treatments A, B, C and D were randomly placed in a square arrangement with 16cm intervals between plants in each cage. Plants were removed 48 hours later and the numbers of *E. balteatus* eggs on each plant counted. Three replicate bioassays were made over a four-week period from 21 November to 11 December 2001.

Temperature was maintained at 22^{0}C ± 1^{o}C throughout the experimental period. Ceiling mounted fluorescent bulbs provided ambient lighting (5000lux/L16: D7 photoperiod).

Analysis

Numbers of eggs laid on plants treated with aphids, squashed aphids, honeydew and controls were compared using Kruskal-Wallis non-parametric one-way analysis of variance. As it was expected that oviposition on untreated plants would be low, a second analysis compared numbers of eggs on the three aphid related treatments.

2.4. Results

A total of 378 eggs overall was found on all treatments combined with the greatest numbers of eggs (61%) being laid on plants treated with live aphids. Few eggs were found on the control plants (Table 2.1). Differences in the numbers of eggs laid on the different plants were highly significant (Kruskal-Wallis test, $X^2 = 33.79$; df = 3; $P < 0.001$), with more eggs laid on plants with live aphids than on control plants. When numbers of eggs on plants with aphids, squashed aphids and honeydew were compared there were no significant differences between them, but there was a trend for more eggs to be laid on plants with live aphids than on the other treatments. The Kruskal-Wallis test results are shown in Table 2.2.

Date	Live aphids(A)	Squashed aphids (B)	Honeydew (C)	Control
21/11/2001	13	14	17	7
28/11/2001	142	52	12	2
04/12/2001	70	19	12	1
11/12/2001	5	2	10	0
Totals	**230**	**87**	**51**	**10**

Table 2.1. Numbers of eggs laid by *E. balteatus* on the different treatments and the control over the experimental period.

	Mean rank				df	X^2	*P*
	Live aphids (A)	Squashed aphids (B)	Honeydew (C)	Control			
Including control	33.79	28.88	25.54	9.79	3	19.988	*0.000
Without control	22.5	18.54	14.46		2	3.517	0.172

Table 2.2. Results of Kruskal-Wallis one-way analysis of variance comparing the number of *E. balteatus* eggs laid on the different treatments and the control over the experimental period.

2.5. Discussion

Although there was a strong trend for more eggs to be laid on plants with live aphids, there was also oviposition on plants treated with squashed aphids and honeydew. Squashed aphids presumably produce many of the same olfactory stimuli as live ones and it is known that honeydew alone, particularly in high concentrations (see Budenberg & Powell, 1992) can be an effective oviposition stimulus for *E. balteatus*. In fact, in the last experimental week, more eggs were laid on the plants treated with honeydew than on the plants treated with live aphids. There is some evidence to suggest that older *E. balteatus* become less selective in the choice of an oviposition site (e.g. Sadeghi & Gilbert, 2000a) and this may have been the reason. There was also some oviposition on the control plants; this may have occurred in response to stimuli from nearby plants. Chandler (1968a) suggests olfactory stimulation from aphids and/or honeydew to be a possible reason for oviposition on non-infested bean plants in the field. However, there were very few (10 in total) eggs laid on controls.

Ideally, nectar and pollen from floral sources known to attract would have been used to rear *E. balteatus*, as the nutrients obtained may affect growth, development, survival and reproduction (Haslett, 1989a). However, nectar and pollen from flowers known to attract *E. balteatus* were not available at the time. *E. balteatus* used in the experiment were the product of first generation flies, which had also been reared on pollen from *P. deltiodes* and blended honey.

In order to produce completely standardised bait plants in the field, it would be best to use known numbers of squashed aphids or known amounts of honeydew. However, there was a strong trend for eggs to be laid on plants with aphids. It was also thought possible that in the field, squashed aphids might desiccate and lose their attractant properties, although this was not tested in the laboratory, and honeydew might be washed off the bait plants if it rained. Finally, it was felt that as high numbers of bait plants would be used and distributed randomly, any differences between numbers of aphids on individual pots would be unlikely to affect the results. For these reasons, it was decided to use live aphids on the standardised bait plants in the field.

There was no evidence from laboratory work or the literature to suggest *M. viciae* to be an unsuitable oviposition stimulant for *E. balteatus.* However, Rüžička (1975) found this species of aphid to be toxic to *E. corollae* larvae, mainly due to the level of alkaloids and glycosides present in the host plant. *M. viciae* is also known to be toxic for some ladybird larvae (e.g. *Exochomus quadripustulatus* (L), *Harmonia axyridis* (Pallas)) (Dixon & Agarwala, 1999). Sadeghi and Gilbert (2000) showed the pea aphid (*Acyrthosiphon pisum* (Harris)), followed by the rose aphid (*Macrosiphum rosae* (L)) to be the preferred oviposition stimulant in *E. balteatus.* Therefore, it was decided to use *A. pisum* on bait plants in the field.

2.6. Field experiments

The model flowers in these investigations combined three of the attributes exhibited by real flowers and thought to be important in hoverfly foraging: colour, pollen and nectar (see Introduction above). Standardised bait plants were placed in the vicinity of the model flowers and the controls and were used to measure oviposition.

2.7. General Methods and Materials

2.7.1. Design of model flowers

Model flowers consisted of plastic flowerpot trays (diameters 19 cm) fixed to the top of wooden stakes. 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 (Glocote 1263, Goo-Var Ltd) was applied 12 hours later. Fluorescent yellow is known to be highly attractive to Syrphidae (Kirk 1984; Finch 1992). In previous work (see Appendix), water traps painted with Glocote 1263 caught large numbers of aphidophagous syrphids. Four holes (diameters 4mm) were drilled in the base of each tray for drainage of rainwater. Each tray was then screwed to a wooden stake ((2.5 x 2.5 cm cross section) and the other end of the stake cut to a 10cm point to allow it to be inserted easily into the soil (Fig.2.1). Food resources (when used) consisted of a sprinkling of *P. deltiodes* pollen and/or a sucrose cube soaked in a 25% solution of honey. A white cotton pad (diameter 5cm) was placed in the centre of each tray and when food resources were used they were placed on this.

In each experiment, flowers were set out in groups consisting of three flowers of different heights (125, 92 and 32cm) which were randomly arranged in an equilateral triangle with sides of 45cm (Fig. 2.1).

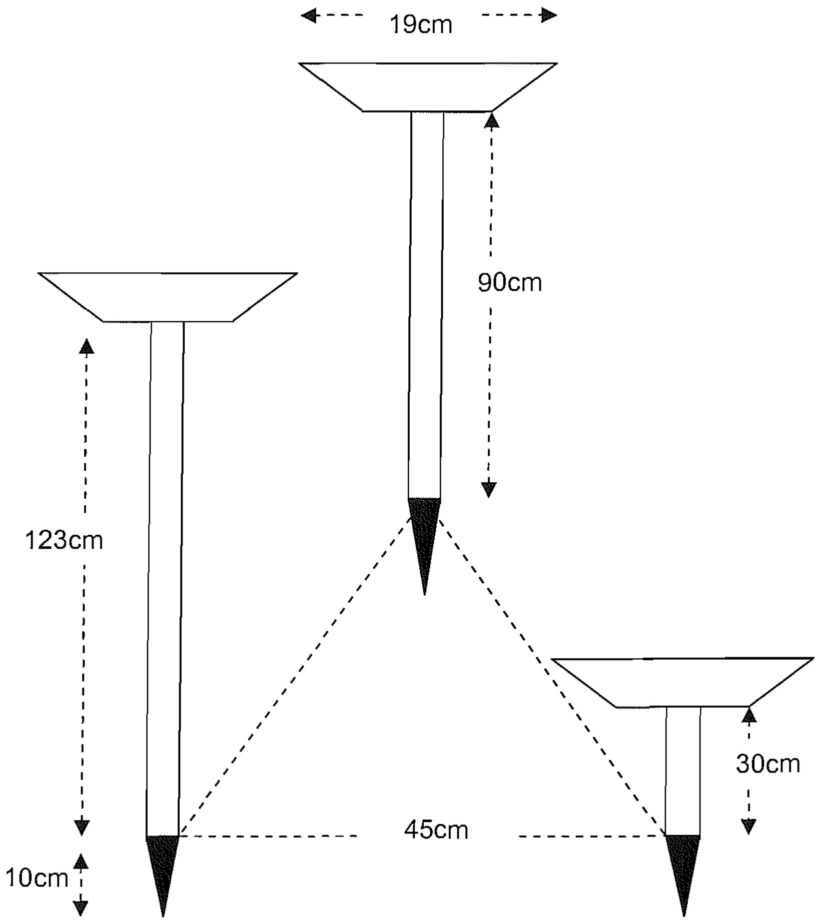


Figure 2.1. The model flower set-up used in winter wheat fields in 2002 and in 2003. The arrangement of each model flower within the set was at random.

2.7.2. Bait plants.

Broad bean (*V. faba*) seeds were sown weekly in plastic plant pots (diameters 6cm) each filled with peat-based compost. Plants were grown under glasshouse conditions at 15-18°C with 16h-day length. After two weeks (four leaf stage), each plant was infested with approximately 12 winged and non-winged *A. pisum* taken from non-clonal laboratory stock. The plants were then left for one week, for the pea aphids to establish, before being taken to the field.

3.7.3. Experimental sites.

The experimental fields were located at Uggford farm, Wilton, Wiltshire, UK. Fields 1 (2002/3) and 2 (2002) had well-established hawthorn (*Crataegus monogyna* (Jacq.)) hedgerows situated approximately two metres 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.)) interspersed by hawthorn hedges. A grass strip (width 20 metres) separated the tree and hedgerow border from the crop in these two fields. Field 5 (2003) was bordered by a farm track. No insecticide was used on the experimental fields during either season. The winter wheat crops were harvested on 23 August (2002) and on 13 August (2003).

To avoid confounding the results, natural flowers in the hedgerows bordering the experimental side of each field were removed regularly with a scythe. During all experiments in both years, winter wheat plants within a radius of 5 metres of the bait plants were randomly checked for aphid infestations each time bait plants were put out and collected.

2.7.4. Field Experiment 1 (2002)

Oviposition near model flowers and at control sites

Four sets of three model flowers and four sets of controls (stakes without flowerpot trays) were used in each winter wheat field (Fields 1, 2 and 3). All model flowers were painted yellow and contained pollen and honey and these were renewed weekly before each set of oviposition bait plants were put out. Sets of three model flowers alternated with sets of three stakes and were positioned in the field margins, approximately one metre from the crop edge, with an interval of 50 metres between treatments. Treatments were placed apart as far as possible to reduce the possibility of more than one treatment being visible to a hoverfly at a time.

At weekly intervals, two bait plants were selected at random and placed on the ground midway between the stakes and the edge of the crop (approximately 50 cm from the stakes). The bait plants were retrieved 48 hours later and the number of eggs counted, and where possible identified to syrphid species. Some eggs were reared to adulthood in the laboratory for easy identification.

The experiment was repeated four times at weekly intervals between 8 and 30 July 2002.

2.7.5. Field Experiment 2 (2002/3)

Relative importance of colour, pollen and honey

This experiment was carried out at weekly intervals and repeated three times in 2002 (12 - 22 August) and five times in 2003 (12 July – 11 August). Four sets of yellow and four sets of unpainted (brown) model flowers were used in each experimental field (Fields 1, 4 and 5). Brown was chosen as it reflects fairly evenly and dully across the insect visual spectrum (Kevan, 1972). It was thought that this colour would provide less of a visual stimulus to syrphids than yellow.

For each colour treatment in each field, one set of three model flowers contained pollen, one set contained honey, one set contained honey and pollen and one set contained no food resources. In each of the three fields, sets of flowers were positioned randomly approximately one metre from the crop edge at intervals of 50 metres. Prior to each replication the positions were re-randomised. The flowerpot saucers were unscrewed from their stakes and put in their new positions. Pollen and honey resources were renewed immediately before bait plants were put out.

In 2002, bait plants were put out and collected as in Experiment 1. Hoverfly eggs which could not be identified to species were kept and reared to adulthood.

In 2003, the experiment was repeated. During the last three weeks of the experiment, two additional bait plants were placed on the ground in the wheat crop at 5m from each set of model flowers and two at 10m. These plants were placed on a line running from the model flower stakes into the crop at right angles to the crop edge.

In 2003, during the last three weeks of the experiment (26 July – 11 August), as well as the bait plants beside the model flowers, two bait plants were placed on the ground in the wheat crop at 5m from the yellow painted and unpainted model flowers, and also at 10m. These plants were placed on a line running from the stakes into the crop at right angles to the crop edge.

Analysis

Mann-Whitney *U*-tests were used to test the differences between the numbers of syrphid eggs on bait plants in close proximity to sets of yellow model flowers and controls (Experiment 1), and between the numbers of eggs on bait plants at distances of 50cm, 5 and 10 metres from the yellow painted and unpainted model flowers (Experiment 2). For yellow painted and unpainted treatments separately, Kruskal-Wallis tests were used to determine differences between egg numbers at each distance between different food treatments. All statistical analyses were performed using SPSS11.

2.8. Results

2.8.1. Field experiment 1

Oviposition near model flowers and at control sites

In total, 61 hoverfly eggs were found on bait plants placed by yellow model flowers and 15 on bait plants at control positions (Table 2.3). This difference was highly significant (Mann-Whitney *U*-test; U = 747.00; n_1n_2 = 48, 48; $P <$ 0.001). During the experimental period, one or more eggs were found on the bait plants associated with 26 out of the 48 model flower sets and 11 out of 48 control (stakes only) positions. The highest number of eggs at any one position was 11 (model flower, field 2). For sets of bait plants with one or more eggs, there was a trend for more eggs on those near model flowers (x = 2.35, s.e. 0.42) than at control positions (x = 1.36, s.e. 0.20) although this difference was not significant (Mann-Whitney *U*-test, *U*=98; n_1n_2 = 11, 26; P>0.05)

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

	Number of syrphid eggs	
Date (2002)	**Model flower sets**	**Controls (stakes)**
8 -10 July	8	0
13-15 July	18	2
23-25 July	28	9
28-30 July	7	4
Totals	**61**	**15**

Table 2.3. Numbers of syrphid eggs laid on bait plant near model flowers sets and the controls over the experimental period.

2.8.2. Field experiment 2

In both years a higher total number of eggs was found at all distances on bait plants near (50 cm) from the yellow model flowers than near the unpainted ones (Table 2.4). These differences were highly significant at 50cm (Mann-Whitney tests, 2002: U = 402; n_1n_2 = 36, 36, $P < 0.001$; 2003 U = 1195.0; n_1n_2 = 60, 60; $P < 0.001$). In 2003, significantly more eggs were found at 10m near coloured than unpainted models (U = 484.5; n_1n_2 = 36, 36; $P < 0.05$). Results were not significant at distances of 5 metres (U = 549.0; n_1n_2 = 36, 36; $P > 0.05$), although a trend was found for more eggs to be laid on plants near the yellow models compared to the non-coloured models (Table 2.4).

No significant differences in oviposition, in either year or at any distance, were found between different food treatments 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.*

Colour	**Fluorescent Yellow**				**Brown (unpainted)**			
Food resources	**Pollen & Honey**	**Pollen**	**Honey**	**None**	**Pollen & Honey**	**Pollen**	**Honey**	**None**
No. of syrphid eggs (2002) 50cm	24	10	13	15	1	3	11	0
No. of syrphid eggs (2003) 50cm	13	18	14	25	1	6	10	2
No. of syrphid eggs (2003) 5m	2	7	4	11	0	1	1	6
No. of syrphid eggs (2003) 10m	6	4	10	9	1	6	4	1
Totals	**45**	**39**	**41**	**60**	**3**	**16**	**26**	**9**

Table 2.4. Numbers of syrphid eggs on bait plants at distances of 50cm, 5 and 10m from model flower treatments in 2002 and 2003.

No. of syrphid eggs	Mean Rank		*U*	*P*
	Treatment	Control		
Experiment 1 (2002) 50cm	56.94	40.94	747.00	*0.001
Experiment 1 (2002) 50cm (positions with eggs)	20.73	14.91	98.00	0.141
Experiment 2 (2002) 50cm	43.33	29.67	402.00	*0.001
Experiment 2 (2003) 50cm	70.58	50.42	1195.00	*0.000
Experiment 2 (2003) 5m	39.25	33.75	549.00	0.116
Experiment 2 (2003) 10m	41.04	31.96	484.50	*0.017

Table 2.5. Results of Mann-Whitney tests on numbers of syrphid eggs on bait plants at yellow painted and unpainted (brown) model flower positions (50cm, 5 and 10 metres) in the different collection periods. * indicates significant differences between treatments.

Colour of trays	**Mean rank**				**df**	X^2	*P*
	Honey	**Pollen**	**Honey & pollen**	**No food**			
Yellow 50cm (2002)	17.06	16.61	21.56	18.78	3	1.383	0.709
Unpainted 50cm (2002)	18.22	21.89	17.89	16.00	3	4.083	0.253
Yellow & unpainted 50cm (2002)	35.19	37.39	38.67	34.75	3	0.601	0.896
Yellow 50cm (2003)	30.57	27.63	28.40	35.40	3	2.064	0.559
Unpainted 50cm (2003)	34.93	33.57	25.83	27.67	3	5.602	0.133
Yellow & unpainted 50cm (2003)	66.00	59.82	54.17	62.02	3	2.451	0.484
Yellow 5m (2003)	17.33	17.94	16.72	22.00	3	2.225	0.527
Unpainted 5m (2003)	17.89	17.89	16.00	22.22	3	4.682	0.197
Yellow & unpainted 5m (2003)	34.72	35.17	32.50	43.61	3	5.841	0.12
Yellow 10m (2003)	20.17	15.44	18.56	19.83	3	1.473	0.689
Unpainted 10m (2003)	20.00	18.22	17.89	17.89	3	0.69	0.876
Yellow & unpainted 10m (2003)	39.42	33.47	36.14	36.97	3.00	1.24	0.74

Table 2.6. Results of Kruskal-Wallis one-way analysis of variance on the number of syrphid eggs laid in the presence or absence of food resources on bait plants at distances of 50cm, 5 and 10 metres from yellow and unpainted (brown) model flower positions in 2002 and 2003.

2.9. Discussion

Oviposition response to model flowers in the field

Although artificial flowers have been used by a number of workers to investigate the foraging behaviour of honey bees (Waddington, 1980; Spaethe *et al.,* 2001), they have not previously been used in an experiment to assess their effect on hoverfly oviposition. The model flowers used in these investigations combined three attributes of natural flowers (colour, pollen and nectar) thought to be of importance in attracting syrphids to them. The fact that significantly more eggs were laid near model flowers than near control positions, strongly supports the findings of those workers who found an increase in oviposition associated with the presence of real flowers (e.g. Fluke, 1937; Dixon, 1959; van Emden, 1965; Hickman & Wratten 1996). The results also strongly suggested colour to be more important than pollen and honey resources in eliciting this response. The results were strengthened by the fact that significant differences were found in all experiments and that the same trend was shown throughout each experimental period.

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 another possible source of variation was eliminated. The field scale of the experiments also avoided the problems associated with small-scale experiments on highly mobile organisms such as hoverflies, which may have contributed to the negative results obtained in some small scale experiments (Chandler, 1968a).

Ideally, as there is a positive correlation between syrphid oviposition and number of aphids (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. Although the plants were of the same age, and all were initially infested to the same extent, it was not possible to ensure this. However the bait plants were allocated at random and with more than 1000 plants used in total, it was very unlikely that this compromised the overall results.

Flowers produce pollen, which is required by immature syrphids to mature their reproductive organs (Schneider, 1969; Svensson & Janzon, 1984; Cowgill, 1989) and by gravid females for ovigenesis (Schneider, 1948). It also appears from these results, that yellow model flowers do attract gravid female syrphids, which oviposit nearby, but that this does not depend on the presence of food rewards.

The results showed that yellow coloured targets, rather than those with food rewards had the main effect on oviposition. Even though the chosen colour was not optimal (see Chapter 4), gravid syrphids appeared to be more attracted to the yellow model flowers than the unpainted models. It can therefore be assumed that colour was an important cue in enabling them to locate the model flowers. However, in this experiment, there was no evidence of increased oviposition near coloured targets with food rewards compared with those without such rewards. Indeed, in 2003 more eggs were laid near yellow targets with no food resources that any other treatment. It might be expected that if the yellow targets represented potential sources of food, then visiting syrphids would continue searching elsewhere if none was available at the target. The results suggest that, even if gravid syrphids 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 is available. It can be assumed that cues for hoverfly oviposition include visual stimuli (Chandler, 1968b; Sanders, 1979; Kan, 1988a,b) and aphid volatiles (Volk, 1964; Budenberg & Powell, 1992). As there was a significant response to coloured targets at 10m into the crop, and at this distance, it is unlikely that small bait plants could be seen by a hoverfly in the field margin, it seems likely that females responded first to the coloured target and then to aphid volatiles, which directed them towards the oviposition site.

Another possible mechanism arises from the fact that many flowering plants e.g. broom and sunflowers, will support colonies of aphids. Gravid females could move towards coloured targets primarily as a likely source of oviposition sites rather than from hunger.

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 provided with both pollen and honey (Table 2.5). These findings suggest that olfactory cues from pollen and nectar are less important than colour in orientating hoverflies towards flowers.

However, the honey from unknown sources and wind-dispersed pollen used, were unlikely to have been optimal. They were chosen because they had been used for many years as food for successive generations of insectary reared *E. balteatus* at Southampton University (J. Hickman, pers. Comm). However, unlike *Melanostoma* and *Platycheirus* spp., which visit plants with anemophilous pollen (Stelleman, 1978), studies by gut analysis (Haslett, 1989) and observational studies (Cowgill *et al.*, 1993; Branquarte & Hemptinne, 2000) have shown that the commonest species found in this project, *E. balteatus,* feeds on pollen and nectar from many different insect pollinated flower species in the field. Had nectar and pollen from flowers known to be exploited by *E. balteatus* and other common species, been used in this project, it is possible that they might have enhanced the attraction of the 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 the naturally occurring flower species 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; Bell 1985; Schmid-Hempel & Speiser, 1988). Although Sutherland (1998) reported that *E. balteatus* preferred small flowers (7cm diameter), the results described here suggest that large (19cm diameter) yellow model flowers were highly attractive to them.

In both years, the majority of eggs laid on aphid-infested bait plants were *E. balteatus*. The larvae of this species have been known to consume between 137-190 *Sitobion avenae* (F.) (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). *E. balteatus* has also been implicated at 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 could be of great practical importance to the agricultural community.

For biological control in crops, artificial flowers possess many advantages over natural ones. For example, they could be put out early in the season when aphid numbers are beginning to increase or in areas where densities of aphids are high. Model flowers could be used in fields with or without margins and also at predetermined distances into the crop without disrupting it. As it appears that colour is the only necessary component to attract gravid females and enhance oviposition, all that would be required would be a coloured disc and something to stand it on; virtually no maintenance would be required other than the initial set up.

This study did not investigate the impact of model flowers on the dynamics of aphid populations in the crop and the economic effects of using this method to enhance oviposition by aphidophagous syrphids still need to be assessed. However, the results may be of interest to farmers and horticulturists, especially those who grow organic crops, as they suggest that it may be possible to enhance the biological control of aphids, using a novel and inexpensive method which requires little labour and does not reduce the area of the crop.

2.10. Laboratory experiment

The effect of food deprivation on the landing behaviour and oviposition responses of gravid *E. balteatus*.

The results described above suggest strongly that the presence of flowers enhances hoverfly oviposition and that colour is more important than food resources in determining this behaviour. However, the relationship between feeding and oviposition is not well understood. The experiments described below were carried out in an attempt to gain a deeper understanding of the oviposition behaviour and landing responses of *E. balteatus* in relation to food availability and deprivation.

The aim of these experiments was to assess whether hunger firstly, had any impact on syrphid oviposition, and secondly any effect on the numbers of landings on a yellow target, by comparing the behaviour of gravid females when starved for 24 hours and when given *ad libitum* access to honey and pollen.

2.11. Methods and Materials

2.11.1. Experiment 1

The oviposition response of starved and normally fed *E. balteatus*

Two perspex cages (40 x 60 x 40cms) each containing 24 gravid *E. balteatus* females (second generation, three weeks old at the start of the experiment) from laboratory stock, were used for the experiment.

The flies were provided with pollen, honey and water (see section 2.3.2 for details). 24 hours before the start of the first experiment, pollen and honey were removed from one cage, but the water was left. Three singly potted three-week-old broad bean plants (*V. faba*) infested with 200 adult *M. viciae* (from stock cultures) were then arranged at intervals of 20cm in an equilateral triangle in each cage. Plants were removed three hours later, pollen and honey which had been removed was replaced, and the numbers of eggs were counted. Each set of flies was alternately starved for 24h or fed normally for the 24h before an experiment. Six replicate bioassays were performed from 9 February to 16 March 2003.

2.11.2. Experiment 2

The landing response of starved and normally fed gravid *E. balteatus* on yellow model flowers

For each bioassay, eight model flowers were constructed using white card discs (diameters 23mm) secured horizontally with Sellotape on thin 18cm lengths of green, plastic-coated gardener's wire (B & Q). Card discs had previously been hand-sprayed with florescent yellow Plasti-Kote 655 paint (B & Q), which was available at the time, and left to dry for 28 days to eliminate any possible odour emanation. Each model flower was secured by placing the stem through a previously drilled 1mm hole in the centre of a white plastic vial lid (diameter 2.5mm). Flowers were held upright by weighting the underside of the vial lid with Plasticine.

Two perspex cages (40 x 60 x 40 cm) were used for each bioassay. In one cage, 12 gravid *E. balteatus* (2 - 3 weeks old at the start of the experiment, second generation) were deprived of honey and pollen, but not water, for 24 hours. In a separate cage, 12 gravid *E. balteatus* were given *ad libitum* access to honey, pollen and water. Until 24 h before the experiment all flies had had access to pollen and honey.

In each cage, four model flowers were placed in a square arrangement at 16cm intervals. The numbers of landings on the model flowers by the starved and normally fed flies were observed for a two-hour period, and at different times of the day. Six replicate bioassays were carried out from 2 February to 8 March 2004 at one week intervals. Each set of flies was alternately starved for 24h or fed normally for the 24h before an experiment.

To maintain the numbers of flies used throughout the experimental period, gravid females from stock were used to replace any dead flies.

In both experiments, temperature was maintained at 22^0C ± 1^oC. Ceiling mounted fluorescent bulbs provided ambient lighting (5000lux/L16: D7 photoperiod).

Analysis

Mann-Whitney *U* tests were used to compare the numbers of landings, and the numbers of eggs laid, by starved and normally fed flies.

2.12. Results

2.12.1. Experiment 1

Numbers of eggs laid by starved and normally fed *E. balteatus*

Over the experimental period a total of 8114 eggs were laid altogether with approximately the same number laid by starved flies and those that had been normally fed (Table 2.7). The number of eggs laid during an experimental session declined over time for each group. There were no significant differences in the numbers of eggs laid by starved and normally fed flies. (Mann-Whitney *U* test: $U = 16$; $P > 0.05$). (See Table 2.9)

Date (2003)	**Starved flies**	**Normally fed flies**
09 February	1062	998
16 February	1063	990
23 February	902	859
02 March	655	589
09 March	285	459
16 March	123	129
Totals	**4090**	**4024**

Table 2.7. Numbers of eggs laid on broad bean plants by starved and normally fed *E. balteatus* over the experimental period.

2.12.2. Experiment 2

The landing response of starved and normally fed *E. balteatus* to the model flowers

A total of 405 landings were made on the model flowers by starved and normally fed *E. balteatus* over the experimental period (Table 2.8). No significant differences between the numbers of landings by the starved and normally fed flies were seen (Mann-Whitney *U* test; $U = 8$; $P > 0.05$) (Table 2.9), although there was a trend for more landings by the starved flies.

Date (2004)	Starved flies	Normally fed flies
02 February	39	37
09 February	42	29
16 February	48	38
23 February	32	28
01 March	44	38
08 March	19	11
Totals	**224**	**181**

Table 2.8. Numbers of landings on the yellow model flowers by starved and normally fed *E. balteatus* over the experimental period.

Starved /fed flies	Mean Rank		*U*	*P*
	Starved	Normally fed		
Experiment 1: No of eggs laid on broad bean plants	6.83	6.17	16.00	0.818
Experiment 2: No of landings on model flowers	8.17	4.83	8.00	0.132

Table 2.9. Results of Mann-Whitney tests comparing numbers of eggs laid on bait plants (Experiment 1), and numbers of landings on model flowers (Experiment 2) by starved and normally fed gravid *E. balteatus*.

2.13. Discussion

Oviposition response of starved and fed *E. balteatus*

Although it was assumed that the starved females were hungry and would be actively seeking food, they nonetheless laid as many eggs as flies that had been fed normally, rather than continuing to search for food as might have been expected. It seems probable that the presence of aphids was an over-riding stimulant. Assuming that at least some of the hoverflies approaching yellow model flowers in the field did so because they were hungry and seeking pollen or nectar, this would help explain why as many eggs were laid in the field near model flowers without food resources as with them. The field experiment was carried out at a time of year when many natural pollen and nectar resources were available, and it seems unlikely that gravid females arriving at the model flowers in the field would have been at the level of starvation of the experimental flies in the laboratory. Unfortunately, few studies have involved measurement of the effects of food deprivation or food type on the numbers of eggs laid *per se* (but see Heimpel *et al.*, 1997). Gilbert and Jervis (1998), however, found that food deprivation had an effect on life span. The results of this experiment might have been different if food resources more optimal for *E. balteatus* had been used. Therefore, it is suggested that the effect of different pollens and nectar extracts are investigated for their effect on the growth, development and subsequent oviposition performance of captive-reared *E. balteatus*, and that the attractiveness of those food resources found most efficient under insectary conditions, be tested in the field. Almohamad *et al.* (2007), for example, found bee-collected pollen and sugar to be suitable foods for *E. balteatus* in the laboratory.

In the second experiment, both starved and normally fed flies landed on the model flower targets, with no significant differences between the number of landings, although there was a trend for more landings by the starved flies, presumably because they were actively seeking food. This again helps to explain the success of model flowers in attracting gravid syrphids to crops;

although the models are presumably recognised as a potential food source, it appears that even flies that have been exposed to a continuous food supply may be attracted towards them and then respond to a nearby oviposition stimulus.

2.14. Conclusions

Although oviposition may be affected by a number of things unexplored here, the results of the field experiments described above showed that syrphid eggs, in particular *E. balteatus,* were laid on bait plants in the vicinity of yellow model flowers with or with out food resources. Laboratory experiments which followed, suggested that food deprivation had no apparent effect on oviposition behaviour or on attraction towards a yellow target. Indeed the above investigations strongly suggested that the oviposition needs of *E. balteatus* were greater than their food requirements. It is possible that, if different food resources were used, then targets with food might be found to be more attractive than those without. However, yellow targets without food did enhance oviposition and would be easier and less expensive for farmers to deploy than targets containing food resources.

CHAPTER 3

COLOUR PREFERENCES IN APHIDOPHAGOUS SYRPHIDS

From the work described in the previous chapter, it appeared that placing model flowers in the field margins of crop fields enhanced oviposition nearby, and that the most important cue in attracting gravid hoverflies to the model flowers was colour. This Chapter describes laboratory experiments followed by large-scale field experiments, which attempted to assess the optimum colour of a model flower to attract gravid hoverflies.

3.1. General introduction

The importance of flower colour in attracting insect pollinators has been recognised for some time and reviewed on several occasions (e.g. Wyatt, 1997; Sutherland 1998; Kevan *et al.,* 2001). The colour of a flower is obviously important, since it enables insects to tell known from unknown flowers and to discriminate profitable food resources and inefficient ones (Chittka & Menzel, 1992). However, success in foraging behaviour is critically dependent on a sensory system which is tuned such as to allow insects to distinguish one flower species from another (Kevan *et al.*, 2001; Chittka & Menzel, 1992). An important component of this equipment is the colour vision system of the insect (Kevan *et al.*, 2001). Consequently, particular insects show a tendency to restrict their visits to flowering plant species of a given colour signal which they have experienced as rewarding (Backhaus *et al.,* 1987; Chittka *et al.*, 1992). Indeed, Sutherland *et al.* (1999) suggested that resources could be effectively partitioned between pollinators, based in part upon flower colour. Lunau and Maier (1995a, b) discuss colour preferences on the basis of what is known about the physiology of colour vision in Diptera.

Many authors (e.g. Daumer, 1956; Kevan, 1978; Feinsinger, 1983; Menzel, 1985; Menzel & Backhaus, 1991) have discussed the evolutionary relationship between flower colour and insect perception. From an evolutionary aspect, the development of the sense of colour in insects probably arose early in the phylogenies of the Arthropoda and Chordata (Kevan *et al.,* 2001). Many insects and vertebrates have been shown to have multiple classes of photoreceptors that contribute to colour vision. For example, some butterflies (e.g. *Gonopteryx rhamni* and *Pieris brassicae*) possess five colour receptors and are attracted to colours which reflect in the red part of the spectrum (about 600nm) (Arikawa, *et al.*, 1987). This suggests that red flowers have evolved exclusively with respect to the perception of the pollinators (Chittka & Menzel, 1992).

In colour discrimination tests with numerous Hymenoptera, Chittka and Menzel (1992) found that honeybees have trichromatic vision based on ultraviolet, blue and green receptors and are most sensitive to flowers with reflections within the blue-green (430-520nm) part of the spectrum (Peitsch *et al.*, 1992; Chittka & Menzel, 1992). Syrphids such as *Episyrphus balteatus* have been shown to have waveband-specific receptors most sensitive in the green-yellow (490-600nm) part of the spectrum (Stavenga *et al.,* 1993; Lunau & Maier, 1995a, b). Collett and Land (1975) suggest that green-yellow sensitivity may help male *E. balteatus,* and related species, to detect yellow coloured females. Stavenga (1979) investigated the peripheral retinular cells of *E. balteatus* and found that different visual pigments were present in the ventral part of the eye in the male, but not in the female. O'Carroll *et al.* (1997) and Nordström *et al.* (2006) suggest that tracking females that might be moving either against a bright sky or cluttered foliage requires a different neural control system. Having established the existence of colour vision in hoverflies, research has also focused on the question of how many spectral types of photoreceptors are involved.

In the case of flower visiting, green-yellow receptors may have much to do with the attraction to yellow flowers (Stavenga, 1989). Sutherland *et al.* (1999) showed that *E. balteatus* exhibited enhanced behavioural responses to the colour yellow, as previously seen in *Eristalis tenax* (L.) by several workers pollen (e.g. Isle, 1949; Horridge *et al.*, 1975; Kay, 1976; Stavenga, 1989; Lunau & Wacht, 1994; Dinkel & Lunau, 2001). *E. tenax* is known to have photoreceptors with double-peaked curves between 350 and 520nm, which explains the sensitivity to ultraviolet and to green and yellow light (Horridge *et al.,* 1975). Detection of the colour yellow might also explain the preference that *E. tenax* has for yellow pollen: feeding is elicited only by stimulation between 520-600nm, which corresponds to the spectral reflection of pollen (Isle, 1949; Horridge *et al.*, 1975; Lunau & Wacht, 1994; Kelber, 2001). Long wavelength light, which converts metarhodopsin into rhodopsin, accelerates pupil opening in hoverflies (Stavenga, 1979). This might explain the preference hoverflies have for yellow over green stimuli (Kelber, 2001).

Hoverflies are known to visit a wide variety of coloured flowers including red flowers (Chittka & Menzel, 1992; Mondor, 1995; Chittka & Waser, 1997) and light blue to lavender coloured flowers (Sol, 1966; Kevan, 1983; Hickman & Wratten, 1996). Sol (1966), for example, observed that *Eupeodes corollae* were attracted to violet-blue bluebells (*Endymion non-scriptus* (L)). Hickman & Wratten (1996) also found the blue flowers of *Phacelia tanacetifolia* (Benth) to be particularly attractive to syrphids such as *E. balteatus* and *E. corollae.* Colour preferences in hoverflies have also been investigated in the laboratory using artificial flowers. Sutherland (1998) found that *E. balteatus* exhibited enhanced behavioural responses to the colour yellow, as previously seen in *Eristalis* by several workers (Isle, 1949; Lunau, 1993; Lunau & Wacht, 1994). Field studies have also shown yellow to be one of the preferred colours of most syrphid species (Kirk, 1984: Finch & Collier, 1989; Wacht *et al.,* 1996). Indeed, the association of hoverflies with yellow flowers is particularly well documented (e.g. Wacht *et al.,* 1996; Sutherland, 1998).

Ultraviolet is also an important component in insect and flower inter-relationships (Kevan *et al.*, 2001). Ultraviolet receptors are generally frequent and are often concentrated in the dorsal part of the eye, as reported by Peitsch *et al.* (1992) and Kevan *et al.* (2001). Most insects are sensitive to ultraviolet wavelengths around 340nm (Chittka, 1996). Although the actual leaf reflects little ultraviolet, hairs (or glaucous coverings) on the surface of the leaf are responsible for bright ultraviolet reflections (Eisner *et al.*, 1973). In other plants, flavonoids in the petal parenchyma are presumed to be responsible for ultraviolet reflection (Frohlich, 1976). It is assumed that ultraviolet reflecting nectar guidelines orientate insects towards the food reward (Kevan *et al.*, 2001). However, it has been suggested that ultraviolet light has no more importance beyond that of reflections in other wavebands (Lutz, 1924). Kevan *et al.* (2001) argued that ultraviolet in *combination* with other reflections elicited flower-visiting behaviour in some insects. In studies with honeybees, Giurfa *et al.* (1996) showed that if the colour contrast was absent, bees had difficulty in detecting the target at all, even if the ultraviolet component was present. Other workers (e.g. Spaethe *et al.*, 2001: Kevan *et al.*, 2001) have also demonstrated the effect of ultraviolet in diminishing the detectability of targets. Spaethe *et al.* (2001), for example, noted that white targets with ultraviolet reflectance attracted fewer bees when placed on a green background. In contrast, white model flowers without ultraviolet reflectance were more attractive to the insects. Kevan and Baker (1983) found that flowers that were prominent against the background attracted hoverflies over long distances and that yellow flowers showed up particularly well against green vegetation. However, the most striking contrast was found in bright yellow flowers which were highly reflective of ultraviolet light (Frohlich, 1976).

Although ultraviolet is unrelated to fluorescent reflectance, the reflectance patterns often appear to be similar (Eisner *et al.*, 1973; Frohlich, 1976). Flowers which fluoresce or appear very bright are visited by a wide variety of Diptera (Isle, 1949; Finch, 1992; Sutherland, 1998: Kevan *et al.,* 2001) and Hymenoptera (Werner *et al.*, 1988; Kevan *et al.,* 2001). Fluorescent yellow is known to be particularly attractive to hoverflies (Hickman, 1996; Sutherland, 1998).

Fluorescent yellow traps have been used by a number of workers to attract hoverflies (e.g. Haslett, 1989a; Finch, 1992; White *et al.*, 1995; Kula, 1997; Hickman, 1996; Sutherland, 1998). Parameter (1951) was the first to report the attraction of syrphids to yellow, on observing *Metasyrphus luniger* (Meigen) hovering over a patch of paint. In New Zealand, Wratten *et al.* (1995b) observed that colour attraction varied between two species of syrphid. Although *Melangyna novaezelandiae* (Macquart) were attracted to yellow water traps, there were no significant differences in the numbers of *M fasciatum* caught in yellow, blue and white traps. However, Sol (1966), found blue to be more attractive to hoverflies than yellow, while Cowgill (1990) reported white to be the preferred colour. Despite the conflicting data, yellow water traps are frequently used in monitoring programmes to catch syrphids (e.g. Schneider, 1969; Dean, 1982; Finch & Collier, 1989; Wyatt *et al.*, 1997; Sutherland, 1998).

In studies using yellow water traps, most workers (e.g. Sol, 1966; Lewis & Taylor, 1967; Haslett, 1989a; Cowgill, 1990; Wyatt *et al.*, 1997; Sutherland, 1998) have concentrated on the effectiveness of the traps in catching the insects rather than on the type of colour used. From the perspective of the insect, floral hue (predominant wavelength), saturation (purity of colour) and intensity (percentage reflectance) may all be important (Moericke, 1969). Vernon & Bartel (1985) suggest that such attributes should be considered when determining the shade of the paint to be used in programmes for monitoring insects.

In the investigation described below, the aim of which was to find the optimum colour for use on model flower targets to attract gravid females to crop fields, it was decided to confine the investigation to the effects of using different shades of yellow, rather than to use a wider range of colours. Yellow is attractive to *E. balteatus* and to *E. corollae* (see above), the aphidophagous species most important in biocontrol of aphids. By looking at yellow shades alone, it was possible to undertake an in depth analysis of syrphid responses to yellows of different wavelengths and reflectances, which would not have been possible if several different colours were being compared. Laboratory work first assessed the landing response of *E. balteatus* to a range of yellow shades in the laboratory and based on the results of this, four fluorescent yellow shades, two of which reflected UV light, were tested in the field.

3.2. Laboratory experiment

In view of the amount of evidence that *E. balteatus* is attracted by the colour yellow (e.g. Isle, 1949; Horridge *et al.*, 1975; Kirk, 1984; Stavenga, 1989; Finch & Collier, 1989; Finch, 1992; Wacht *et al.,* 1996), and the importance of this species in the biocontrol of aphids in the UK, it was decided to test the landing responses of *E. balteatus* to a range of yellow trays in the laboratory. The aim was to try to establish the best shades of this colour to be tested in large scale field experiments to find the optimum yellow to be used for model flowers to attract gravid syrphids, in particular *E. balteatus,* to crop fields.

3.3. Methods and materials

3.3.1. Experimental insects

Twelve male and 12 female *E. balteatus* (first generation), reared in the Insectary at the University of Southampton, were taken at random before each bioassay. Flies were two weeks old at the start of the experiment. Between experiments, flies had access to three Petri dishes with pollen, a 10% honey solution and tap water on cotton (see Chapter 2, Methods section 2.3.2). Flies also had access to bean plants (*Vica faba*) infested with the vetch aphid, *Megoura viciae* supplied by Mambotox (University of Southampton). During bioassays, flies had access to water, but not to food.

3.3.2. Experimental arena

The floor of a perspex cage (40 x 60 x 40cm) was covered with brown wrapping paper (W.H. Smith), which was replaced after each experimental run. Brown was chosen because it reflects fairly evenly and dully across the insect visual spectrum (Kevan, 1972). The entrance to the cage was covered with 'tubi-gauze' netting (20 x 20cm) through which treatments and insects could be transferred. Male and female *E. balteatus* were then released into the cage and allowed to settle for one hour before making observations. Ceiling mounted fluorescent bulbs provided ambient lighting (5000lux/L16: D7 photoperiod). Temperature was maintained at 22^0C ± 1^oC during the experimental period.

3.3.3. Yellow paints

Four fluorescent and five non-fluorescent yellow paints were tested. Eight were commercially available pre-formulated paints supplied by B & Q. Glocote 1263 was obtained from the manufacturers (Goovar, Ellenshaw Works, Hull HU2 OHN). Yellow paints were selected that appeared to be visually different to the human eye. The four fluorescent paints that were available at the time were Plasti-Kote fluorescent enamel 142S; Plasti-Kote 655 fluorescent spray; Glocote fluorescent gloss 1263 and Revell fluorescent enamel SM312. Five non-fluorescent paints were chosen at random. These were Plasti-Kote 'Buttercup' gloss B12; Daler Rowney lemon yellow gloss 651; Plasti-Kote sunshine yellow gloss B11; Tamiya Acrylic X-8 and Crown Soleil matt emulsion 0202458.

3.3.4. Preparation of the yellow trays

Nine flowerpot saucers (diameters 6 cm) were sanded and treated with a base coat (see Chapter 2, Methods section 2.7.1). When dry, trays were hand-painted or sprayed with yellow paint. To eliminate any possible odour emanation, trays were left in a well-ventilated room for two months before use. Trays were placed 2cm apart at random in a 3 x 3 square arrangement in the centre of the cage. Tray positions were re-randomised within the experiment every 30 minutes to eliminate positional preference. The numbers of landings on the yellow trays were observed continuously over four two-hour periods from 19 January to 9 February 2004. Between experiments, the trays were rinsed with tap water to remove contaminants and left to dry in a well ventilated room.

3.3.5. Reflectance spectrophotometry

Reflectance spectrophotometry was used to obtain an objective description of the paint colours. Data on the visible reflectance spectra for the yellow paints were obtained at the University of Southampton by means of an Ocean Optics B.V. S2000 dual channel fibre optic spectrometer. A DT-MINI Deuterium Tungsten halogen flash bulb illuminated a fibre optic reflectance probe and transmitted the light to the spectrometer. Three fast scans were carried out on each of paints. The mean values were calculated to produce spectral reflectance data between 250 and 600nm. The graduate potential of the yellow paints was determined by calculating the intensity values of the maximum and minimum wavelengths. A barium sulphate plate was used as a calibration standard.

Analysis

Numbers of landings on the different yellow trays by *E. balteatus,* and by male and female flies separately, were compared using Kruskal-Wallis non-parametric one-way analysis of variance. Because it was expected that there might be a different response to fluorescent and non-fluorescent yellows, the numbers of landings on fluorescent and non-fluorescent trays were compared using a Mann-Whitney test. All statistical analyses were performed using SPSS11

3.4. Results

3.4.1. Visits to the yellow painted trays

Table 3.1 (a) shows the numbers of landings by male and female *E. balteatus* on each of the different yellow trays. Differences between the numbers of *E. balteatus* landings on the yellow trays were highly significant (Kruskal-Wallis test; $X^2 = 22.03$; df = 8; $P < 0.01$) with more landings on fluorescent Plasti-Kote 142S than on non-fluorescent Plasti-Kote B11. Similar results were seen for male landings (Kruskal-Wallis test; $X^2 = 19.27$; df = 8; $P < 0.05$) and for females (Kruskal-Wallis test; $X^2 = 18.81$; df = 8; $P < 0.05$) separately, with significantly more visits made to fluorescent Plasti-Kote 142S than non-fluorescent Tamiya X-8. Table 3.1 (b) shows the results of the Kruskal-Wallis tests for each observation. Differences between the fluorescent and non fluorescent trays were confirmed by a Mann-Whitney test (Mann-Whitney test; $U = 29.0$; n= 16, n =20; $P < 0.001$).

(a)

	Treatment									
Dates	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**Totals**
	♂ / ♀	♂ / ♀	♂ / ♀	♂ / ♀	♂ / ♀	♂ / ♀	♂ / ♀	♂ / ♀	♂ / ♀	
19/01/04	6 / 9	3 / 3	7 / 4	2 / 0	2 / 4	1 / 1	0 / 1	1 / 2	4 / 4	**26 / 28**
26/01/04	9 / 13	7 / 4	6 / 3	3 / 4	3 / 5	1 / 1	0 / 2	1 / 2	4 / 5	**34 / 39**
02/02/04	10 / 9	8 / 5	5 / 5	5 / 3	3 / 0	5 / 1	4 / 3	3 / 3	5 / 3	**48 / 32**
09/02/04	8 / 11	4 / 2	7 / 4	2 / 4	1 / 3	3 / 5	6 / 2	6 / 2	2 / 5	**39 / 38**
Totals	**33 / 42**	**22 / 14**	**25 / 16**	**12 / 11**	**9 / 12**	**10 / 8**	**10 / 8**	**11 / 9**	**15 / 17**	**147 / 137**

(b)

	Mean rank									df	X^2	*P*
Males & females	34.5	21.75	26.63	13.75	12.63	10.38	10.88	12.13	21.88	8	22.032	*0.005
Males	33.00	24.63	28.25	14.25	10.88	12.00	12.50	13.00	18.00	8	19.270	*0.013
Females	34.50	19.50	22.88	15.88	17.50	10.75	9.88	11.13	24.50	8	18.807	*0.016

Table 3.1 (a). Numbers of landings on the different treatments by *E. balteatus* **(b).** Results of Kruskal-Wallis one-way analysis of variance on numbers of *E. balteatus* landing on the yellow trays. **1** = Plasti-Kote 142S; **2** = Glocote 1263; **3** = Revell SM312; **4** = Plasti-Kote B12; **5** = Daler 651; **6** = Plasti-Kote B11; **7** = Tamiya X-8; **8** = Crown 0202458; **9** = Plasti-Kote 655. * indicates significant differences between treatments.

3.4.2. Reflectance curves

A sharp step in the spectrum at about 500nm was noted for the four fluorescent paints (Plasti-Kote 142S, Plasti-Kote 655, Glocote 1263 and Revell SM312) (Fig. 3.1), but not for the non-fluorescent paints. Reflective intensities (RI) for three of the fluorescent paints, Plasti-Kote 142S, Plasti-Kote 655 and Revell SM312 were 200%. RI for the fourth fluorescent paint, Glocote 1263, was 160%. Reflective intensities for the non-fluorescent paints varied between 120% and 80%. Fluorescent Plasti-Kote 142S produced a secondary peak in the ultraviolet at about 350nm. Non-fluorescent Crown 0202458 also produced a second spectral curve in the blue part of the spectrum at about 400nm.

To confirm the original result, a second scan was carried out on the fluorescent yellow paints. Fluorescent yellow Plasti-Kote B29 was also included in the spectrometry as this was available at the time. The mean values were calculated to produce spectral reflectance data between 500 and 520nm. Plasti-Kote B29 and Plasti-Kote 142S produced a secondary peak in the ultraviolet at about 350nm. Glocote 1263 produced a second spectral curve in the blue part of the spectrum at about 420nm (Fig. 3.2).

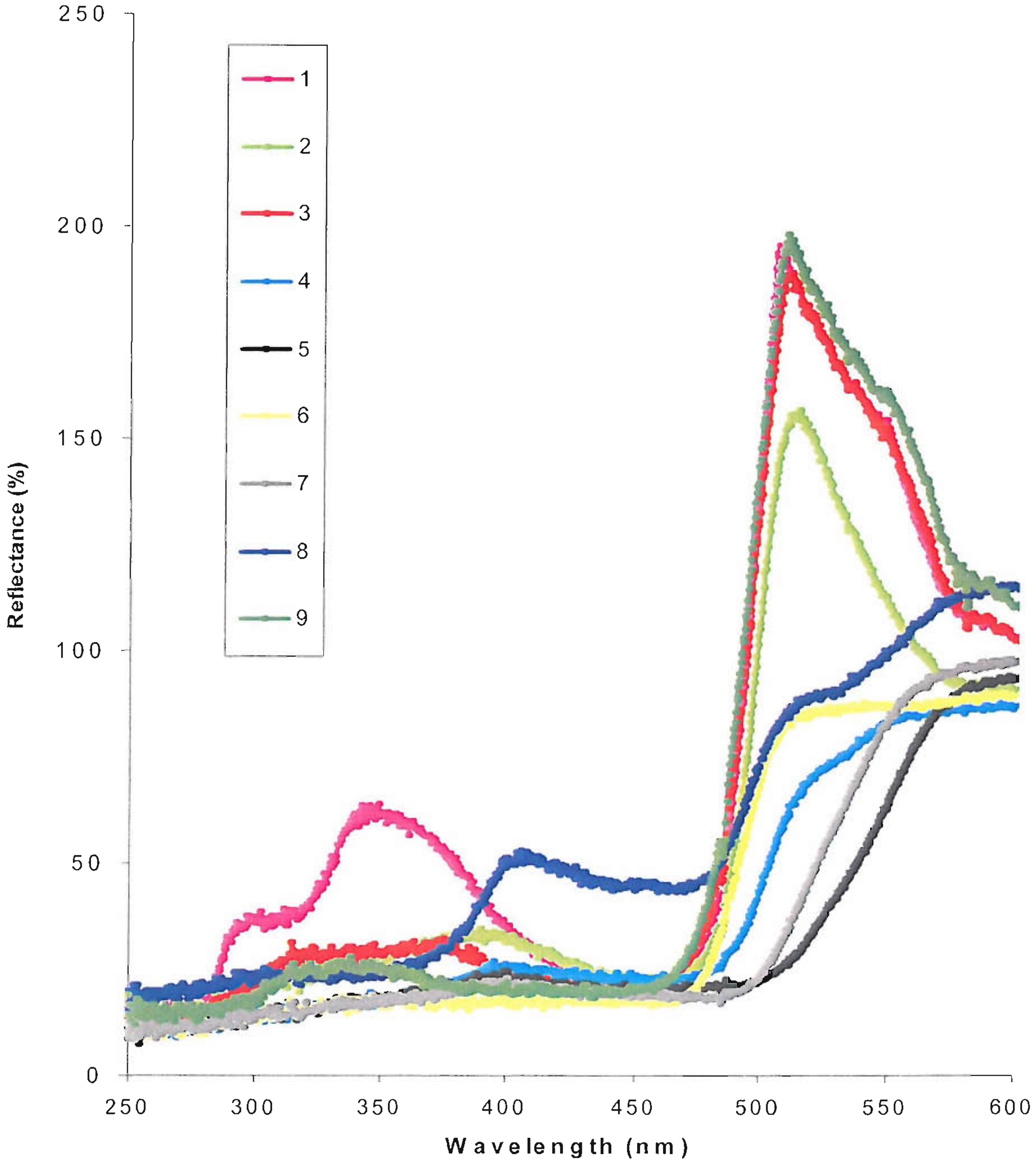


Figure 3.1. The dashed lines mark the spectral reflection of the 9 colours tested in the laboratory. Wavelength positions were determined by taking the mean value of three spectral scans (1= Plasti-Kote 142S*; 2 = Glocote 1263*; 3 = Revell SM312*; 4 = Plasti-Kote B12; 5 = Daler 651; 6 = Plasti-Kote B11; 7 =Tamiya X-8; 8 = Crown 0202458; 9 = Plasti-Kote 655*). * indicates fluorescent paint.

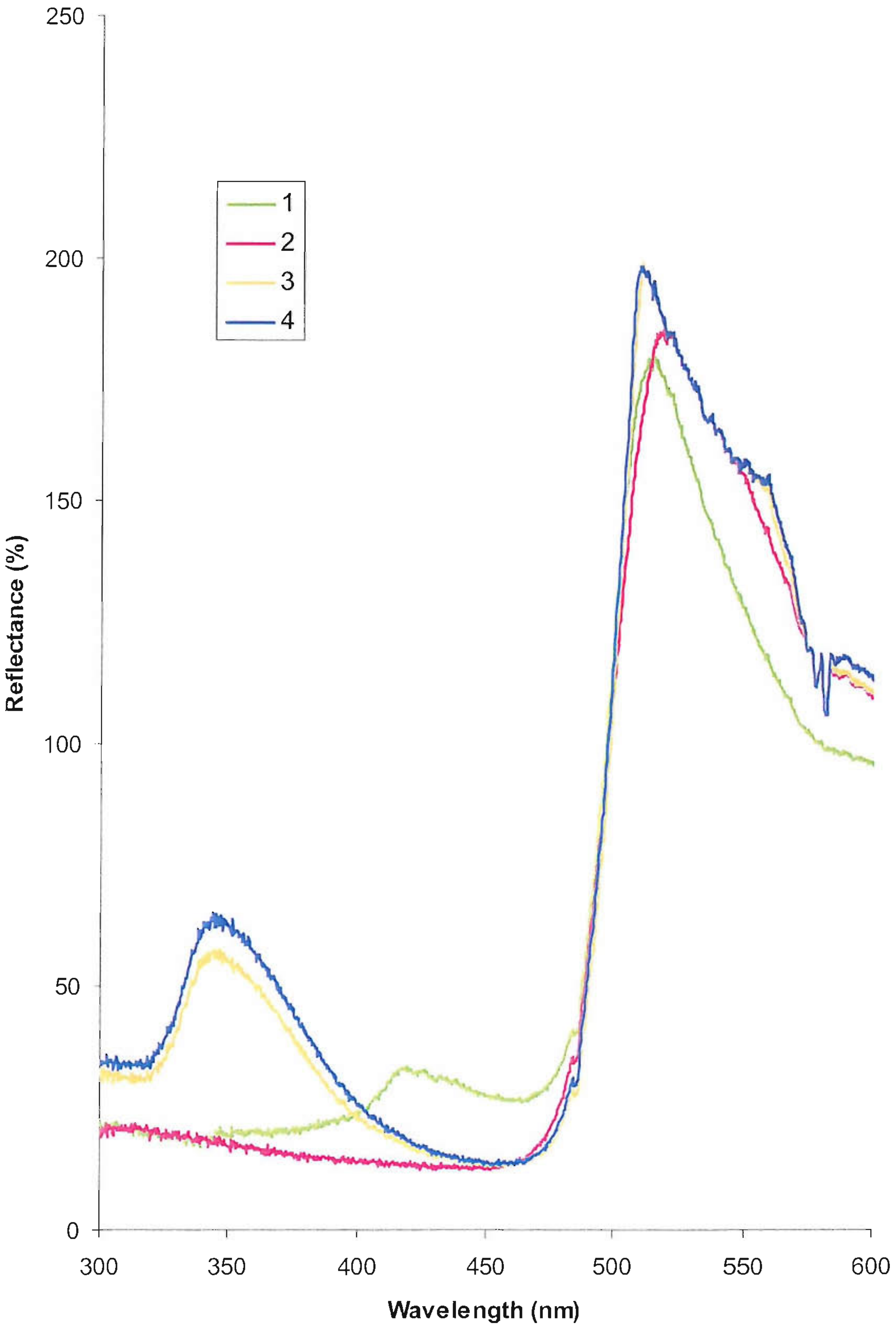


Figure. 3.2. The coloured lines mark the spectral reflection of the four colours tested in the field (1= Glocote 1263; 2 = Plasti-Kote 655; 3 = Plasti-Kote B29; 4 = Plasti-Kote 142S).

3.5. Discussion

The attraction to the fluorescent yellow trays correlated well with the findings of other workers (e.g. Isle, 1949; Horridge *et al.*, 1975; Gilbert, 1981; Kevan 1983; Sutherland, 1998) who found that *E. balteatus* showed a strong preference for yellow flowers such as dandelion (*Taraxacum offinale* (Weber)), ragwort (*Senecio jacobea*) and buttercup (*Ranunculus repens* (L)) with spectral properties between 490 and 580nm. Fluorescent yellow trays had much higher reflectance intensities than the non-fluorescent ones and elicited significantly more visits by *E. balteatus.* Fluorescent yellow trays also produced sharp peaks in the yellow part of the light spectrum (520 – 580nm). However, such spectral peaks were not observed for the non-fluorescent yellow trays.

It was also found that fluorescent yellow Plasti-Kote 142S produced a secondary spectral curve in the ultraviolet part of the spectrum (350nm). This paint elicited more landings by *E. balteatus* than any other yellow shade tested. It is possible that this paint mimicked the reflectance of *Taraxacum* and *Senecio* flowers, which have a secondary peak in the ultraviolet at about 350nm (Kevan *et al.*, 2001). These flowers are known to be attractive to hoverflies (Kevan & Baker, 1983).

It was thought that preference to different shades of yellow might change with the increasing age of the flies (flies were aged five weeks at the end of the experiment). Sutherland (1998) and Sadeghi and Gilbert (2000) found a decrease in preference from yellow to blue in *E. balteatus* with increasing age. However, the same general pattern of more landings on the UV reflecting yellow shades was seen throughout the experiment.

Although the laboratory experiment provided an opportunity to investigate the landing responses of *E. balteatus* to different yellow shades under controlled conditions, artificial fluorescent lighting was used and it is very likely that this dulled the effect of the yellow paints. Unlike fluorescent lighting, which does not contain the balance of the full colour spectrum, daylight distributes light of almost all visible wavelengths more evenly and provides better colour rendition (Hashmi, 2002). Natural sunlight also eliminates problems associated with fluorescent lighting such as light flicker and decreases in lighting from the middle to the end of the tube (Hashmi, 2002). It was therefore decided to test the responses of aphidophagous syrphids to yellow painted trays in the field.

3.6. Field experiments

3.6.1. Introduction

Following the work described above, a large scale experiment was carried out to test syrphid colour preference in the field. The laboratory results indicated that, for *E. balteatus* at least, fluorescent yellow model flowers would be more attractive than non-fluorescent yellow ones and it was decided to confine the colour treatments to this category. Two ultraviolet (UV) reflecting yellow fluorescent paints were used, one of these being the paint that received the most visits in the laboratory experiment, and two non-UV yellow fluorescent trays. The aim was to determine the optimum yellow model flower colour to be used in a model flower to attract gravid syrphids.

3.7. Methods and materials

3.7.1. Experimental site 2005

The site in 2005 (Fig. 3.3) consisted of three winter wheat fields of similar size located at Uggford Farm, Wilton, Salisbury, England, UK. Field boundaries for each site consisted primarily of hawthorn (*Crataegus monogyna*) and beech (*Fagus sylvatica*) hedgerows with an understorey of herbaceous plants (see Chapter 2, methods section 2.7.3. for site details). A farm track ran parallel to one side of each field. The winter wheat crops were harvested on 16 August.

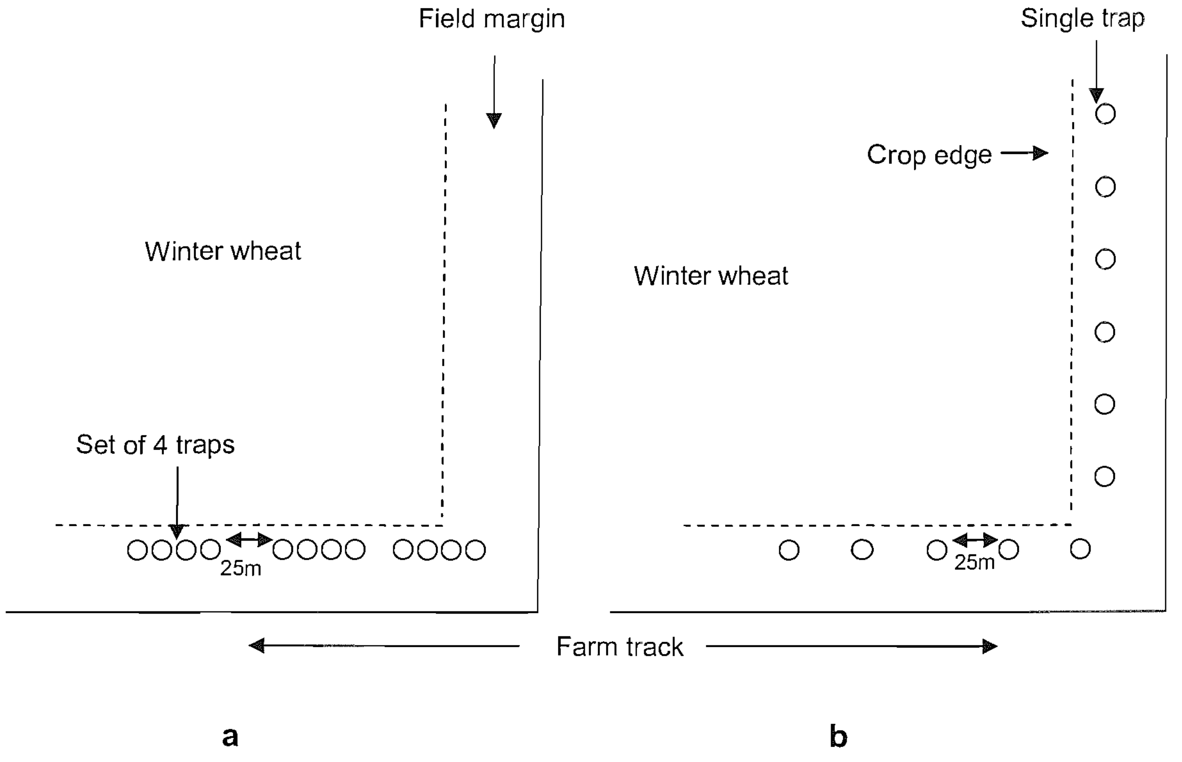


Figure 3.3a, b. Simplified plan showing the layout of yellow water traps in the winter wheat fields in 2005 (not to scale). **a** = arrangement of traps in sets in one field margin; **b** = layout of single traps in two field margins (see text for details).

3.7.2. Water trap preparation

The water traps were 19 cm diameter plastic flowerpot saucers painted with one of the four chosen fluorescent yellows (see Methods above) and filled with tap water and a 1% solution of ordinary household detergent. The UV reflecting paints were Plasti-Kote 142S and Plasti-Kote B29. Non-UV reflecting paints were Plasti-Kote 655 and Glocote 1263. Although Revell SM312 was also found to be attractive to *E. balteatus* in the laboratory, difficulties in obtaining sufficient quantities of the paint made it unsuitable for fieldwork. Storage limitations meant that it was not possible to leave the traps in a ventilated room to eliminate any possible odour emanation. Traps were put out in the field as soon as they were dry.

3.7.3. The treatments

Sets of traps (15 – 22 July 2005)

Sets of the four treatments, randomly placed in a straight line parallel to the edge of the crop and with 45 cm between treatments, were placed on the ground at intervals of 25 metres along the length of the field margin and within one metre of the crop edge (see Fig. 3.3a). In each of the three winter wheat fields, there were 5 replicates of each set Collections of hoverflies were made on four separate occasions from 15 to 22 July. Trap positions within each set were re-randomised after each collection.

Single traps (25 July – 1 August 2005)

As it was possible that the proportions of syrphids trapped in each colour treatment might vary according to whether or not a choice was available, traps were also set out separately, placed in random order on the ground at intervals of 25 metres, and within one metre of the crop edge (see Fig. 3.3b). There were 5 traps of each treatment (total 20 per field) in two field margins in each field. Collections of hoverflies were made on three separate occasions from 25 July to 1 August 2005. Trap positions were re-randomised after each collection.

After each collection, traps were cleaned and reset with tap water and 1% solution of ordinary household detergent. Catches of aphidophagous syrphids were transferred to 70% alcohol in labelled plastic tubes and identified to species and sex using the criteria of Stubbs and Falk (2000).

Vegetation and flowering plants within 10 metres of the traps were removed to ensure that they could be seen from a distance. No insecticide was used on the crops or on any of the surrounding fields during the experimental period.

Analysis

Kruskal-Wallis tests were used to compare the numbers of gravid syrphids caught in the yellow traps, and the numbers of gravid *E. balteatus* and *E. corollae* separately. Single traps and sets of traps were analyzed separately.

Because it was expected that more gravid syrphids would be caught in the UV reflecting traps than the non-UV traps, Mann Whitney tests were carried out to compare numbers caught in UV and non-UV traps in each experiment. All statistical analyses were performed using SPSS11

3.8. Results

3.8.1. Numbers of syrphids

A total of 1408 aphidophagous syrphids, of which 119 were gravid females, were caught between 15 and 22 July (sets of traps) and 9373 (488 gravid) between 25 July and 1 August (single traps). Most syrphid species and gravid females were trapped on the last two collection dates (Table 3.2).

Date of collection	**Plasti-Kote B29 (UV)**	**Plasti-Kote 142S (UV)**	**Glocote 1263**	**Plasti-Kote 655**	**Totals**
Sets of traps					
15/07/2005	113 (10)	133 (22)	20 (5)	16 (1)	**282**
16/07/2005	103 (27)	102 (28)	13 (1)	43 (8)	**261**
21/07/2005	177 (3)	236 (9)	120 (0)	95 (2)	**628**
22/07/2005	96 (0)	89 (2)	31 (1)	21 (0)	**237**
Totals	**489 (40)**	**560 (61)**	**184 (7)**	**175 (11)**	**1408 (119)**
Single traps					
25/07/2005	155 (8)	180 (8)	92 (2)	73 (3)	**500**
29/07/2005	1861 (85)	2158 (133)	1445 (72)	884 (35)	**6348**
01/08/2005	843 (81)	869 (40)	494 (17)	319 (4)	**2525**
Totals	**2859 (174)**	**3207 (181)**	**2031 (91)**	**1276 (42)**	**9373 (488)**

Table 3.2. Numbers of aphidophagous syrphids caught in different yellow colour treatments in 2005 (figures in brackets represent gravid females).

Gravid females were mainly *E. balteatus* and *E. corollae* (these species together accounted for 74% of the individuals trapped in sets, and 82% in single traps). Other species included *Scaeva pyrastri* (L), *Sphaerophoria scripta* (L), *Chrysotoxum bicinctum Melanostomini* (L), *Syrphus* and *Platycheirus.* Figure 3.4 shows the numbers of gravid females and different species caught in the different treatments over the experimental period.

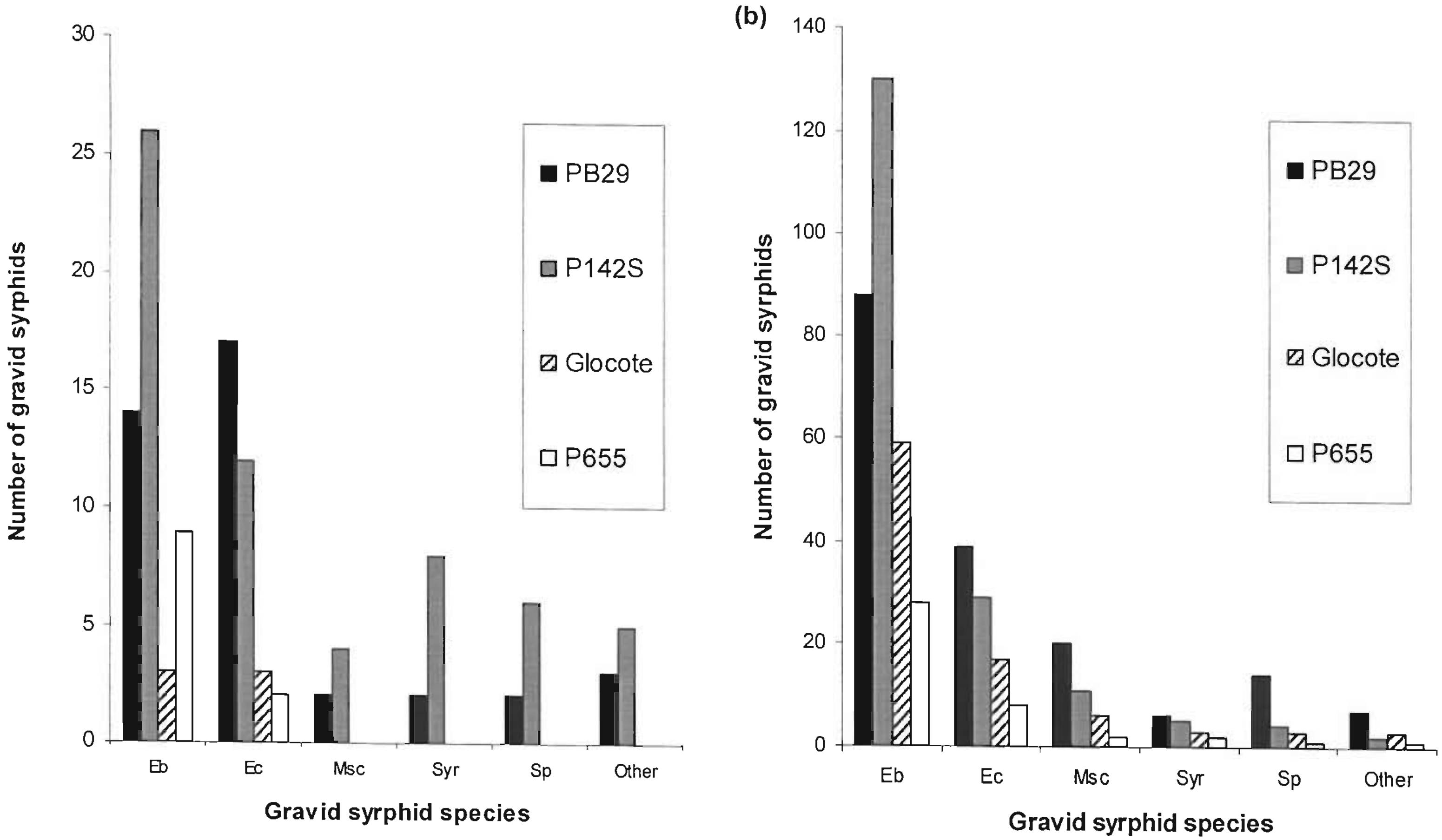


Figure 3.4 (a) & (b). Numbers of gravid syrphids *species* caught in sets of traps **(a)** and single traps **(b)** over the experimental period. (*Eb* = *E. balteatus; Ec* = *E. corollae; Msc* = *Melanostoma scalare*; *Syr* = *Syrphus ribesii* and *S. vitripennis*; *Sp* = *Scaeva pyrastri;* Other = *Sphaerophoria scripta, Chrysotoxum bicinctum* and *Platycheirus* species). UV traps: P B29 and P 142S; non-UV traps: Glocote and P 655.

Kruskal-Wallis analysis (see Table 3.3 for details of analysis) showed that for all aphidophagous syrphids trapped, whether in single or sets of traps, and for all gravid females and for *E. balteatus* and *E. corollae* separately, rankings for the numbers of flies trapped in the two UV reflecting colour treatments were similar and higher than the rankings for the two non UV reflecting fluorescent yellow treatments. In every case the differences between the highest and lowest ranked treatment were very highly significant with P <0.01 in all cases.

For all gravid females, the Kruskal-Wallis mean rank (Table 3.3) for P124S (UV) was higher than the ranking for P B29 (UV) when traps were presented in sets (P124S: 150.42; P B29: 130.71) (Table 3.3). When traps were presented singly, the rankings were very similar with P B29 (UV) slightly higher (P124S: 105.08; P B29: 108.67). When *E. balteatus* and *E. corollae* were analysed separately, for *E. balteatus* the highest ranked treatment was P124S and for *E. corollae* the highest ranked treatment was P B29; in each case this applied whether traps were presented singly or in sets.

Differences between the total numbers of gravid flies trapped in UV and non-UV reflecting traps were very highly significant, with much higher numbers trapped in treatments with a UV component (Mann-Whitney test; U =102352.0 n= 480, n = 480; P < 0.001, for sets of traps and U = 125097.5; n= 540, n = 540; P < 0.001, for single traps).

	Mean rank				df	X^2	*P*
	P B29 (UV)	**P 124S (UV)**	**G 1263 (non-UV)**	**P 655 (non-UV)**			
Sets of traps							
All syrphids	161.11	170.42	76.38	74.08	3	103.257	*0.000
All gravid females	130.71	150.42	96.63	104.23	3	33.941	*0.000
Gravid *E. balteatus*	121.70	137.86	105.28	117.17	3	15.58	*0.001
Gravid *E. corollae*	131.78	125.47	113.35	111.40	3	12.25	*0.007
Single traps							
All syrphids	105.08	108.67	80.61	67.64	3	19.285	*0.000
All gravid females	111.11	105.21	80.47	65.21	3	25.046	*0.000
Gravid *E. balteatus*	104.73	107.39	81.09	68.79	3	20.16	*0.000
Gravid *E. corollae*	105.96	93.96	84.18	77.91	3	12.01	*0.007

Table 3.3. Results of Kruskal-Wallis one-way analysis of variance on the number of syrphids, gravid syrphids, gravid *E. balteatus* and gravid *E. corollae* caught in the different yellow treatments over the experimental period. * indicates significant differences between treatments.

3.9. Discussion

Numerous workers have related ultraviolet reflections from flowers to ultraviolet sensitivity in insect vision (e.g. Chittka & Menzel, 1992; Kevan *et al.*, 2001). Although most studies have concentrated on bee sensitivity to ultraviolet reflections (Backhaus, 1993; Giurfa *et al,* 1996; Spaethe *et al.*, 2001; Lunau, 2005), it appears that hoverflies are also sensitive to ultraviolet reflections. It was demonstrated under laboratory conditions that fluorescent yellow model flowers elicited more visits by *E. balteatus* than non-fluorescent ones and that ultraviolet reflections enhanced this response. It was also evident that the ultraviolet reflecting traps were more attractive to *E. balteatus* (and to syrphids generally) than the non-ultraviolet reflecting ones under natural conditions in the field. Whether the treatments were arranged in sets or separated, ultraviolet reflecting traps were chosen more frequently than the non-ultraviolet reflecting ones which always ranked last. Although there are a few examples in the literature of ultraviolet eliciting landing behaviour in insects, most studies have concentrated on honeybees (Dafni *et al.*, 1997; Lehrer, 1997) and butterflies (*Papilio* spp. and *Pieris brassicar*) (Scherer & Kolb, 1987). However, flowers pollinated primarily by butterflies and bees have nectar guidelines in the human-visible range (Kevan *et al.,* 2001). Simpler flowers with open corollae are less likely to have nectar guides but more likely to have ultraviolet reflections (Kevan, 1983) and hoverflies are known to be frequent visitors. Guldberg and Atsatt (1975) noted that smaller flowers were much less likely to have ultraviolet reflecting patterns than large flowers. As is shown in Chapter Five, gravid females predominated in large traps and traps without patterns.

Kevan *et al.* (2001) suggest that some insects may use ultraviolet wavelengths in feeding, oviposition and mating, but that the relative importance of UV *vis ā vis* other primary colours is probably no more important than blue, green or red reflections. As yellow water traps were used, the possibility exists that the combination of colour, water and ultraviolet signals enhanced syrphid responses to them. Water can enhance ultraviolet reflections, but model flowers were used in the laboratory under artificial lighting and preference to the ultraviolet reflecting model was shown. However, in the absence of the yellow stimuli, ultraviolet may be no more significant than other wavelengths. The near absence of naturally occurring pure ultraviolet reflecting flowers (Kevan *et al.,* 2001) may explain why no attempt was made to identify the response of syrphids to pure ultraviolet signals.

An interesting feature was that the highest rank for *E. balteatus* was always ultraviolet reflecting Plasti-Kote 142S and for *E. corollae*, UV reflecting Plasti-Kote B29. It is known that not all syrphid species react to colour in the same way (Sabota & Twardowski, 2004). Wratten *et al.* (1995) observed species-specific differences in colour attraction between two species of syrphid, *Melangyna novaezelandiae* (Macquart) and *Melanostoma fasciatum* (Macquart), in New Zealand. Haslett (1989a) suggests different colour preferences between species to be a mechanism for resource partitioning and the avoidance of competition for resources. Kevan *et al.* (2001) proposes differences in choice behaviour to be the result of different perceptual dimensions. Although there was a very small difference in ultraviolet reflectance between the two paints, it did appear that they might be perceived differently by *E. balteatus* and by *E. corollae*. However, this investigation only provided information about the reflectance spectra of the yellow trays in relation to the number of *E. balteatus* landings in the laboratory, and attraction to them in the field. It did not consider the visual system of *E. balteatus* and *E. corollae* in relation to ultraviolet perception, which was outside the scope of this work. Further investigations may provide insight into the mechanisms which underlie colour choice in these two species of hoverfly.

Although time did not permit a detailed investigation into responses to more than one colour during this project, it would have been interesting to look at syrphid responses to green targets as well as yellow ones. The reflection of green radiation is known to be extremely important in the detection of leaf size, shape and form in honeybees (Dafni *et al.*, 1997; Lehrer, 1997). Green reflections are also known to stimulate butterflies to oviposit (Kolb & Scherer, 1982). However, in New Zealand, Laubertie *et al.* (2006) caught fewer *M. fasciatum* and *M. novaezelandiae* in traps that were painted green on the outside, than in ones that were completely yellow, presumably because it made them less easy to see. It is known that *E. balteatus* has waveband-specific receptors most sensitive in the green-yellow (490-600nm) part of the spectrum (Stavenga *et al,* 1993; Lunau & Maier, 1995a, b) and it has been postulated that perception of the colour green may be important in eliciting close range oviposition behaviour (Vernon & Bartel, 1985; Chittka & Menzel, 1992). Sutherland (1998) found an enhanced response from yellow to green in three-week old *E. balteatus*, suggesting that older females were more concerned with the search for potential oviposition sites than foraging (Giurfa *et al.*, 1996).

3.10. Conclusions

While there is little evidence in the literature to suggest that ultraviolet is of special significance to hoverflies, from the work described above, it appears that there is good potential for the use of ultraviolet reflecting yellow paint to attract gravid syrphids, including *E. balteatus* and *E. corollae*, to the vicinity of crop fields. Several workers (e.g. Price, 1975; Kevan *et al.*, 2001; Kruess & Dauber, 2004) have demonstrated the potential of ultraviolet reflecting yellow flowers such as dandelion (*Taraxacum offinale*), St. John's Wort (*Hypericum maculatum* (Crantz)) and ragwort (*Senecio jacobea*) in and around gardens and fields to attract hoverflies. Where agricultural practices such as frequent cultivation and herbicide applications have reduced flowering plants, the use of ultraviolet reflecting flowers may enhance the potential benefit of hoverflies for biological control of crop pests. It has already been established (see Chapter 2) that oviposition by aphidophagous syrphids increased in the presence of artificial yellow flowers. A fluorescent yellow which reflects ultraviolet therefore seems to be the optimum colour for the model flowers.

CHAPTER 4

THE RESPONSES OF APHIDOPHAGOUS SYRPHIDS TO AN APHID-DERIVED PHEROMONE AND A PLANT-DERIVED VOLATILE IN THE FIELD

This Chapter describes experiments in which an aphid-derived volatile, nepetalactone, and a plant-derived volatile, *cis*-jasmone, were tested to assess their potential as an attractant to gravid syrphids.

4.1. General Introduction

It is now generally agreed that chemical cues play a major role in attracting insects to particular plants for feeding and oviposition (see Rockstein, 1978; Ritter, 1979; Birch & Hayes, 1982; Bell & Carde, 1984). (See Introduction 1.5.4. for the role of honeydew in stimulating oviposition). Selection of the oviposition site by hoverflies may rely on the detection of prey pheromones and plant green leaf volatiles (Sutherland, 1998). Plant volatiles may also be used to locate potential food resources (Harbourne, 1994).

Many plant chemicals are highly volatile and these are the basis for floral odours generally contained in the 'essential oil' fraction of the flower (the part that can be separated by steam distillation or ether extraction) (Harborne, 1994). Within the essential oils, organic sequiterpenes, simple aliphatic alcohols, ketones and esters may all be present (Kaiser, 1993). Usually, one component reinforces the effectiveness of a second and third in producing a characteristic odour (Beck & Reese, 1976). The concentration of a compound is important; small changes in the concentration of a particular volatile can either increase or abolish its attractant or deterrence value (Rhoades & Cates, 1976). However, for a volatile to be active over a distance of several kilometres it must be of a relatively low molecular weight (Harborne, 1994). Many long-distance volatile compounds e.g. linalool are known to direct bees and moths to specific flowers from almost a mile away (Adams, 2007). However, heavier molecules that do not disperse far from the source may be detected by hoverflies, which may use short-distance olfactory cues to locate potential food resources and oviposition sites (Rashed & Sherratt, 2006).

Of particular importance in the context of this work is the role that pheromones might play in enhancing the oviposition behaviour of aphidophagous hoverflies. The aphid pheromone, nepetalactone, released by females of a number of aphid species in the autumn to attract sexual males shows potential as an odour cue for locating aphids (Wadhams *et al.*, 1999). A mixture of nepetalactone (11) and nepetalactone (12) is liberated from the hind legs of female vetch aphid *Megoura viciae,* the wheat aphid *Schizaphis graminum* (Rondani) and the black bean aphid *Aphis fabae* (Scop) (Dawson *et al.,* 1987). The lactol 12 alone is the sex pheromone of the damson-hop aphid *Phorodon humuli* (Schrank).

There is evidence that nepetalactone attracts aphid parasitoids. Several workers (e.g. Hardie *et al,* 1994; Lilley *et al.,* 1994; Powell & Glinwood, 1998) have found that nepetalactone attracts female *Praon* species, a hymenopteran parasitoid of aphids. Powell & Glinwood (1998), for example, found that female *Praon* species were attracted to field traps baited with aphid sex pheromones, and that numbers of *Aphidius* species greatly increased in the vicinity of pheromone lures. In a later study, Powell (2004) did not find that nepetalactone lures in the field margins of winter wheat crops increased significantly the total number of aphid parasitoids in their vicinity. However, more parasitoids were found further into the crop. In wind tunnel tests, *Praon volucre* (Haliday) and *Aphidius ervi* (Haliday) responded strongly to both plant-extracted and 99% pure synthetic (4a*S*,7*S*,7a*R*)-nepetalactone. However, in the field, there was no significant difference in parasitisation levels by *Praon* spp. between plants baited with synthetic nepetalactone or with plant-extracted 7*S* isomers (Glinwood *et al.,* 1999).

Nepetalactone has also been seen to attract the seven-spot ladybird *Coccinella septempunctata* (L.), (Wadhams *et al.,* 1999), and the lacewing *Chrysoperla carnea* (Steph) (DEFRA, 2002).

Nepetalactone is also one of the major components (~ 40%) of the essential oils from *Nepeta cataria* (Labiatae), a member of the mint family commonly known as Catnip, and is notable as a powerful olfactory attractant for the domestic cat *Felis domesticate* (Erxleben) (Dawson *et al.,* 1987). Leppia (2005) suggested *N. cataria* to be a useful source of pollen and nectar to adult parasitoids and many other beneficial insects. Black (1994) demonstrated that small quantities of pure *cis*-trans nepetalactone applied to the base of a beehive attracted large numbers of bees. A number of field trails in Canada, Korea, the USA and the UK have shown that *Nepeta*-derived compounds attract lacewings, although it was mainly males that responded to the compounds (Powell, 2005). However, the effects of aphid or plant derived nepetalactone on hoverfly behaviour are not yet understood.

In electroantennograph (EAG) tests, responses to nepetalactone have been recorded in *Episyrphus balteatus* (Sutherland, 1998; DEFRA, 2003). In particular, strong electrophysiological activity was observed for (4aS, 7S, 7aR)-nepetalactone, (1R, 4aS, 7S, 7aR)-nepetalactol and for the aphid alarm pheromone (*E*)-*β*-farnesene (DEFRA, 2003). However, EAGs cannot necessarily predict the behavioural response of the insect. Components for which there are few receptors can be missed as may synergies between components which are not usually observed at the peripheral level (Wyatt, 1997).

There is some evidence (e.g. Birkett *et al.,* 2000; Bruce *et al.,* 2003; Hajjar, 2003; Powell & Pickett, 2003) to suggest that plants under attack by aphids and other herbivores produce volatile compounds that attract beneficial predatory insects (Hajjar, 2003). One such volatile is jasmonic acid, which can be activated during damage caused by mechanical wounding or by herbivory. Methylation of jasmonic acid enhances the production of certain glucosinolates, which are emitted from the plant and which stimulate foraging by beneficial insects (Bruce *et al.,* 2003). Engelberth *et al.* (2004) found that corn seedlings naturally emitted methyl jasmonate in response to mechanical wounding and to aphid attack. Bruce *et al.* (2003) demonstrated that methyl jasmonate altered the metabolism of the bean plant *Vicia fabae,* such that plant became less attractive to herbivores and more attractive to beneficial predatory insects. Preston *et al.* (2002) found that release of the volatile had an effect on neighbouring intact plants by regulating defence-related and other genes to withstand herbivore attack (see also Dicke *et al.,* 1990; Karban *et al.,* 1999; Bruce *et al.*, 2003). Although methyl jasmonate has potential for external signalling on intact plants, it can have a deleterious effect on plant development and yields for agricultural crops as a large number of genes are influenced (Pickett *et al.*, 2006). The controlled use of *cis*-jasmone, however, has broad applicability for the expression of commercially relevant trait genes in plants (Hajjar, 2003).

Because of its close structural resemblance to methyl jasmonate, the semiochemical *cis*-jasmone has been investigated both as a plant activator and an aphid repellent (Birkett *et al.*, 2000). The volatile also shows potential as an attractant to predators and parasitoids of aphid pests. When applied in vapour form, *cis*-jasmone has been shown to induce the production of monoterpene (*E*) *β*-ocimene, which affects plant defence, by stimulating the activity of parasitic insects (Birkett *et al.*, 2000). Bruce *et al.* (2003) noted that artificially applied *cis*-jasmone induced the release of the parasitoid foraging stimulant (*E*) *β*-ocimene, resulting in more aphid mummies being formed. Birkett *et al.* (2000) and Bruce *et al.* (2003) also found that when applied to winter wheat seedlings, *cis*-jasmone was sufficient to repel the cereal aphid, *Sitobion avenae* and that the effects were long-lived. Plants were also more attractive to the seven spot ladybird and an aphid parasitoid (Birkett *et al.,* 2000).

EAGs coupled to high-resolution gas chromatography have identified *cis*-jasmone to be an electrophysiologically active compound (Pickett *et al*, 2006). Although there is no published evidence to suggest that *cis*-jasmone exerts an antennal response in aphidophagous syrphids, EAG responses to other plant volatiles (e.g. linalool, 2-Phenylethanol) have been recorded in *E. balteatus* (Sutherland, 1998). However, Hood-Henderson (1982) did not find EAG tests to be a suitable method for showing the effectiveness of odour components as cues in aphidophagous syrphids. Byers (1992) suggested a simple experiment to be the best method for measuring the responses of an insect to a stimulus.

It was decided to test both an aphid pheromone and a plant volatile for their potential as attractants to gravid syrphids. The decision to use nepetalactone and *cis*-jasmone was influenced primarily by the fact that from the literature, both appear to show promise in increasing activity in several species of beneficial predatory insects, but there was no published evidence of their effect on syrphids. Apart from this, nepetalactone was available as a slow release lure, while (E)-*β*-farnesene was much more unstable and not available in this form at the time (but see Pickett *et al.,* 2006). *Cis*-jasmone is an inexpensive, non-toxic natural plant product, with a history of safe use in the perfume industry (Hajjar, 2003) unlike linalool for example, which can heighten sensory nerve activity in insects, thus leading to convulsion and paralysis (Tvedten, 2003).

The aim of this work was to carry out field experiments to find out whether either or both of these compounds had an enhancing effect on syrphid oviposition.

4.2. Nepetalactone experiments

In 2004, a laboratory experiment (similar to an experiment performed by Vet *et al.,* 1983) assessed the landing responses of *E. balteatus* to yellow discs with and without Nepeta lures. This was followed by field trials using slow release nepetalactone lures.

4.3. Method and materials

4.3.1. Preparation of lures

Nepeta lures were obtained from AgriSense-BCS Ltd (product code: BDS030, Treforest Industrial Estate, Pontypridd). Lures were composed of extruded polymer (plasticised PVC) containing *Nepeta cataria* extract (Type 2) produced by English Hop Products Ltd. and the nepetalactol reduction product from IACR-Rothamstead. The formulation was prepared with a 5% loading of the appropriate aphid sex pheromone component. Lures were weighed before and after each bioassay and release rates calculated on the last day of entrainment.

For the handling of the Nepeta lures, standard operating procedures relevant to the handling of any volatile were used. Although inhalation was unlikely, a volatile mask was worn. Disposable gloves were also worn since neat Nepeta oil can cause dermatitis. Lures were double-wrapped in foil and sealed in their packet and kept at 5°C until ready for use. Nepetalactone has a shelf life of approximately six weeks (Powell, 2004).

4.3.2. Model flowers

Four model flowers were constructed using white card discs (diameters 23mm). Card discs had been previously painted with ultraviolet reflecting Plasti-Kote 142S yellow fluorescent paint and left to dry in a well-ventilated room for 28 days to eliminate any possible odour emanation. In previous experiments (see Chapter 3), this paint was more attractive to aphidophagous syrphids than any other colour tested. Two of the discs were each treated with one 2 cm (length) Nepeta lure inserted vertically through a previously drilled 2.5 mm hole positioned 2.5mm off-centre. The centre of each disc was then secured horizontally with Blu-tack to one end of a thin glass tube (L 8cm). The model flower was held upright by placing the other end of the glass stem into a 3 mm (diameter) hole in the centre of a plastic vial lid (diameter 1 cm) weighted with Blu-tack.

4.3.3. Experimental arena

The experimental arena (see Fig. 4.1) was a square-based pyramidal-shaped wind tunnel designed by Poppy (1997). Air flow was maintained by an extractor fan, through which exhaust air was vented out of the top of the cage. Plastic mesh squares (1.5 x 1.5 cm) on the floor of the cage allowed for maximum plume distinction, which was tested using incense sticks. The tunnel was cleaned with ethanol and left in a well-ventilated room for two months to eliminate any possible odour emanation before starting the experiment. A clean muslin cloth was placed on the floor of the cage to prevent the insects escaping through the mesh squares. Temperature was maintained at 20°C ± 1°C (photoperiod 08.30am – 5.30pm). Ceiling mounted fluorescent bulbs provided ambient lighting (5000lux/).

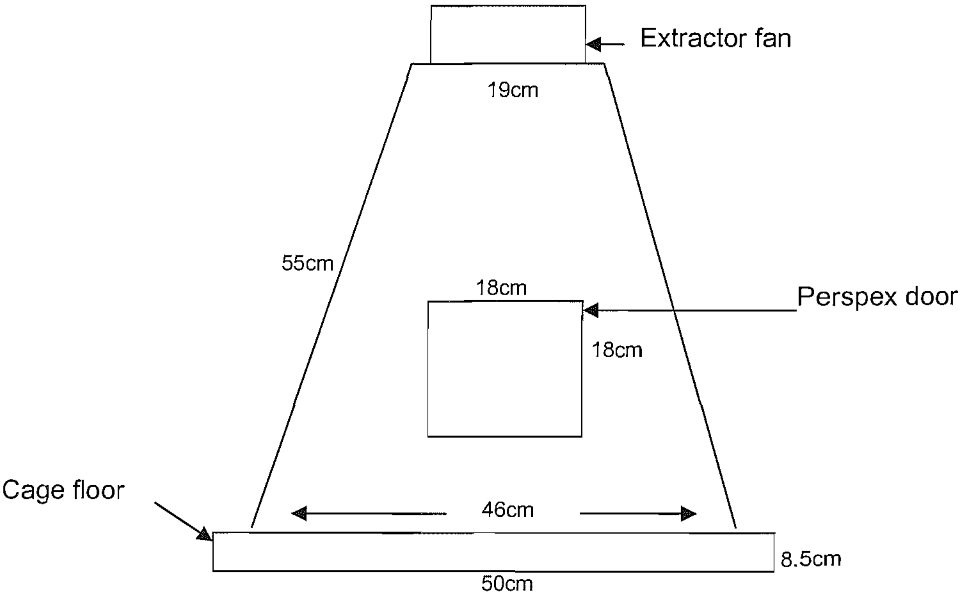


Figure 4.1. Simplified diagram of the wind tunnel used in the laboratory experiment (not to scale).

Model flowers (2 with Nepeta lures and 2 controls) were placed as far as possible apart in the cage, at random, but with equal spacing (11.5 cm) between model flowers. The positions of the flowers were changed every half-hour to eliminate positional preference (gloves were worn during the procedure to reduce the risk of contamination).

Twelve male and twelve female two-week-old second-generation *E. balteatus* (from laboratory stock) were introduced into the cage. Pre-experimental flies had *ad libitum* access to tap water, sieved pollen and a 10% solution of honey. Male and female landings on the flowers were counted over a two-hour period. Observations were made on four separate occasions, and at different times of the day, from 17 May to 1 June 2004.

The extreme sensitivities of insects to volatiles dictated the need for extreme cleanliness in the laboratory to avoid contamination. All glassware was soaked in Decon^R 90, rinsed in distilled water and chlorinated Hexane. Glassware was then removed with clean forceps and placed on tin foil in a drying oven between experiments. The experimental cage was thoroughly cleaned with ethanol and rinsed with distilled water to remove any contaminants before each bioassay. Muslin, flower discs and Blu-tack were discarded at the end of each bioassay and replaced with new ones.

Analysis

Chi-squared tests were used to compare the numbers of landings by *E. balteatus* on the model flowers with Nepeta lures and the controls, and the numbers of landings by male and female *E. balteatus*.

4.4. Results

Table 4.1 shows the number of landings on the model flowers with and without Nepeta lures by male and female *E. balteatus* over the experimental period. No significant differences were observed in the total numbers of landings on the model flowers with Nepeta lures and the controls ($X^2 = 1.318$; df = 3; $P > 0.05$). Although more landings were made by females (46) than males (16), there was no association between sex and flower treatment (X^2 = 1.032; df = 1; $P > 0.05$).

Date	Model flowers with lures	Controls
	♂/ ♀	♂/ ♀
17/05/04	2 /10	3 / 7
20/05/04	1 / 7	2 / 7
26/05/04	0 / 0	3 / 5
01/06/04	3 / 4	2 / 6
Totals	**6 / 21**	**10 / 25**

Table 4.1. Number of landings by male and female *E. balteatus* on the model flowers.

The mean release rate of the formulated Nepeta lures was estimated to be 0.24mg/day at 20°C ± 1°C.

4.5. Discussion

Although there were no significant differences in the numbers of landings by *E. balteatus* on the model flowers with Nepeta lures and the controls, it was felt that different concentrations of the pheromone might have had an effect on the landing response of the flies. Unfortunately, time limitations prevented further investigation.

As discussed above (see Introduction), olfactory cues are thought to play an important role in attracting insects to plants for both feeding and oviposition. Although this preliminary experiment was useful in allowing the investigator to record the landing responses of *E. balteatus* to nepetalactone, it did not allow the insects to use the pheromone at a distance from the source. It was therefore decided to carry out a more extensive field-based study comparing the oviposition responses of aphidophagous syrphids to model flowers with and without Nepeta lures.

4.6. Preliminary field experiment

4.6. 1.Introduction

The aim of this experiment was to compare the response of gravid syrphids to different concentrations of nepetalactone in order to assess the number of Nepeta lures to be used in the main experiment.

4.7. Methods and materials

4.7.1. Experimental site

The preliminary experiment was conducted in the field margins of a 14-ha spring barley field located at Hossiers Farm, Upper Woodford, Salisbury in Wiltshire UK. There was some flowering vegetation in the field margins, the most common species being bindweed (*Convolvulus arvensis* (L.)), red clover (*Trifolium pratense* (L.)) and white clover (*T. repens* (L.)). The surrounding area was very poor in floral resources, mainly due to the cutting of hedgerows and verges, which left few flowers. The spring barley crop was harvested on 12 August 2004.

4.7.2. Nepeta lures

The Nepeta lures were secured with fuse wire 50 cm above the ground on bamboo canes (after Powell, 1994), so that the pheromone was released at crop height. Canes (total 16) had one, two, three or four lures attached. A further four canes were used as controls (no lures). Each cane was inserted into the ground directly behind a flowerpot tray (total 20) (diameter 19 cm), which had previously been treated with Plasti-Kote 142S yellow fluorescent paint (see Chapter 2, Methods section for preparation details). A bait plant infested with the pea aphid *Acyrthosiphon pisum* (see Chapter 2, Methods section for details) was placed beside each tray. The treatments were separated at intervals of 25 metres (after Lösel *et al.*, 1999) in the field margins and were within one metre of the crop edge. Bait plants were retrieved 48 hours later and the numbers of syrphid eggs were counted.

The experiment was repeated eight times from 27 May to 9 July 2004, and the positions of the canes were re-randomised each time.

Analysis

A Kruskal-Wallis test was used to test for differences between the numbers of syrphid eggs laid on bait plants beside one, two three or four Nepeta lures and the controls. Statistical analysis was performed using SPSS11.

4.8. Results

In total, 33 syrphid eggs were found on the bait plants with Nepeta lures and the controls (Table 4.2), the majority being *E. balteatus* and *Eupeodes corollae*. Significantly more eggs were laid at control positions than by stakes with four lures (Kruskal-Wallis test, $X^2 = 16.48$; df = 4; $P < 0.01$). The numbers of eggs laid beside one, two or three Nepeta lures were very similar (Table 4.2).

Date of collection	**No lure**	**1 lure**	**2 lures**	**3 lures**	**4 lures**
29/05/04	1	1	1	0	0
05/06/04	2	1	0	0	0
10/06/04	2	0	2	1	0
17/06/04	2	0	0	0	0
23/06/04	2	2	0	1	1
29/06/04	3	2	1	2	0
05/07/04	2	0	0	1	0
09/07/04	1	0	1	1	0
Totals	**15**	**6**	**5**	**6**	**1**

Table 4.2. Number of eggs found on bait plants beside yellow trays with one or more Nepeta lures and the controls in 2004.

4.9. Discussion

Overall few eggs were found on the bait plants, even by the control targets there were less than 0.05 eggs per plant. There was a reduced oviposition response to four lures compared to that for one, two or three lures, which were very similar. Concentration of the pheromone at this level (four lures) possibly acted as a deterrent to gravid females. Although Pickett & Birkett (2004) found that water traps baited with combinations of nepetalactone led to a significant increase of *Aphidius ervi* parasitoids and *Proan* species, it appeared that high concentrations might have the opposite effect in hoverflies. Due to the very low number of syrphids eggs present at the time of the trial, it was decided to repeat the experiment on a much larger scale. It was also decided not to use a combination of four lures.

4.10. Main field experiment

4.10.1. Introduction

Although there was no evidence from the previous experiment that there was higher oviposition near nepetalactone lures than near controls, different conditions may lead to different results. For example, the oviposition response might vary at different distances from the lures. Powell (2004) showed that more parasitoids were found within the crop than at positions with nepetalactone lures. It was therefore decided to carry out a large scale field experiment.

The aims of this experiment were to discover whether nepetalactone in different concentrations had an effect on syrphid oviposition, either in the vicinity of the pheromone or at a distance, and whether there might be any synergistic effect when yellow painted targets (already shown to lead to enhanced oviposition in their vicinity) and nepetalactone were used together.

4.11. Methods and materials

4.11.1. Experimental site

The experimental site consisted of three winter wheat fields located at Uggford farm, Wilton, in Wiltshire, UK (see Chapter 2, Methods section for site details). No insecticide was used on the experimental fields during either season. The crop was harvested on 18 August 2004.

4.11.2. Yellow targets and Nepeta lures

Targets consisted of 12 brown flowerpot trays (diameters 19 cm) painted with Plasti-Kote 142S fluorescent yellow paint and 12 unpainted flowerpot trays (See Chapter 2, Methods section for details of tray preparation). Four holes (diameters 4 mm) were drilled in the base of each tray for drainage of rainwater. Each tray was secured to one end of a wooden stake (125 cm, diameter 5 cm) using 'Cerafix' Decorators Caulk (Henkel Consumer

Adhesives, Winsford, Cheshire, UK). The other end of each stake had been previously cut to a 10 cm point to allow it to be inserted easily into the soil (see Fig. 4.2). Traps bonded well to the top of each stake, but were also easy to remove. Treatments could then be re-randomised at the start of each experimental run.

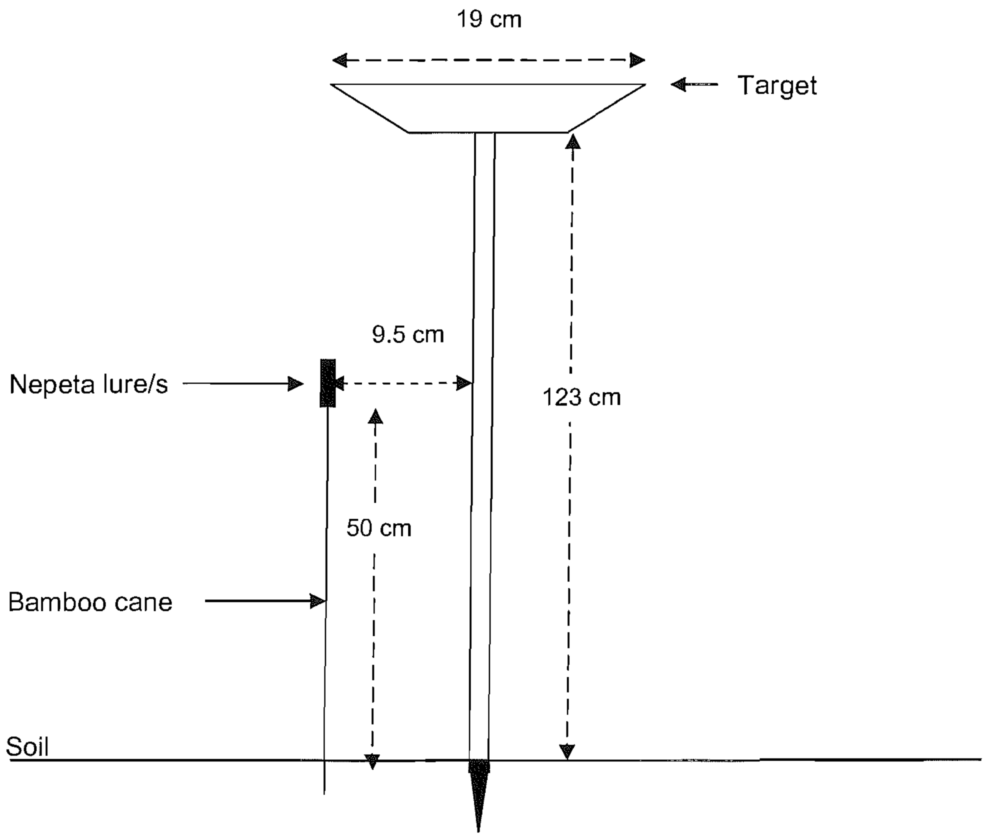


Figure 4.2. The Nepeta and target set-up used in winter wheat fields in 2004 (not to scale).

In each winter wheat field, there were eight targets (4 yellow, 4 brown) randomly positioned at 25 metre intervals, within one metre of the crop edge, in each of the three winter wheat fields. A bamboo cane, with or without Nepeta lure(s) attached at a height of 50 cm, was inserted into the ground (9.5cm from the stake) beside each target (see Fig. 4.2), and canes were also placed in a straight line at right angles to the crop edge at distances of 5 and 10 m into the crop from each target. One yellow and one brown target had no lures at any distance, one of each colour had lures at 0 m, one of each colour had lures at 5 m and one of each colour had lures at 10 m. One set of treatments was used in each of the three fields and within the field treatments were allocated at random. Figure 4.3 shows the random arrangement of the targets and the lures on one date in one winter wheat field.

Two standardised bait plants (See Chapter 2, Methods section for full details) were placed on the ground beside each cane 10 cm from the cane and approximately 2 cm apart. Bait plants were retrieved 48 hours later and the number of syrphid eggs counted. After each set of bait plants were collected, the treatments were re-randomised and new bait plants were set out.

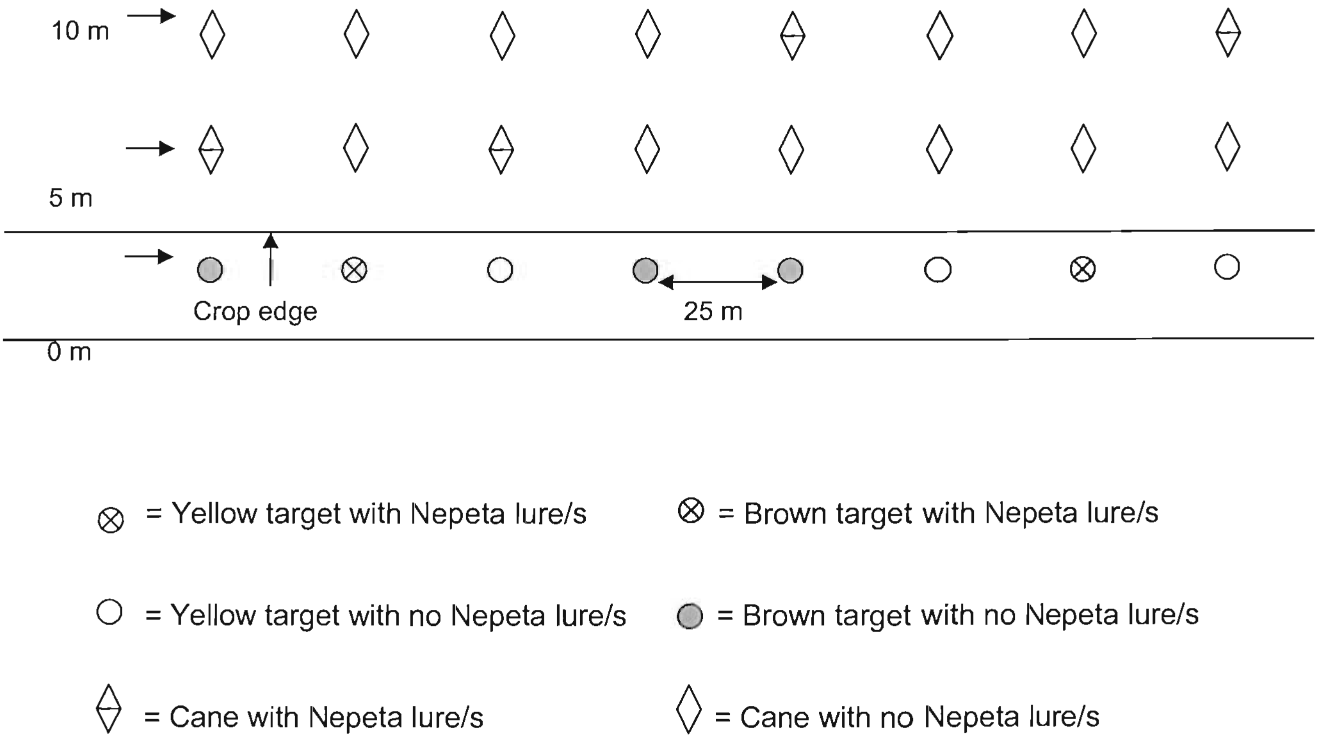


Figure 4.3. The random arrangement of the targets and lures in one winter wheat (Field 1) between 10 & 12 August 2004. Note that that control targets had no lures at 0, 5 or 10 metres. Treatments were re-randomised after each collection of eggs.

Between 12 and 30 July, three lures were used on all targets and canes with lures, two lures were used between 1 and 8 August and one lure was used between 12 and 16 August 2004. As it was felt that a combination of four lures might have a deterrent effect on hoverfly oviposition, it was decided to use one, two or three lures (see previous experiment).

Analysis

Kruskal-Wallis tests were used to compare numbers of eggs laid at different distances from one, two or three Nepeta lures, for yellow and brown targets separately. Mann-Whitney *U*-tests were carried out to test for differences between the numbers of eggs (combined total of eggs laid at 0, 5, and 10 m) laid near yellow compared to brown targets with one, two or three lures. All statistical analyses were performed using SPSS11.

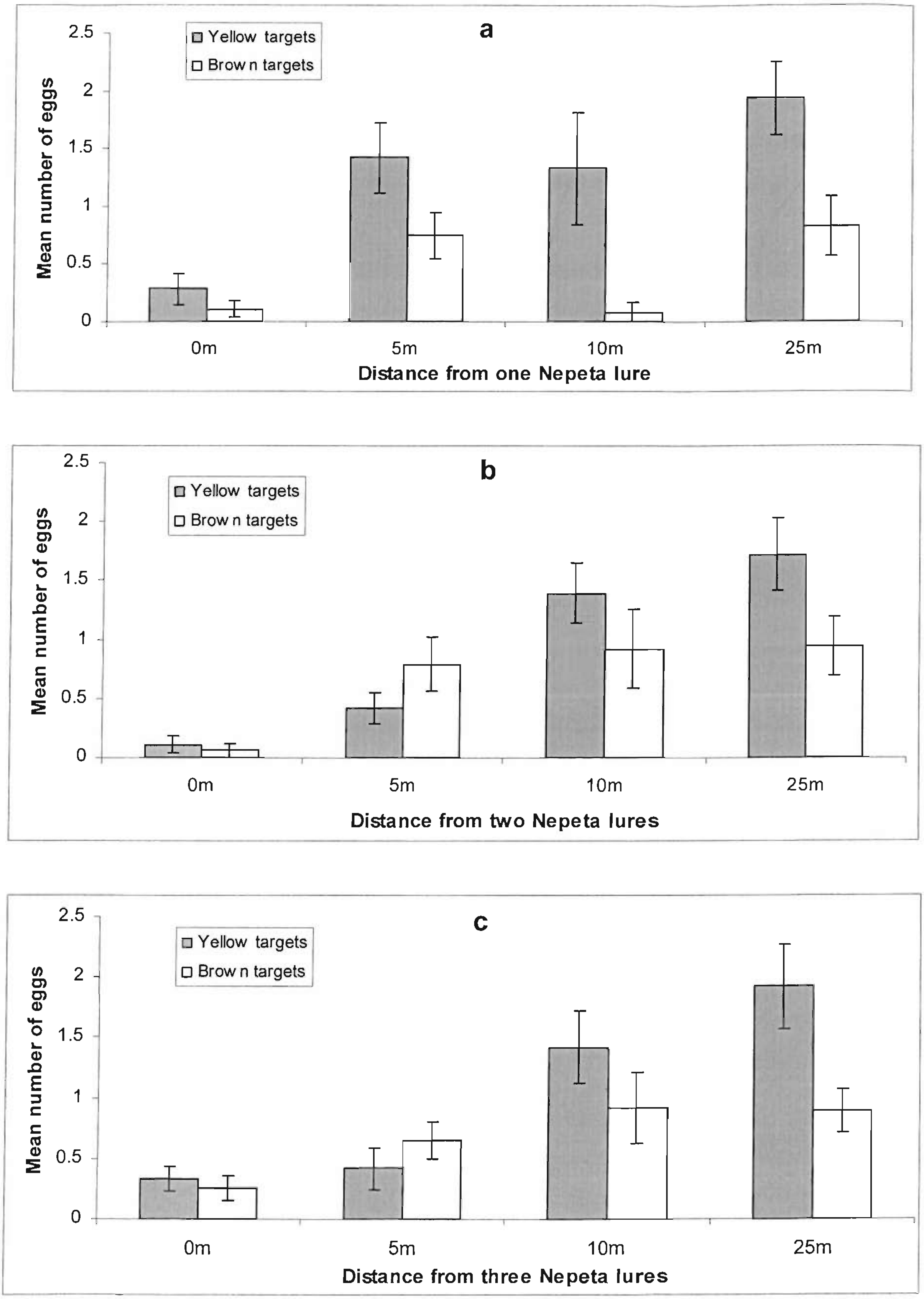
4.12. Results

In total, 233 syrphid eggs were found on bait plants. Of these, 156 were associated with yellow targets and 77 were associated with brown targets. Figures 4.4a,b,c show the mean numbers of eggs found on bait plants at 0, 5, 10 and 25 m from Nepeta lures. There were significant differences between the numbers of eggs found at 0 m and at 25 m distances from lures associated with yellow (Kruskal-Wallis tests: $P < 0.01$ in all cases) and brown (Kruskal-Wallis tests: $P < 0.05$ in all cases) model flowers, with significantly more eggs being found at 25 m in all cases. The results of the Kruskal-Wallis tests are shown in Table 4.3.

For treatments including Nepeta lures, there were no significant differences between brown and yellow treatments for the total numbers of eggs laid at the three positions when three lures (Mann-Whitney *U*- test: $U = 5675.00$; $P > 0.05$) or two lures (Mann-Whitney *U*- test: $U = 1401.5$; $P > 0.05$) were used. However, when one lure was used there were significantly more eggs found by yellow than by brown model flowers (Mann-Whitney *U*- test: $U = 1112.00$; $P < 0.05$).

Treatment	**Mean rank**				**df**	X^2	***P***
	Distance from field margin						
	0 metres	**5 metres**	**10 metres**	**25 metres**			
Yellow targets							
1 Nepeta lure	22.50	38.79	36.58	47.30	3	14.866	*0.002
2 Nepeta lures	24.67	31.83	40.21	52.08	3	21.862	*0.000
3 Nepeta lures	60.56	57.63	80.65	98.85	3	31.474	*0.000
Brown targets							
1 Nepeta lure	29.33	41.38	28.50	42.50	3	10.372	*0.016
2 Nepeta lures	25.06	38.67	41.33	41.83	3	10.156	*0.017
3 Nepeta lures	58.04	72.11	79.52	82.79	3	9.836	*0.020

Table 4.3. Results of Kruskal-Wallis one-way analysis of variance on numbers of eggs found at 0m and at 25m distances from yellow and brown targets with one or more lures. * indicates significant differences between treatments.



Figures 4.4a, b & c. Mean number of syrphid eggs found near yellow and brown targets with Nepeta lures in 2004 (bars represent standard errors).

4.13. Discussion

More syrphid eggs were laid on bait plants near the controls, than on bait plants near Nepeta lures, whether these were beside targets or in the field at any position. From the results, the Nepeta lures appeared to act as an oviposition deterrent, not an enhancer as hoped. If the flies were attracted from a distance towards the yellow targets, they were presumably deterred from ovipositing on the bait plants when they got there, with the result that the effect of using yellow targets (see Chapter 2 Results section) was nullified. The results also suggested that the deterrent effect increased as more lures were used.

Despite the evidence (e.g. Birkett *et al.,* 2000; Powell & Glinwood, 2003; Wadhams *et al.,* 2004) demonstrating the role of nepetalactone in enhancing parasitoid activity, it would not necessarily be expected that the pheromone would have an equivalent effect in enhancing syrphid oviposition and therefore, their effectiveness as biocontrol agents.

Nepetalactone is known to mediate mating/host plant behaviour in some species of aphid (see Introduction 4.1) in the autumn (Park *et al.*, 2000). Nepetalactone is released when aphids are leaving the crop for an alternative host. Usually winged virginoparous aphids move from the summer host to the primary winter host plant, where mating occurs (Emden *et al.*, 1969). The move appears to be assisted by the sex pheromone released by sexual females, already present on that host, acting as an aggregation pheromone. Even though Sutherland (1998) found that *E. balteatus* responded well to nepetalactone in EAG tests, from the results, nepetalactone did not appear to be an optimal pheromone.

The lifecycles of parasitoids and syrphids are very different. While parasitoids need just one host for the development of the larva, the success of a syrphid larva depends on the consumption of large numbers of aphids (see Chapter One, Section 1.4). *E. balteatus* for example has been shown to operate a ‘buy futures’ tactic of avoiding large aphid colonies and preferentially ovipositing by small colonies containing young nymphs (Kan, 1988a), thus making it more likely that there will still be aphids available when the larvae emerge. As the production of nepetalactone may signal the imminent departure of aphids from the crop, and therefore a reduction in food supply for syrphid larvae, it is perhaps not surprising that it appears to act as a deterrent, rather than an enhancer of syrphid oviposition.

What is known, however, is that the structure of nepetalactone closely resembles the terpenoids irododial and dolichodial, used in defence against predation and parasitism by some insects (e.g. the devil's coach horse beetle, *Staphylinus olens*) (Harbourne, 1994). Therefore, the *raison d'être* of nepetalactone could well be its ability to repel some insects from attack. This argument was tested by Eisner *et al.* (1973) who demonstrated that 17 out of 24 insect species were repelled by a pure solution of nepetalactone. Nepetalactone has been shown to be an active repellent for cockroaches (Eisner, 1964) and recent tests (Geier, 2004) on yellow fever mosquitoes showed it to be a more effective repellent than DEET (N, N diethyl-*m*-toluamide). Sutherland (1998) also caught fewer syrphids in nepetalactone baited sticky traps than the controls. The results of this work clearly demonstrated that nepetalactone did not increase the numbers of syrphid eggs laid on the bait plants at any distance.

Even though hoverflies appeared to be repelled by the nepetalactone lures, it is possible that different ratios of the pheromone or extra components (e.g. nepetalactol) would attract them. Most insect pheromones appear to be composed of more than one synergistic component acting together (Wyatt, 1997). Further experiments could seek to determine whether there is a behavioural response to different synergistic compounds.

However, if it is determined that nepetalactone has the role of an oviposition repellent in aphidophagous syrphids, then any decision on whether to use the pheromone to enhance biocontrol of aphids by aphid predators would have to consider both its potential as parasitoid attractant, and the fact that it might diminish syrphid activity in the crop.

4.14. *Cis*-jasmone experiments

4.14.1. Introduction

Cis-jasmone is known to have roles in inducing plant defence and as an insect semiochemical, and the potential to exploit beneficial organisms such as predators and parasitoids of pests (e.g. Powell *et al.,* 1991; Poppy *et al.,* 1997; Pickett *et al.,* 2000; Bruce *et al.,* 2003; Engleberth *et al.,* 2004; Pickett *et al.,* 2006). The aim of the following experiments was to ascertain whether *cis*-jasmone acted as an attractant to gravid syrphids and if so, whether there might be a synergistic effect when a yellow colour stimulus was combined with the volatile.

4.15. Methods and materials

2004

The experiments took place in the field margins of three winter wheat fields (between 14 and 16ha) located at Uggford Farm, Wilton (see Chapter 2 Methods section for site details). No insecticide was used on the crop or on any of the surrounding fields at any time during the experimental period.

Four yellow and four brown targets were randomly positioned at 50 metre intervals, within one metre of the crop edge, in each of the three winter wheat fields. *Cis*-jasmone is a highly volatile chemical (Bruce *et al.*, 2003), so the targets were set as far as possible apart in each field. Targets consisted of yellow or brown (unpainted) flowerpot trays (diameters 19 cm) glued to wooden stakes (125 cm, diameter 5 cm) using 'Cerafix' Decorators Caulk (see Methods 4.11.2 for full details of the target preparation). At each position a cane was set into the ground at a distance of 9.5 cm from the stake supporting the flowerpot tray and a standard brown Chromocol vial was secured to it 10 cm above ground level. For work in olfaction, Byers (1988) suggested the use of open tubes to be particularly appropriate for field work. It was thought that the colour brown would offer little or no colour signal to hoverflies because its spectral reflection is virtually constant against the entire spectral absorbance range of insect photopigments (Kevan, 1983). Four vials (two randomly placed on yellow targets and two on brown) contained 1 ml of *cis*-jasmone (*Cis* 90%, Trans 10%, supplied by Aldrich Chemicals (batch no. 134-13)) which was transferred to the vial using a plastic syringe. The other four vials were left empty as controls. A plastic lid, through which a 1 mm hole had been drilled, prevented rainwater from entering the vials (confirmed by preliminary tests) but allowed the volatile to escape. Release rates of *cis*-jasmone under standard conditions were estimated to be 0.94 g/mL at 25 °C (lit.) per day (Aldrich, UK, 2007).

Two standardised bait plants (See Chapter 2, Methods section 2.3.1 for full details) were placed on the ground between the target and the cane. Bait plants were retrieved 48 hours later and the number of syrphid eggs counted, and as far as possible, identified to species. The experiment was run five times from 6 to 16 August 2004. The treatments were re-randomised at the start of each experimental run and new bait plants were used.

4.16. Introduction

2005

As the results from 2004 were not conclusive, it was decided to carry out a further experiment in 2005. Time and labour considerations meant that it was not possible to prepare bait plants and test oviposition directly. Therefore attraction was measured by comparing the number of gravid female syrphids caught in yellow water traps in the vicinity of and distant from *cis*-jasmone sources.

4.17. Methods and Materials

See start of 2004 experiment methods for site details.

Twenty flowerpot trays (diameters 19cm) were painted with Plasti-Kote 142S fluorescent yellow paint (see Chapter 2, Methods section for full details of trap preparation), filled with water and a 1% solution of ordinary household detergent, and placed on the ground in the field margin within one metre of the crop edge in one winter wheat field (16-ha). Because *cis*-jasmone is known to be active over long distances (Bruce *et al.*, 2003), the traps were separated at intervals of 100 metres. This had not been possible in 2004 because of the lack of available space. Experimental and control vials (as in 2004) were secured at random to canes 10cm above the ground. Trays were left for 24h and then emptied. Trapped syrphids were counted and then transferred to 70% alcohol in labelled plastic tubes for later identification. The experiment was run four times from 15 to 25 July 2005. Before each run, the yellow trays were cleaned and reset and the positions of the experimental and control vials re-randomised. Weather conditions were also recorded.

As rainwater had collected in the lids of the vials on the last two collection dates, it was not possible to calculate the release rate of the volatile.

Analysis

2004

Kruskal-Wallis tests were used to test for differences in the numbers of syrphid eggs from bait plants beside yellow and unpainted targets with and without *cis*-jasmone. Mann-Whitney *U*-tests compared numbers of eggs laid near yellow targets with and without the volatile.

2005

Mann-Whitney *U*-tests were used to compare numbers of gravid females caught in water traps with and without *cis*-jasmone overall. Because the weather was dry until the 21 July and wet between 22 and 25 July (Met. Office, 2005), and it was believed that the weather could have affected dispersal of the volatile (see discussion), the results were also analysed separately for these two periods.

All statistical analyses were performed using SPSS11.

4.18. Results

2004

A total of 38 eggs were laid on the bait plants underneath the targets. These were visually assessed to be *E. corollae* (24) and *E. balteatus* (14). For model flowers with *cis*-jasmone, 20 eggs were laid near yellow and 5 eggs near brown targets. For treatments without *cis*-jasmone, 10 eggs were laid near yellow and 3 eggs near brown targets (see Table 4.4). There were highly significant differences in the number of eggs laid by the different treatments with more being found by yellow targets with *cis*-jasmone than by brown targets with no *cis*-jasmone (Kruskal-Wallis test: $X^2 = 11.82$; df = 3; $P < 0.01$). The ranks for the brown targets were very similar. The results of the Kruskal-Wallis test are shown in Table 4.5.

	Number of eggs							
	Yellow model flowers				Brown model flowers			
Date of collection	**Cis-jasmone**		**Control**		**Cis-jasmone**		**Control**	
	E.corollae	*E.balteatus*	*E.corollae*	*E.balteatus*	*E.corollae*	*E.balteatus*	*E.corollae*	*E.balteatus*
08/08/04	5	2	2	1	3	0	1	0
10/08/04	0	1	3	0	0	1	0	0
12/08/04	1	2	2	1	0	0	0	0
14/08/04	1	3	0	1	0	1	1	0
16/08/04	4	1	0	0	0	0	1	0
Totals	**11**	**9**	**7**	**3**	**3**	**2**	**3**	**0**

Table 4.4. The total number of *E. corollae* and *E. balteatus* eggs found on bait plants near yellow and brown model targets with and without *cis*-jasmone in 2004.

Treatment	Mean rank
Yellow targets	
Cis-jasmone	29.50
No *cis*-jasmone	22.50
Brown targets	
Cis-jasmone	15.80
No *cis*-jasmone	14.65

df = 3; X^2 = 11.820; *P* = 0.008

Table 4.5. Kruskal-Wallis test ranking for yellow and brown targets with or without *cis*-jasmone.

Differences between the number of eggs were not significant when the yellow treatments were considered separately, although there was a trend for more eggs to be laid by yellow targets with *cis*-jasmone than targets without the volatile (Mann-Whitney *U*–test: *U* = 30.5; *P* = 0.143).

2005

Numbers of syrphids

A total of 1914 syrphids were caught in the yellow water traps, the main species being *E. balteatus* (62%), *M. scalare* (16%) and *E. corollae* (15%). Table 4.6 shows the numbers of adult syrphids and gravid females caught in traps by *cis*-jasmone and at control positions on each collection date.

Date	*Cis*-jasmone	Controls	Totals
15-16July	370 (61)	249 (54)	**619 (115)**
20-21 July	327 (10)	205 (1)	**532 (11)**
22-23 July	134 (5)	205 (2)	**339 (7)**
24-25 July	215 (10)	209 (8)	**424 (18)**
Totals	**1046 (86)**	**868 (65)**	**1914 (151)**

Table 4.6. Total number of aphidophagous syrphids and of gravid females (numbers in brackets) caught in traps by *cis*-jasmone and by control vials between 15 and 25 July 2005.

A total of 151 gravid females were caught in the traps, the most abundant species being *E. balteatus* (42%) and *E. corollae* (36%) with *M. scalare, Syrphus ribesii,* S. *vitripennis, Sc. pyrastri* and *Chrysotoxum bicinctum* making up the rest. Most gravid females were collected on 16 July (see Table 4.6). Figure 4.5 shows the numbers and species of gravid female caught in traps by *cis*-jasmone and traps by control vials over the experimental period.

There were no significant differences between the numbers of gravid females caught in traps by *cis*-jasmone and the numbers caught in control traps for all gravids or for *E. balteatus* or *E. corollae* for any of the time periods, although the mean ranks for catches by *cis*-jasmone were higher than for controls in all cases (Mann-Whitney *U*-test: *P* >0.05 in all cases). See Table 4.7 for full details of the analyses.

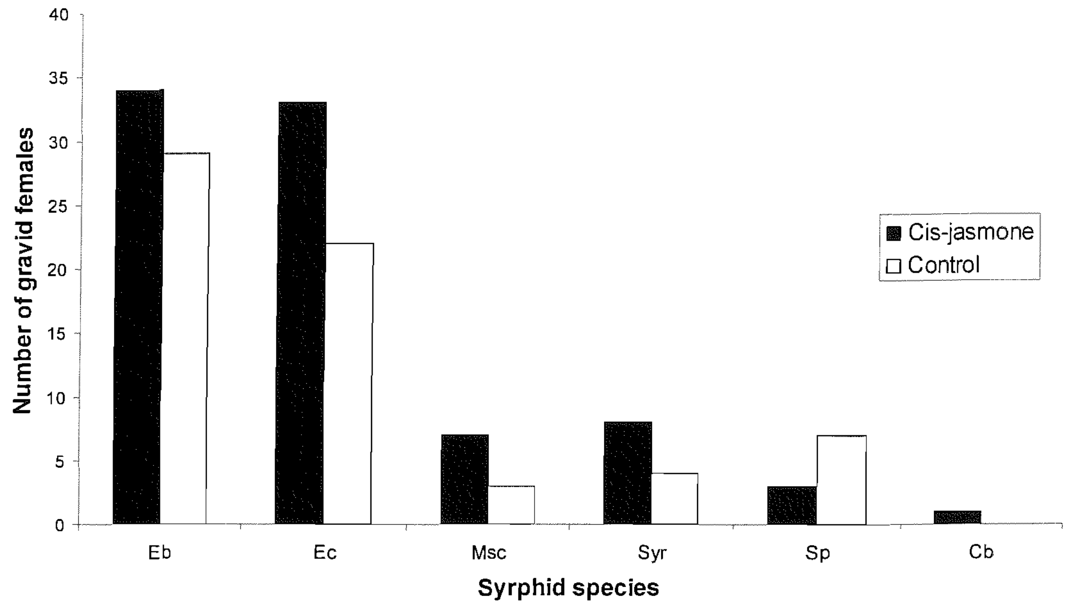


Figure 4.5. Total numbers of gravid females of each species caught in traps by *cis*-jasmone and by control vials between 15 and 25 July 2005 (Eb = *E. balteatus;* Ec = *E. corollae*; Msc = *M. scalare*; Syr = *S. ribesii* & *S. vitripennis*: Sp = *S. pyrastri*; Cb = *Chrysotoxum bicinctum*).

Gravid females	**Mean rank**		**Mann-Whitney *U***	***P***
	Cis-jasmone	Control		
15-25 July				
All gravids	42.90	38.10	704.0	0.322
E. balteatus	41.55	39.45	758.0	0.641
E. Corollae	41.80	39.20	795.0	0.530
15-21 July				
All gravids	21.78	19.22	174.5	0.480
E. balteatus	21.22	19.78	185.0	0.678
E. Corollae	21.52	19.48	179.5	0.542
22-25 July				
All gravids	21.58	19.42	178.5	0.493
E. balteatus	20.65	20.35	197.0	0.907
E. Corollae	20.92	20.08	191.5	0.689

Table 4.7. Results of Mann-Whitney *U*-tests on the total number of gravid syrphids, gravid *E. balteatus* and gravid *E. corollae* caught in traps by *cis*-jasmone and in control traps in 2005.

4.19. Discussion

In 2004, there was an enhanced oviposition response by *E. corollae* and *E. balteatus* to bait plants near yellow targets with *cis*-jasmone compared to brown targets without the volatile. There was also a trend for more eggs to be laid on plants near yellow targets with *cis*-jasmone, than by yellow targets alone, although the difference was not significant. Neither was any significant effect of *cis*-jasmone on yellow water trap catches of gravid syrphids as a whole, or on either *E. balteatus* or *E. corollae* individually, seen in the follow up experiment in 2005. From these results it seems unlikely that the addition of *cis*-jasmone to model flowers is likely to provide a synergistic effect in terms of enhanced oviposition.

It has been demonstrated that parasitoid populations increase in winter wheat crops sprayed with *cis*-jasmone (e.g. Birkett *et al.*, 2000; Bruce *et al.*, 2003; Powell & Pickett, 2003) as with nepetalactone the fact that *cis*-jasmone applications enhance parasitoid activity does not necessarily have any implications for its effects on syrphids as their life cycles and needs in terms of numbers of prey are so different.

However, a number of different factors other than *cis*-jasmone not being attractive to gravid syrphids might have contributed to the negative results in 2005. One factor that could have played a role was the weather. During the first two collecting periods it was mainly dry, but during the second two it rained (Table 4.7). When emptying the water traps, it was noticed that rainwater had collected in the dips in the lids of the vials being used, which probably prevented the volatile from dispersing. However the results of the analysis were very similar when these two time periods were analysed separately. If, in fact, *cis*-jasmone does not attract gravid female syrphids then this result is what would be expected. It is clear that in any future experiments with volatiles, it would be important to choose a dispensing method that allowed for wet conditions. If vials were used to dispense the chemical it would be important to shield the dispensing aperture from rain. Other possible techniques might include delivering *cis*-jasmone in an emulsifiable concentrate (see Bruce *et al.*, 2003) or in vapour form (see Birkett *et al.*, 2000).

After each collection, the treatments were re-randomised and it is possible that odour cues left behind at the site of previous *cis*-jasmone treatments could have affected the results. There are reports in the literature (e.g. Pickett *et al.* 1992; Birkett *et al.,* 2000; Bruce *et al.*, 2003) that plants within the vicinity of *cis*-jasmone act as a sink for the volatile. Couch grass grown adjacent to barley plants treated with *cis*-jasmone has been shown to increase foraging by predators and parasitic wasps for up to 8 days after application (Pickett *et al.*, 1992; Bruce *et al.,* 2003). Birkett *et al.* (2001) found that bean and wheat plants treated with *cis*-jasmone had elevated volatile profiles and that the effects lasted for up to 196 hours after treatment.

Little work has been carried out on the use of volatiles to attract syrphids, but there is evidence that some plant derived volatile compounds do have this effect. For example, Laubertie *et al.* (2006) found that the addition of rose water to yellow water traps significantly increased the number of hoverflies they caught. Sutherland (1998) observed that *E. balteatus* individuals hovered close to linalool baited traps, but were not necessarily caught in the traps themselves. The effectiveness of *E. balteatus* and *E. corollae* in particular in the bological control of aphids (e.g. Dean 1982; Ankersmit, 1986; Chambers & Adams, 1986; Tenhumberg & Poehling, 1995) means that the identification of a compound or compounds that could be used to increase the numbers of gravid females in the vicinity of crops where aphids are a problem could be of great value to farmers and growers.

4.20. Conclusions

Of the two of the volatiles tested, nepetalactone had a clear deterrent effect on syrphid oviposition. It would certainly not be recommended as a compound suitable for use in conjunction with model flowers designed to attract gravid syrphids to crops. The evidence as to whether *cis*-jasmone acted as an attractant to gravid syrphids or not was less clear. A possible trend towards this was seen in 2004, but this was not supported by the results from 2005. However problems with dispersal of the volatile and possible contamination with *cis*-jasmone of positions that were subsequently used as controls may have affected the results. There is evidence that some flower derived volatiles are attractive to hoverflies (e.g. Laubertie *et al.* 2006). With a better experimental design, it would be worth continuing research into *cis*-jasmone as a possible attractant for gravid syrphids.

CHAPTER 5

THE RESPONSES OF APHIDOPHAGOUS SYRPHIDS TO TRAPS OF DIFFERENT HEIGHT, SIZE AND PATTERN IN THE FIELD

5.1. General Introduction

Kevan and Baker (1983) found flower choice in syrphids to be dependent on a variety of different factors including height, corolla size and morphology, colouration, scent, nectar and pollen resources and suitability as a landing site. In the time available for this project it was not possible to test all of these factors as attributes of model flowers, but three of the factors thought to be important, height, inflorescence size and pattern, were investigated in the work described in this chapter.

There is evidence that different hoverfly species have preferred heights for the vegetation they visit (e.g. Kevan and Baker, 1983; Lövei *et al.*, 1992). Size of inflorescence also appears to have an effect on the number of syrphid visits to flowers. Some workers (e.g. Kevan and Baker, 1983; Conner, 1997; Branquart & Hemptinne, 2000), have established that larger flowers attract more syrphids than do smaller ones, although others (e.g. Sutherland *et al.*, 1999; Golding *et al.*, 1999) have found the opposite. Flower pattern has been extensively researched for its effect on bee visiting (e.g. Butler, 1951; Manning, 1956; Free, 1970; Johnson & Dafni, 1998). There is less information about the effects of pattern on syrphid visits to flowers. However, evidence from other insects, suggests that it could be an influencing factor.

It seems likely that factors which affect the visiting frequency of hoverflies to natural flowers will also affect visits to model flowers. The effect of these three characteristics, height, size and pattern, on the attractiveness of model flowers to gravid syrphids, were therefore investigated in the work reported in this chapter, with a view to ultimately incorporating the optimum features into one model and testing it in the field (see Chapter Six). The large scale of the experiments and the fact that sets of different treatments would be offered, meant that assessing preference by comparing levels oviposition directly would have been impracticable. Instead, the yellow targets were used as water traps and attractiveness was assessed by comparing the numbers of gravid syrphids caught in different treatments.

5.2. General Methods and Materials

5.2.1. Experimental Site

All experiments, except the preliminary laboratory pattern work, were carried out in 2005 at Uggford Farm at Wilton, in Wiltshire, UK. The sites consisted of three winter wheat fields (between 14 & 18-h) (harvested 16 August). See Chapter 2, Methods section for site details.

At each site, flowering vegetation present within 20 metres of the flower traps was cleared on a regular basis to ensure that naturally occurring flowers did not act as a counter-attractant to the traps. No insecticide was used on the winter wheat crops during the experimental period.

5.2.2. Model Flower Traps

The model flower traps used in all experiments consisted of flowerpot trays (19 cm diameter unless otherwise stated) painted with fluorescent yellow ultraviolet reflecting paint (Plasti-Kote 142S) (see Chapter 2, Methods section for details of preparation). This paint was chosen because in previous work (see Chapter 3), it was found to be more attractive than non-UV reflecting Glocote 1263 (see Chapter 2). UV-reflecting Plasti-Kote B29 was also found to be equally attractive to aphidophagous syrphids, but was not available in the quantities required for large-scale field work. In order to trap visiting syrphids so that they could be identified and counted, the trays were filled with tap water and a 1% solution of ordinary household detergent.

Traps were emptied at 2-3 day intervals, cleaned with a paintbrush and reset at the beginning of each experimental run. All aphidophagous hoverflies were transferred to 70% alcohol in labelled plastic tubes, counted and identified to species and sex. Female syrphids were dissected to assess egg content. It was necessary to identify gravid females in this way as in many cases it was not possible to tell for certain whether a female was gravid without dissecting it.

5.3. Height Experiments

5.3.1 Introduction

Up to now, there is no information on the potential importance of flower height in attracting gravid syrphids to crop fields for the biocontrol of aphids. However, there is some evidence that different species have preferred heights at which they fly and for oviposition. Chandler (1968a) found that *Episyrphus balteatus* preferentially oviposited on bean plants at heights of 30cms, but that *Eupeodes corollae* laid more eggs on plants at 123cms above the ground. Oviposition by *E. corollae* was also recorded by McEwan *et al.* (2004) in wheat aphid (*Rhopalosiphum padi* (L)) colonies under maize ear husk leaves. Almohamas *et al.* (2006) however, showed that stakes positioned 30cms above the ground were the most attractive heights of aphid colony location for oviposition both in *E. balteatus* and in *E. corollae.*

Most workers (e.g. Kevan, 1978; Kevan & Baker, 1983; Lövei *et al.,* 1992) agree that flower visibility is important, particularly in fields where the vegetation is high. Lövei *et al.* (1992), for example, found the top of the vegetation to be a favourite flying height for many species of syrphid. Kevan and Baker (1983) noted that tall flowers were visited more frequently by insects flying overhead than flowers close to the ground, but that preference was influenced by the availability of food resources at the time. *E. balteatus* and *E. corollae* are known to visit flowers that are low on the ground and also large tall flowers and are commonly found in habitats where there are trees, shrubs and herbs of different heights (Gilbert, 1993). Other species such as *Melanostoma* and *Platycheirus* seemingly prefer low vegetation (Stubbs & Falk, 2000). In New Zealand, Wratten *et al.* (1995) caught both common syrphid species in ground level traps although they had different preferred flying heights. Hickman *et al.* (2001) caught significantly more *E. balteatus* in yellow water traps at crop height than in traps located on the ground, although these were mainly immature flies with empty guts. Flies caught in ground traps were more likely to be female and have full guts but no gravid females were trapped.

There is also evidence to suggest that flower height is important in eliciting behaviours in other insects groups. For example, Weigmann *et al.* (2000) found that bumble bee foragers *(Bombus impatiens* (Cresson)) showed a significant preference for medium-height flowers over tall ones. Whitting (2006) in work with parasitic wasps, determined flower height to be important with higher levels of parasitism by *Trichogramma minutum* (Riley) at greater heights and higher parasitism by *T. pretiosum* (Riley) at lower heights. To maintain a high diversity of insect visitors in crop fields, Sjödin (2007), recommended the best strategy to be the provision of flowers at all heights.

The aim of the work described here, was to find the most effective height of yellow model flowers to attract gravid female syrphids.

5.3.2. Methods and materials

See General Methods and Materials (section 5.2) in this chapter for a description of the site and details of yellow water trap preparation and hoverfly collection and identification details.

Arrangement of traps

Traps were placed at four different heights; 0 cm (on the ground) and 30, 90 and 123 cm above the ground. Traps sited above ground level were glued to wooden stakes (2.5 x 2.5 cm cross section) using 'Cerafix' Decorators Caulk (Henkel Adhesives, Winsford, Cheshire, UK). This bonded the traps well to the stakes but the traps were easy to remove when the positions of the stakes were re-randomised and the traps cleaned. The decision on trap heights at 123 and 30cms was based on evidence that these may be preferred oviposition heights for some species (Chandler, 1968a) (see Introduction 5.3.1). Traps heights at 90 cm and ground level were based on evidence that large numbers of syrphids may be trapped at these heights (e.g. Bowie *et al.,* 1999; Hickman *et al.,* 2001).

Single traps in field margins

Five traps of each height were randomly positioned in the field margins, approximately one metre from the crop edge, and at intervals of 25 metres in each of the three fields (20 traps per field). Collections of hoverflies were made from 13 to 22 July 2005. Treatments were re-randomised each time the traps were emptied and reset.

Sets of traps in field margins

Five sets of four traps, each set containing one trap of each height, and arranged randomly in a square with sides of 45 cm, with one side of the square parallel to the crop (Fig 5.1), were positioned with intervals of 25 m between sets in one field margin approximately one metre from the crop edge in each of the three fields. Collections of hoverflies were made from 25 July to 3 August 2005. Treatments within each set were re-randomised each time the traps were emptied and reset.

Traps in tramlines

From 8 to 15 August 2005, ten sets of traps were positioned at intervals of 25 metres along the central tramline (a track made by tractor wheels, within the field and at right angles to the crop edge) of one field, and five single traps at each height were positioned at 25m intervals along each of two tramlines in the two other fields. The different height treatments were assigned randomly to their individual positions (single traps) or within their sets (sets of traps). Treatments were re-randomised each time the traps were emptied and reset.

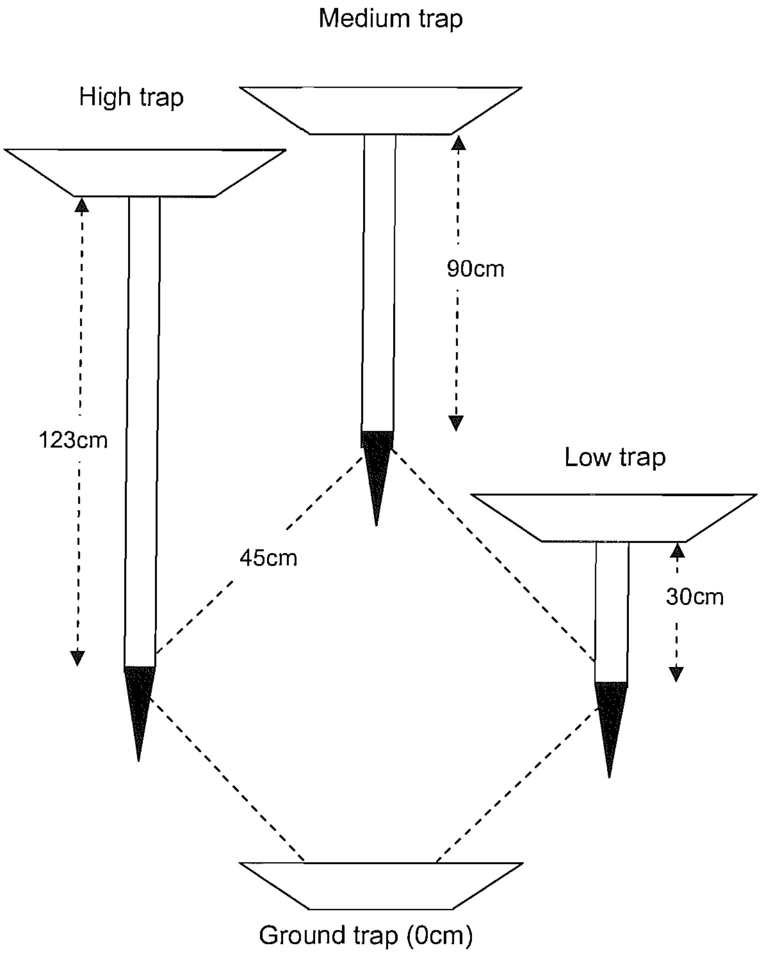


Figure 5.1. Simplified diagram illustrating the height of each flower trap and the general trap layout for sets of traps (not to scale). The traps were arranged randomly at each corner of a 45cm side square.

Analysis

The total numbers of gravid syrphids, and the numbers of gravid *E. balteatus* and gravid *E. corollae*, caught at different heights in single traps and sets of traps in the field margins and tramlines were compared separately using Kruskal-Wallis tests. All statistical analyses were performed using SPSS11

5.4. Results

Table 5.1 shows the total number of adult aphidophagous syrphids and the number of gravid females collected on each date. A total of 2299 aphidophagous syrphids were caught at 123 cm, 3968 at 90 cm, 6305 at 30 cm and 3608 at ground level. For gravid females the numbers were 187, 333, 475 and 267 respectively. The numbers and species of gravid syrphid caught in single traps and the numbers caught in sets of traps in the field margins and tramlines over the experimental period are shown in Figure 5.2 (a) & (b); the most abundant species were *E. balteatus* and *E. corollae*. 64% of all gravid females were caught between 25 July and 3 August, with peak numbers collected on 29 July (Table 5.1).

When all aphidophagous species were considered together, there were highly significant differences between treatments for gravid females caught in sets of traps in field margins (Kruskal-Wallis test: $P < 0.01$) and in single traps in tramlines (Kruskal-Wallis test: $P < 0.05$) (Table 5.2) with higher numbers being caught in low traps (30 cm above the ground) than in high traps (123 cm above ground level). There were no significant differences between treatments when the total number of gravid females caught in single traps in tramlines or in sets of traps in the tramlines were analysed (Kruskal-Wallis tests: $P > 0.05$ in each case), although the same trend was seen in the latter case (Table 5.2).

When gravid *E. balteatus* and *E. corollae* were analysed separately, significantly more *E. corollae* were found in low than in high traps for all four different trap layouts (Kruskal-Wallis test: $P < 0.05$ for all trap layouts) (Table 5.2). Significantly more gravid *E. balteatus* were trapped in low traps arranged in sets in field margins than in high traps (Kruskal-Wallis test: $P < 0.01$) but for other trap arrangements there were no significant differences between numbers caught in the different treatments (Kruskal-Wallis test: $P > 0.05$ in all cases) (Table 5.2).

Collection dates	**Height of trap above ground level**				**Totals**
	123cm (High)	90cm (medium)	30 cm (low)	0cm (ground)	
Single traps in field margins					
13/07/05	27 (10)	24 (4)	33 (2)	30 (4)	**114 (20)**
15/07/05	30 (3)	21 (3)	37 (7)	46 (7)	**134 (20)**
16/07/05	119 (9)	77 (14)	165 (28)	184 (27)	**545 (88)**
21/07/05	128 (5)	346 (17)	421 (15)	390 (6)	**1285 (43)**
22/07/05	187 (7)	310 (18)	411 (12)	142 (8)	**1050 (45)**
Totals	**491 (44)**	**778 (56)**	**1067 (64)**	**792 (52)**	**3128 (216)**
Sets of traps in field margins					
25/07/05	177 (3)	184 (6)	388 (10)	148 (2)	**897 (21)**
29/07/05	565 (62)	1042 (128)	2128 (180)	1209 (94)	**4944 (464)**
01/08/05	390 (44)	693 (41)	921 (89)	647 (40)	**2651 (214)**
03/08/05	263 (16)	467 (35)	631 (36)	303 (22)	**1664 (109)**
Totals	**1395 (125)**	**2386 (211)**	**4068 (315)**	**2307 (158)**	**10156 (808)**
Single traps in tramlines					
08/08/05	109 (5)	194 (11)	323 (34)	253 (14)	**879 (64)**
10/08/05	51 (2)	144 (12)	81 (7)	103 (5)	**379 (26)**
12/08/05	23 (0)	41 (0)	72 (4)	40 (3)	**176 (7)**
15/08/05	10 (0)	34 1)	55 (1)	27 (0)	**126 (2)**
Totals	**193 (7)**	**413 (24)**	**531 (46)**	**423 (22)**	**1560 (99)**
Sets of traps in tramlines					
08/08/05	111 (7)	222 (35)	382 39)	325 (30)	**1040 (111)**
10/08/05	57 (4)	96 (5)	122 (6)	87 (3)	**362 (18)**
12/08/05	32 (0)	40 (1)	84 (3)	38 (2)	**194 (6)**
15/08/05	20 (0)	33 (1)	51 (2)	27 (0)	**131 (3)**
Totals	**220 (11)**	**391 (42)**	**639 (50)**	**477 (35)**	**1727 (138)**

Table 5.1. Total number of aphidophagous syrphids and of gravid females (numbers in brackets) caught in single and sets of traps at different heights in the field margins and tramlines of winter wheat fields on each date in 2005.

Gravid females	**Mean rank**				**df**	**X^2**	***P***
	Height of trap above ground						
	123 cm (High)	90 cm (medium)	30 cm (low)	0 cm (ground)			
Field margins							
Single traps (all gravids)	880.81	910.99	913.61	896.59	3	4.239	0.237
Sets of traps (all gravids)	673.53	736.91	782.04	689.51	3	25.419	*0.000
Single traps (*E. balteatus*)	140.18	156.89	154.73	150.20	3	2.893	0.408
Sets of traps (*E. balteatus*)	104.79	125.06	143.48	108.69	3	13.193	*0.004
Single traps (*E. corollae*)	136.60	150.27	166.19	148.94	3	11.687	*0.009
Sets of traps (*E. corollae*)	98.62	122.93	143.68	116.78	3	15.396	*0.002
Tramlines							
Single traps (all gravids)	456.30	478.66	504.73	482.30	3	17.673	*0.001
Sets of traps (all gravids)	451.77	490.32	501.95	477.95	3	16.484	*0.001
Single traps (*E. balteatus*)	77.70	78.20	88.40	77.70	3	4.523	0.210
Sets of traps (*E. balteatus*)	75.81	88.28	79.93	77.99	3	4.834	0.184
Single traps (*E. corollae*)	66.00	81.55	92.20	82.25	3	14.585	*0.002
Sets of traps (*E. corollae*	64.75	86.40	87.75	83.10	3	11.357	0.010

Table 5.2. Results of Kruskal-Wallis one-way analysis of variance on the total number of gravid syrphids, gravid *E. balteatus* and gravid *E. corollae* caught in single or sets, of yellow traps in the field margins and tramlines of winter wheat crops in 2005. * indicates significant differences between treatments.

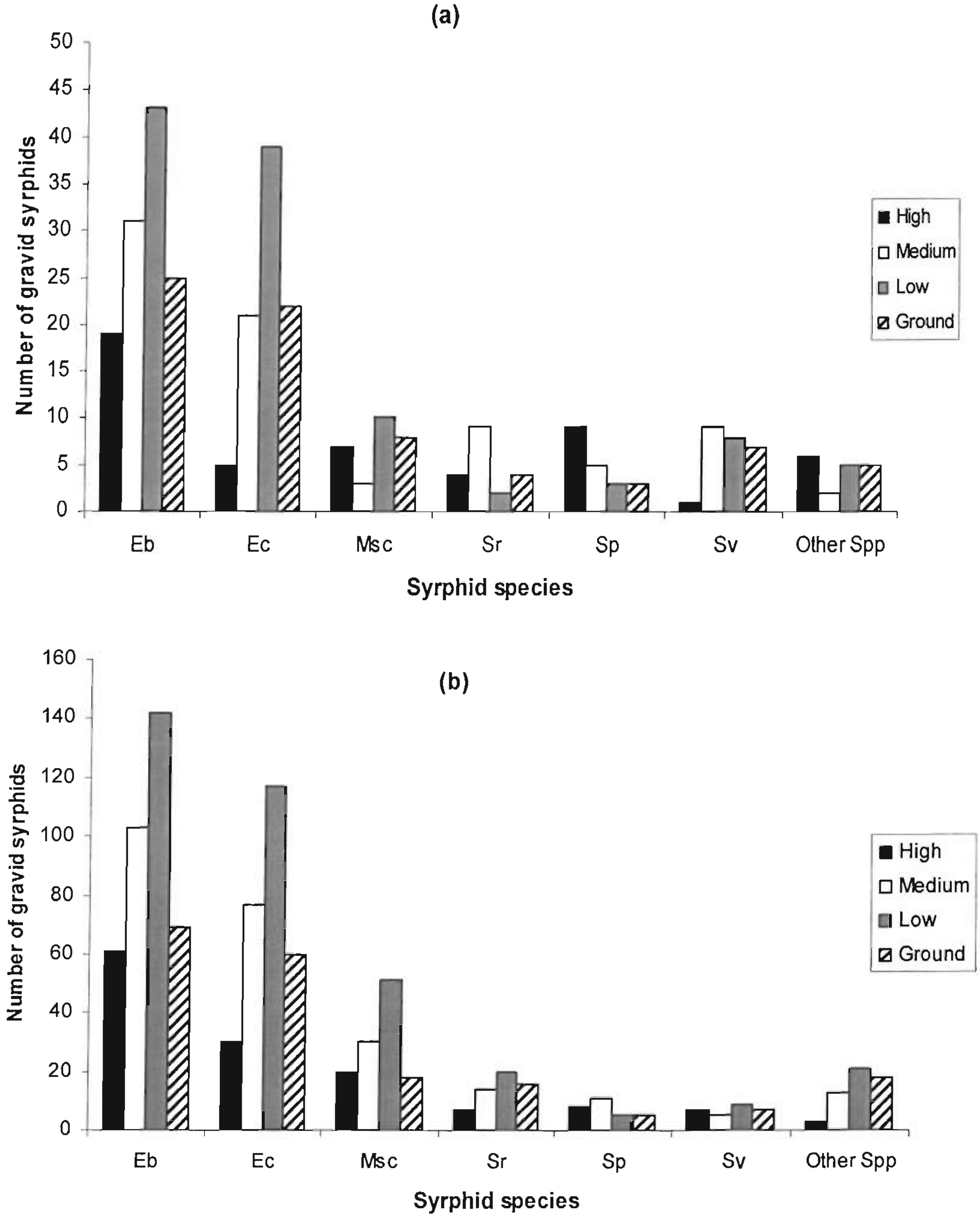


Figure 5.2 (a) and (b). Number and species of gravid syrphid caught in single traps **(a)** and sets of traps **(b)** at different heights in the field margins and tramlines over the experimental period in 2005 (Eb = *E. balteatus*; Ec = *E. corollae*; Msc = *Melanostoma scalare*; Syr = *Syrphus ribesii*; Sp = *Scaeva pyrastri*; Sv = *Syrphus vitripennis*; Other Spp = *Sphaerophoria scripta, Chrysotoxum bicinctum*, *Xanthandrus comtus* and *Platycheirus* spp.).

5. 5. Discussion

The results of the large-scale experiments described here strongly suggest that from the range of heights tested here, gravid females, including those of the two most important species, *E. balteatus* and *E. corollae*, are attracted to targets at a height of 30 cm with traps above crop height being much less attractive. Although it could not be assumed that gravid females would prefer targets (or real flowers) at their preferred oviposition height, this did seem to be the case for *E. balteatus* (Chandler 1968a; Almohamas *et al*., 2006) and possibly *E. corollae* (Almohamas *et al*., 2006). Chandler (1968a) found that the latter species preferentially oviposited at 123 cm rather than 30cm, but for *E. corollae* as well as for *E. balteatus* traps at 123 cm trapped the fewest gravid females. In fact attractiveness of traps at 30 cm compared to those at 123 cm appeared stronger in *E. corollae* than in *E. balteatus* (Table 5.2). When trapped syrphids were considered as a group the trends seen, in terms of numbers caught in each treatment, were the same as for gravid females.

In this work, traps at each height in the field margins were placed near to the crop, but not within it. Flowering plants within the vicinity of the traps were removed to avoid any bias towards real flowers occurring, and vegetation surrounding the traps was cleared regularly to ensure that each trap could be seen. Because of this, it was felt that all the yellow traps in the field margins, whatever their height, offered a strong visual cue to approaching syrphids. However, along the tramlines within the crop it was expected that lower placed traps might be more difficult to see, and that therefore different results might be found for traps sited here. As part of an aphid control programme model flowers might be sited both in field margins and within the crop itself and it was important to investigate this. However the pattern of catches was the same as for traps placed in the field margins.

It was also expected that less defined preferences might be shown when traps were presented singly than when they were presented in sets as a sub optimal choice might be made when no alternative was present. There is some evidence that this occurred in the field margins. Although the highest numbers of gravid females were found in the 30 cm single traps, these differences were not significant for gravid females as a group or for *E. balteatus* although they were highly significant for *E. corollae* (Table 5.2). However, single and sets of traps in the tramlines were put out at the same time, and there was no evidence that single and sets of treatments were responded to differently (Table 5.2). In the field margins, single traps were put out in mid July when populations of syrphids were small compared to the large numbers at the end of July/early August when treatments were presented in sets (See Appendix A). The average age of the trapped gravid females may have differed and this could have confounded the results as it is known that the behaviour of gravid female syrphids changes as they become older; they become less discriminating in their choice of oviposition sites (Budenberg, & Powell, 1992) and height preferences change (Chandler, 1968c). Ideally, all sets of treatments and single treatments should have been put out at the same time, but this was logistically impossible.

Overall it appears that traps at a height of 30 cm would be the optimum choice out of the heights compared, for attracting gravid females to the crop.

5.6. Size Experiments

5.6.1. Introduction

Hoverflies have frequently been shown to prefer large flowers (e.g. Kevan, 1978; Branquart & Hemptinne, 2000) to small flowers. Elle and Carney (2003) and Bell (1985) suggested that when given a choice, pollinators discriminated against small flowers because flower size advertised potential floral reward. The visual stimulus provided by conspicuous, colourful large flowers is thought to attract hoverflies at greater distances than smaller ones (Kevan, 1978; Haslet, 1989a; Chittka & Menzel, 1992). Kevan and Baker (1983) observed that the larger flowers of the Arctic and of Canada had more hoverfly visitors than the smaller flowers. Branquart & Hemptinne (2000) noted that hoverflies exploited pollen and nectar produced by plants having large inflorescences and flat corollae (e.g. Apiaceae, Asteraceae, Ranunculaceae and Rosaceae). Connor (1997) also found strong, consistent evidence that increases in flower size increased visitation by syrphid flies. In contrast, Sutherland *et al.* (1999) found that in the laboratory, small flowers elicited a higher response in *E. balteatus* than the large ones. Golding *et al.* (1999) made some similar generalisations noting that when the petals of oil-seed rape were removed, this had no effect on the frequency of visits by *E. balteatus.* However, Brunel *et al.* (1994) did not find flower size to be important in pollinator choice when flowers were at a high density.

At present, there is no quantitative information on the relationship between hoverfly visiting (and therefore size of trap catches) and trap size in the field. The aim of this investigation was to determine the response of gravid aphidophagous syrphids to targets (yellow water traps) of different size to establish the dimensions of the optimum model flower to attract them.

5.7. Methods and Materials

See General Methods and Materials (section 5.2.) for a description of the site, and details of yellow water trap preparation and hoverfly collection and identification details.

The Treatments

Traps of diameters 25cm, 19cm and 13.5 cm were compared. Smaller traps were not used, as in a preliminary field trial it became evident that, in hot weather, traps with diameters less than 13.5 cm were prone to evaporation. Windy conditions also increased the chance of catches in small traps being blown away (see Sutherland, 1998).

Single traps

Five traps of each size were randomly positioned in the field margins, approximately one metre from the crop edge, with intervals of 25 metres between traps, in each of the three fields (20 traps per field). Collections of hoverflies were made from 13 to 22 July 2005. Treatments were re-randomised each time the traps were emptied and reset.

Sets of three traps

Five sets of three traps, with intervals of 25 m between sets, were positioned in each field. Each set was positioned in the field margin approximately one metre from the crop edge and parallel to it with 45 cm between treatments. Within the set, treatments were in random order. Collections of hoverflies were made from 25 July to 3 August 2005. Treatments within each set were re-randomised each time the traps were emptied and reset.

Sets of six traps

Five sets of six traps were positioned in the field margin of one field with intervals of 25 m between sets. A set consisted of one large trap (total area 490.9 cm^2), two medium traps (total area 567.2 cm^2) and three small traps (total area 429.6 cm^2). Although the trap areas were not exactly the same, they were the closest match available at the time. The two medium traps were arranged side by side and the three small traps were placed side by side in an equilateral triangle. It was intended that the arrangement of the medium and small traps should resemble the arrangement of real flowers, which are frequently found in pairs or clumps. A 45 cm gap was left between different sized traps. Collections of hoverflies were made from 8 to 15 August.

Analysis

Trap catches for single and sets of traps were analysed as the number of syrphids trapped per cm^2 of trap surface. Kruskal-Wallis tests were used to compare the numbers of all gravid females and the numbers of *E. balteatus* and of *E. corollae* caught in traps of different sizes for single traps, sets of three traps, and sets of six traps separately.

5.8. Results

Numbers of gravid syrphids

Table 5.3 shows the numbers of all adult syrphids and gravid females caught in the different treatments over the experimental period. A total of 1047 adult aphidophagous syrphids per 100 cm^2 were collected from large (25 cm diameter) traps of which 62.8 were gravid. The equivalent figures for medium size traps (19 cm diameter) were 934.9 and 58.6, and for small traps (13.5 cm diameter) 1516.7 and 56.9 (Table 5.3). The main species were *E. balteatus* and *E. corollae* and peak numbers were caught at the end of July/early August when traps were presented in sets of three treatments together.

There were no significant differences between the different treatments when the overall numbers of gravid females caught in single traps were compared (Kruskal Wallis test: $P > 0.05$) (See Table 5.4 for details of Kruskal-Wallis analyses). For sets of three traps (one of each size) and for sets of six traps (one large, two medium and three small), differences between the overall numbers of gravid flies caught in the different treatments were highly significant (Kruskal-Wallis test: $P < 0.01$ in each case) (Table 5.4), with more gravid females caught per cm^2 in large than in small traps.

For *E. balteatus* and for *E. corollae* separately, there were no differences between numbers of gravid females caught in single traps or in traps presented in sets of six (Kruskal Wallis tests: *E. balteatus* $P > 0.05$; *E. corollae*: $P > 0.05$ in each case) (Table 5.4). For flies caught in traps presented in sets of three differences between treatments were highly significant for *E. balteatus* (Kruskal Wallis test: $P < 0.01$) and very highly significant for *E. corollae* (Kruskal Wallis test: $P < 0.001$) with higher numbers caught per cm^2 in large than in small traps in each case (Table 5.4). In each case where significant differences were found, the rank for numbers of gravid females caught in medium size traps was intermediate between the rank for large traps which was highest and the rank for small traps which was lowest.

Figure 5.3 (a), (b), (c) shows the species and actual number of gravid females caught in single traps, sets of three traps and sets of six traps over the experimental period.

Collection dates	Diameter of yellow water trap						Totals	
	25 cms		19 cms		13.5 cms			
Single traps	All ♂♀	Gravid ♀♀	All ♂♀	Gravid ♀♀	All ♂♀	Gravid ♀♀	All ♂♀	Gravid ♀♀
11/07/2005	17 (3.5)	0 (0.0)	15 (5.3)	0 (0.0)	4 (2.8)	0 (0.0)	36 (11.6)	0 (0.0)
13/07/2005	18 (3.7)	1 (0.2)	19 (6.7)	6 (2.1)	4 (2.8)	0 (0.0)	41 (13.2)	7 (2.3)
15/07/2005	101 (20.6)	9 (1.8)	26 (9.2)	2 (0.7)	45 (31.5)	6 (4.2)	172 (61.3)	17 (6.7)
16/07/2005	124 (25.6)	12 (2.4)	49 (17.3)	6 (2.1)	109 (76.2)	10 (7.0)	282 (119.1)	28 (11.5)
22/07/2005	290 (59.1)	7 (1.4)	120 (42.3)	8 (2.8)	171 (119.6)	6 (4.2)	581 (221.0)	21 (8.4)
Totals	**550 (112.5)**	**29 (5.8)**	**229 (80.8)**	**22 (7.7)**	**333 (232.9)**	**22 (15.4)**	**1112 (326.2)**	**73 (28.9)**
Sets of three traps								
25/07/2005	82 (16.7)	2 (0.4)	113 (39.8)	6 (2.1)	37 (25.9)	2 (1.4)	232 (82.4)	10 (3.9)
29/07/2005	1765 (359.5)	136 (27.7)	942 (331.7)	33 (11.6)	1001 (700.0)	20 (14.0)	3708 (1391.2)	89 (33.3)
01/08/2005	1604 (326.7)	121 (24.6)	843 (296.7)	51 (17.9)	509 (355.9)	16 (11.2)	2956 (979.3)	188 (53.7)
05/08/2005	508 (103.5)	50 (10.2)	345 (121.5)	38 (13.4)	207 (144.8)	17 (11.9)	1060 (369.8)	105 (35.5)
Totals	**3959 (806.4)**	**209 (62.9)**	**2243 (789.7)**	**128 (45.0)**	**1754 (1226.6)**	**55 (38.5)**	**7956 (2822.7)**	**392 (146.4)**
Sets of six traps								
08/08/2005	376 (76.6)	40 (8.1)	215 (37.2)	28 (4.9)	121 (28.2)	12 (2.8)	712 (142.0)	80 (15.8)
10/08/2005	118 (24.0)	5 (1.0)	85 (15.0)	3 (0.6)	66 (15.4)	1 (0.2)	269 (54.4)	9 (1.8)
12/08/2005	79 (16.1)	1 (0.2)	42 (7.4)	2 (0.4)	38 (8.9)	0 (0.0)	159 (32.4)	3 (0.6)
15/08/2005	56 (11.4)	0 (0.0)	27 (4.8)	0 (0.0)	20 (4.7)	0 (0.0)	103 (20.9)	0 (0.0)
Totals	**629 (128.1)**	**46 (9.3)**	**369 (64.4)**	**33 (5.9)**	**245 (57.2)**	**13 (3.0)**	**1243 (249.7)**	**92 (18.2)**

Table 5.3. Number of aphidophagous adult syrphids and of gravid females collected from single traps, sets of three traps and sets of six traps on each date (first number in each set is actual number caught, numbers per 100 cm^2 of trap surface in brackets) in the field margins of winter wheat crops in 2005.

Gravid females		**Mean rank**		**df**	X^2	***P***
	Large trap (25 cm)	Medium trap (19 cm)	Small trap (13.5 cm)			
Single traps (all gravids)	271.94	268.47	271.09	2	0.206	0.902
Sets of 3 traps (all gravids)	514.77	441.32	395.41	2	54.14	*0.000
Sets of 6 traps (all gravids)	147.47	138.18	120.84	2	10.932	*0.004
Single traps (*E. balteatus*)	88.53	90.69	92.28	2	0.417	0.812
Sets of 3 traps (*E. balteatus*)	103.47	93.18	74.85	2	10.792	*0.005
Sets of 6 traps (*E. balteatus*)	23.80	25.80	19.40	2	2.927	0.231
Single traps (*E. corollae*)	114.76	111.99	112.25	2	0.472	0.790
Sets of 3 traps (*E. corollae*)	108.88	88.90	73.72	2	18.311	*0.000
Sets of 6 traps (*E. corollae*)	25.27	23.50	20.23	2	1.561	0.458

Table 5.4. Results of Kruskal-Wallis one-way analysis of variance on trap catches for single and sets traps (analysed as the number of gravid syrphids per cm^2 of trap surface). in 2005. * indicates significant differences between treatments.

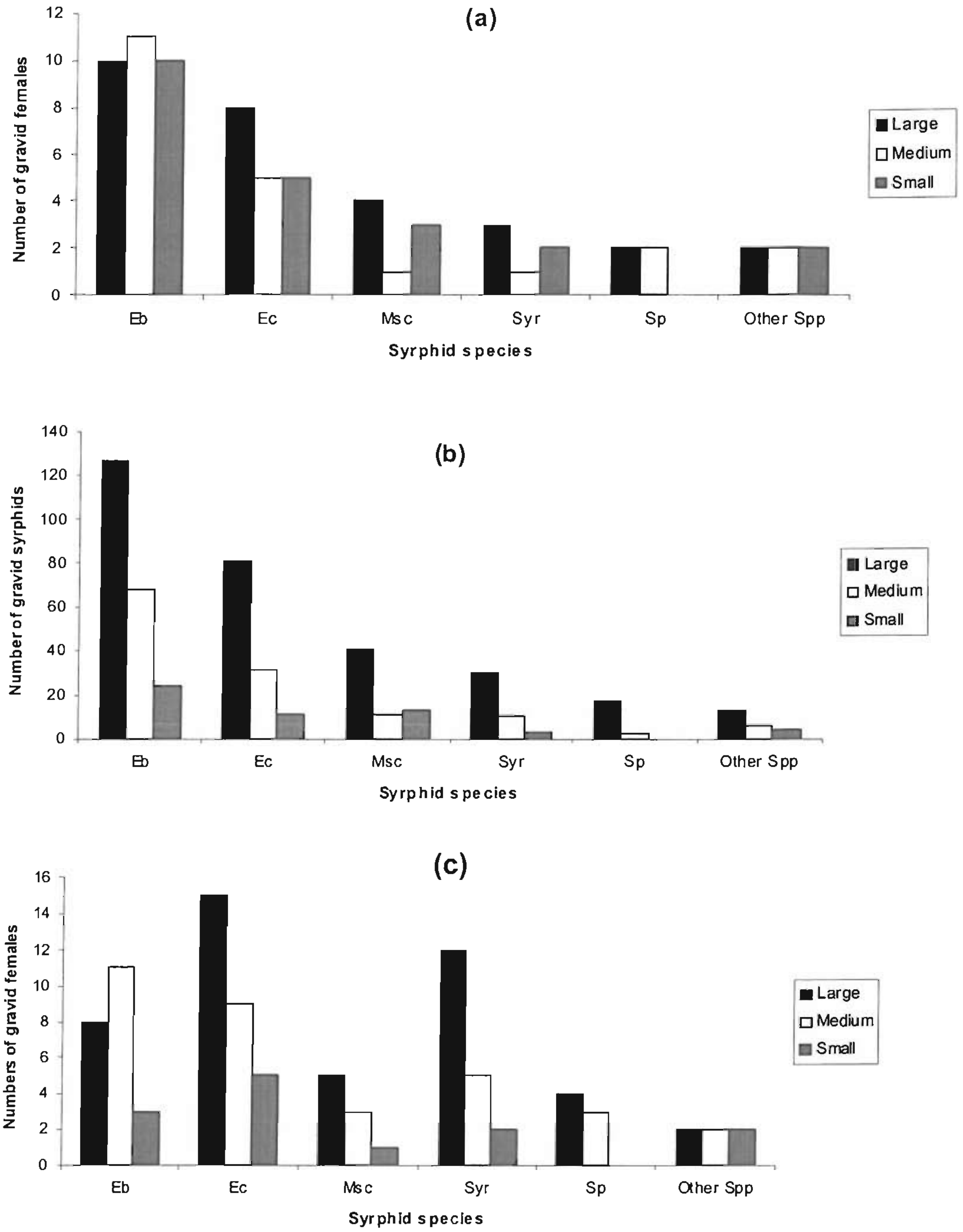


Figure 5.3 (a), (b) and (c). Number and species of gravid syrphids caught in single traps (a), sets of three traps (b) and sets of 6 traps (c) of different size over the experimental period in 2005. (Eb = *E. balteatus*; Ec = *E. corollae*; Msc = *Melanostoma scalare;* Syr = *Syrphus ribesii* and *S. vitripennis*; Sp = *Scaeva pyrastri*; Other Spp = *Sphaerophoria scripta, Chrysotoxum bicinctum* and *Platycheirus* spp.).

5.9. Discussion

Few gravid females were collected during the periods when traps of different sizes were presented singly and no significant differences were found in the numbers caught in the different size traps. One reason for this might be that flies were attracted towards and landed in targets presented singly that they would have rejected if a choice had been offered. High numbers of flies were captured in late July and early August and there were very significant differences between treatments for gravid females trapped during this period, when traps were presented in sets, with higher numbers per cm^2 collected from large than small traps.

The effect of presenting equivalent target areas, but split into units of different size, was tested in the third part of the experiment, the same result was seen with more gravid syrphids cm^2 trapped in the large trays (Table 5.4). Ideally the traps would have been of equivalent area, but in practice this was not possible and the combined area of two medium traps or three small traps was somewhat more and a little less respectively than the area of a single large trap. It was expected that the greater area of the two medium trays might provide an extra stimulus to gravid females. Similarly, it was thought that a cluster of small trays might improve their attractiveness because they appeared to resemble the arrangement of real flowers. However, an insect's perception of a colour or flower signal cannot be directly compared to a human's. Much depends on the receptors that code information and the computational capabilities of the nervous system (Chittka & Menzel, 1992).

In fact, one large target appeared to be preferred to two, or three, smaller targets with an equivalent combined area. However, all the targets used in this experiment were larger than any natural flowers the local syrphid population was likely to encounter and it cannot be assumed that the same results would have occurred using real flowers.

The main aim of carrying out this investigation was to produce the most attractive possible model flower for attracting gravid females and the results suggest that the largest model would be the most effective for this. It would have been ideal to test the response of gravid females to larger trap sizes than those investigated in this project. However, the experiments described here were extremely labour intensive and lack of time prevented further investigation.

When all adults were counted together for both the single and sets of three traps, many more syrphids were caught in small traps than large ones (Table 5.3). This could be because males and /or immature females have different preferences to those of gravid females. This may help explain why there is disagreement over whether syrphids preferentially visit small or large flowers. It supports the work of Sutherland *et al.* (1999), who found small flowers to be more attractive than large to naïve *E. balteatus.* Sutherland *et al.* (1999) found young *E. balteatus* to be highly selective in assessing the resource available to them and suggested that although large flowers may provide increased floral rewards, there may be an upper size limit above which they are no longer attractive. This trend was not seen when sets of six traps, including three small traps, were presented together, however this was the last presentation of treatments to be carried out, and it is possible that the result seen was a consequence of an increase in the average age of the population and changes in preference associated with this.

There is some evidence that bees (Heinrich, 1978) and honeybees (Hodges, 1981) preferentially choose large or small flowers depending on the concentration of nectar rewards. In the laboratory, Sutherland *et al.* (1999) found that female and young *E. balteatus* directed visits to model flowers that provided the greatest honey concentrations. No food rewards were associated with the models used in this experiment, however the small targets may have been perceived as being a better nutritional option. Gravid flies, however, may be less concerned with nutritional requirements and more concerned with the search for oviposition sites, with colour being a primary cue in attraction. There also is evidence to suggest that *E. balteatus* discrimination decreases with increasing age (Sadeghi & Gilbert, 2000). It seems possible therefore, that preference for flower size may change with female age, with larger sizes preferred by older flies. As older males were not identified, their behaviour could not be assessed.

The results show the importance of identifying gravid females. Had this not been done, then, as they were in a minority, their pattern of behaviour would not have been identified and it would have been assumed that they followed the same pattern (with the smallest targets most attractive) as males and immature females and found the smallest targets most attractive.

If further experimentation confirms that gravid syrphids do respond in the same way, or more positively, to large single model flowers than to more abundant smaller models, then these may have an even greater advantage, as far as time and labour costs are concerned, over pairs and clumps of small model flowers in attracting them to crop fields. There may also be potential to use much larger yellow targets to attract gravid syrphids into areas of high aphid density, where natural flowers are poorly available.

5.10. Pattern Experiments

5.10.1. Introduction

This section describes two preliminary laboratory experiments followed by field experiments in which the landing responses of *E. balteatus* to yellow discs with pattern features such as black oriented lines, circles and edges were tested.

Sphengel (1793) first drew attention to the various lines, spots and blotches of contrasting colour visible to the human eye on the petals of many flowers and suggested that these drew insects to the nectaries. Kugler (1963) noted that 83% of flowers pollinated primarily by butterflies had nectar guides. Kugler (1943), von Frisch (1950), Manning (1956) and Free (1970) observed that bees were also drawn to the nectaries by honey guides on the petal. However, some flowers produce ultraviolet reflecting nectar guidelines, which are invisible to the human eye (Kevan & Baker, 1983). Thompson *et al.* (1972) provided the first biochemical evidence that 'invisible' honey guides occurred in flowers such as the yellow Composite, *Rudbeckia hirta* (L)) (Black-eyed Susan). Within flowers, yellow flavonoids (Harborne, 1972), chalcones and aurones (Scogin & Zakar, 1976) and the differential distribution of pigments such as anthocyanin within the flower tissue are usually responsible for these patterns or nectar guides.

It is widely recognised that nectar-guides are used by numerous insect species to orient themselves on flowers to find rewards (Kevan *et al.*, 2001). In bees, a number of cases have been described in which flowers with visible patterns are visited more frequently for pollen than flowers without them (see Manning, 1956; Free, 1970; Johnson & Dafni, 1998). There is also some evidence to suggest that radiating guidelines enable *Eristalis tenax* (L.) to find a central yellow spot on a artificial flowers more frequently than on artificial flowers without them (Dinkel, 1999; Dinkel & Lanau, 2001).

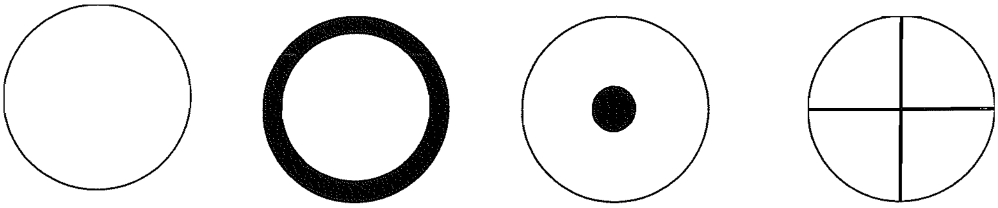
There have been a number of studies on honeybees (e.g. Butler, 1951; Free, 1970), and on bumblebees (e.g. Manning, 1956; Lunau: 1990; Lunau *et al.,* 1996) in relation to pattern discrimination, but other than Finch (1991), who found a reduction in the numbers of hoverflies caught when various parts of the trap were painted black and Laubertie *et al.* (2006), who caught fewer syrphids in traps painted green on the outside than in completely yellow traps, no experimental studies have been carried out to test the effect of pattern on hoverflies. The responses of *E. balteatus* to pattern were therefore tested firstly in the laboratory, and then in the field to find out whether or not gravid syrphids were attracted to them.

5.11. Preliminary laboratory experiment

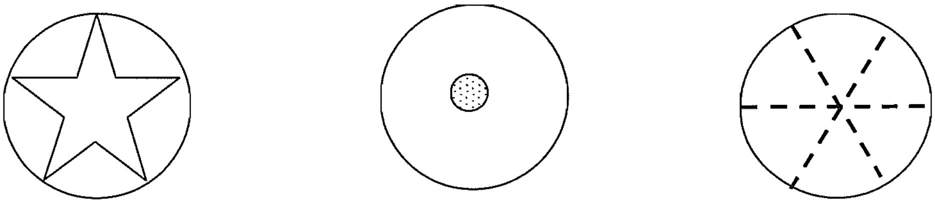
5.12. Methods and materials

5.12.1. Model flowers

Model flowers were constructed using white card discs (diameters 13mm) painted florescent yellow (Glocote 1263, Goovar, Ellenshaw Works, Hull HU2 OHN) (see chapter 2 methods section). The size of the disc was chosen to most accurately represent flowers such as the buttercup (*Ranunculus repens*), which would normally be encountered by hoverflies in the field. Pattern choices were based on Free (1970) who tested the reaction of bees to circular models with radiating guide lines, clusters of dots, circles and star shapes of approximately the same area. Patterns were applied by hand, using a fine (0.5 mm wide) black ink pen (Pilot Hi-Tecpoint V7) (see Fig. 5.4). Black was chosen because this it was thought that this would provide a strong colour contrast to the yellow colour of the disc.



A No pattern **B**. Black outer rim **C**. Black centre circle **D**. Black cross



E. Five-pointed star **F**. Inner circle of dots **G**. Dotted diagonal lines

Figure 5.4. Models used to test landing responses by *E. balteatus* to patterned targets in the laboratory (not to scale). Experiment 1: all models used. Experiment 2: models A, B, C and D used.

The painted discs were left in a well-ventilated room for two months to eliminate any odour emanation before use. Discs were then mounted horizontally with Sellotape on 18cm lengths of green, plastic-coated gardener's wire (B & Q). Stems were inserted into hand-moulded conical Plasticine mounts (100g), which provided support. New model flowers were constructed for each replicate bioassay and used flowers were discarded.

5.12.2. Experimental insects

The experimental insects were first generation gravid female *E. balteatus* reared from stock cultures kept in a perspex cage (40 x 60 x 40cms) under long-day conditions (5000lux/L16: 8h/D7) in the Insectory at Southampton University. Pre-experimentally, flies had *ad libitum* access to tap water, sieved pollen from *P. deltiodes* (Sigma-Aldrich Co Ltd., Poole, Dorset, U.K.) and a 10% honey solution (Gales Original Clear, UK) on cotton. Food and water was provided on Petri dishes on upturned plant pots at the back of the cage. During bioassays, flies had access to water, but not food. Temperature was maintained at 22°C ± 1 °C throughout the experimental period.

5.12.3. Experimental arena

Kevan and Baker (1983) found that bright yellow flowers showed up well against a green background and for this reason, green artificial grass matting (Palmyra Manufacturing Co. Ltd., Maryport, Cumbria) was fitted to the floor of the cage. A circular (diameter 26cm) marble turntable ('Lazy Susan', Horwood Homeware) was also covered with green matting and placed in the centre of the cage. The seven patterned model flowers (see Fig. 5.4) were presented simultaneously and positioned at 9 cm intervals on the outer rim of the turntable at random. Twenty four gravid *E. balteatus* were transferred into the cage and allowed to settle for ten minutes before making observations. The position of the model flowers relative to the cage was altered by a 90-degree clockwise rotation of the turntable every 20 minutes to eliminate positional preference. The numbers of landings by *E. balteatus* on the model flowers were recorded continuously over a three-hour period, on four separate occasions, at different times of day from 22 February to 6 March 2002.

Analysis

The numbers of landings on the seven different treatments were compared using a X^2 test.

5.13. Results

A total of 85 landings were recorded overall. Table 5.5 shows the number of landings on each model. The highest numbers of landings were on the model flower with no pattern. The patterned models on which there were most landings were the central circle (18) and the black cross (16). Differences between the numbers of landings on the seven different treatments were significant (X^2 = 15.49; df = 6; $P < 0.05$) with more landings than expected on the plain yellow model, and the models with a black central circle and a black cross respectively.

No pattern	Black outer rim	Black centre circle	Black Cross	Five-pointed star	Circle of dots	Diagonal dotted lines
19	12	18	16	6	5	9

Table 5.5. Number of landings on model flowers of each pattern by *E. balteatus*.

5.14. Discussion

Although there was no evidence from the laboratory experiment that any pattern would be likely to be more effective at attracting gravid syrphids than a plain painted target, this would not necessarily be the case in field conditions. Only *E. balteatus* was tested in the laboratory and it was possible that other species might react differently. It was therefore decided to investigate the response of syrphids to yellow water traps with and without patterns on a much larger scale in the field.

5.15. Field Experiments

5.16. Methods and Materials

Trap Preparation

Sixty traps were painted with UV-reflecting yellow Plasti-Kote 142S (see General Methods 5.2.2). Black enamel (Hammerite Products, ICI Paints, Slough, UK) patterns were applied by hand using a flat paintbrush (size 14). Equal numbers of trays (15 of each) were painted with a central circle (diameter 2.3cm) an outer rim (width 1cm) a cross (width 1cm) or left without patterns. Patterns used were based on the models elicited the most visits by *E. balteatus* in the first laboratory experiment (see Fig. 5.4: B, C & D). Patterns were enlarged to cover the same proportion of the yellow painted plant pot tray as on the laboratory models.

The treatments

Single traps

Five traps of each pattern were randomly positioned in the field margins, approximately one metre from the crop edge, with intervals of 25 metres between traps, in each of the three fields (20 traps per field). Collections of hoverflies were made from 15 to 22 July 2005. Treatments were re-randomised each time the traps were emptied and reset.

Sets of three traps

Five sets, which consisted of one trap of each pattern and one plain yellow trap, were placed in each field with intervals of 25 m between sets. Each set was positioned in the field margin approximately one metre from the crop edge and parallel to it, with 45 cm between treatments. Within the set, treatments were in random order. Collections of hoverflies were made from 25 July to 5 August 2005. Treatments within each set were re-randomised each time the traps were emptied and reset.

Analysis

The total numbers of gravid syrphids, and the numbers of gravid *E. balteatus* and gravid *E. corollae*, caught in water traps with different patterns, were compared for single traps and sets of traps separately using Kruskal-Wallis tests. All statistical analyses were performed using SPSS11

5.17. Results

Numbers of gravid syrphids

Table 5.6 gives the total number of aphidophagous adult syrphids and the number of gravid females caught in the different treatments over the experimental period. A total of 3363 adult syrphids, of which 213 were gravid, were collected from plain traps. Figures for traps with a black outer rim were 2110 and 152, a black centre circle, 1624 and 110, and 1746 and 88 for traps with a black cross. As for the height and size experiments, which were conducted at the same time, the highest numbers of gravid females were caught at end of July/early August. The main species were *E. balteatus* and *E. corollae* (Fig. 5.5).

When gravid females were analysed as a group, there were highly significant differences between the numbers caught in the different treatments with higher numbers caught in traps with no pattern when treatments were presented as sets (Kruskal Wallis test: $P < 0.001$) and for single traps (Kruskal-Wallis test: $P < 0.01$) Full results of the Kruskal-Wallis analyses are given in Table 5.7. In both cases, the next highest ranked treatment was the black rim, while the ranks for traps with a black cross or a black centre circle were lowest and similar to each other (Table 5.7).

For *E. balteatus,* as for combined species, whether caught in sets of traps (Kruskal-Wallis test: $P < 0.001$) or singly presented traps (Kruskal Wallis test: $P < 0.05$) (Table 5.7) significantly more gravid females were caught in yellow traps without a pattern than in those with a central circle (sets) or a black cross (single traps). As with all gravid females combined, there was greater difference between the ranks for plain traps and the highest ranked patterned trap, than between the different patterned treatments. For *E. corollae* caught in sets of traps, differences between the four treatments were very highly significant (Kruskal-Wallis test: $P < 0.001$) with many more caught in controls than traps with a cross. When treatments were presented in isolation, or single traps, there were no significant differences between numbers of *E. corollae* caught in the different treatments (Kruskal- Wallis test: $P > 0.05$) (Table 5.7).

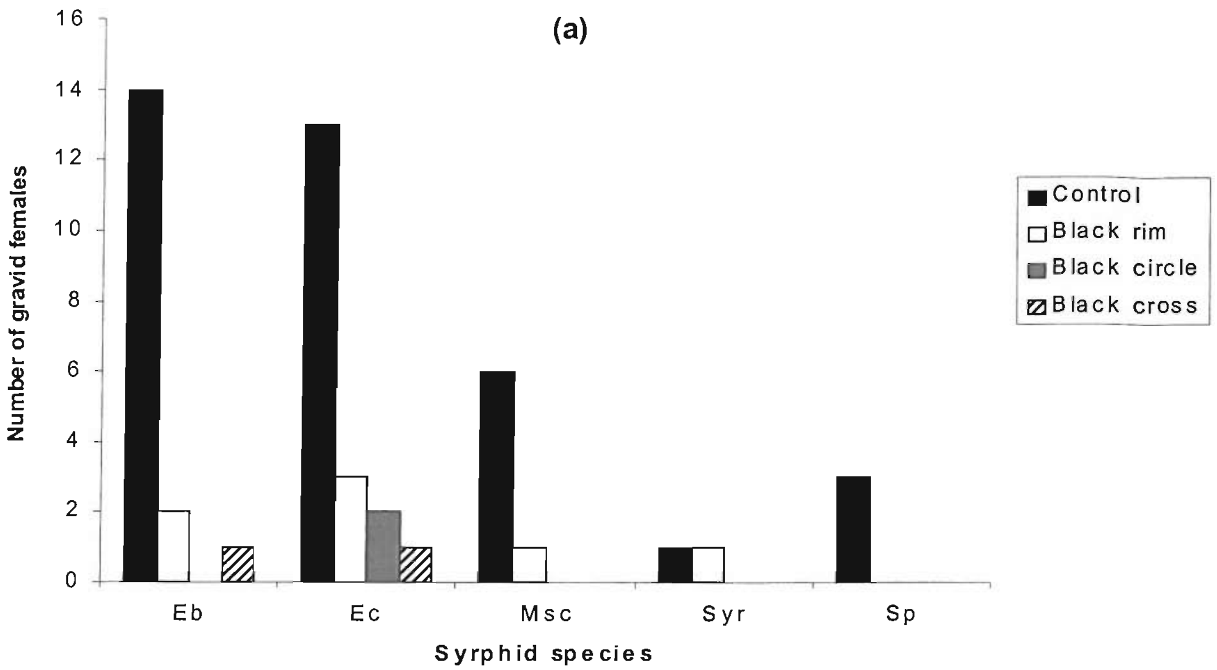
Figure 5.5 (a), (b) shows the number and species of gravid syrphids caught in sets of traps and single traps with and without patterns over the experimental period in 2005.

Date	No pattern		Outer rim		Centre circle		Cross		Total	
Sets of traps										
15/07/05	66	(13)	7	(0)	23	(1)	9	(0)	**105**	**(14)**
16/07/05	91	(21)	23	(1)	23	(1)	21	(1)	**158**	**(24)**
21/07/05	180	(1)	62	(5)	67	(0)	31	(0)	**340**	**(6)**
22/07/05	160	(2)	55	(1)	31	(0)	41	(1)	**287**	**(4)**
Totals	**497**	**(37)**	**147**	**(7)**	**144**	**(2)**	**102**	**(2)**	**890**	**(48)**
Single traps										
25/07/05	33	(2)	39	(1)	24	(2)	20	(1)	**116**	**(6)**
29/07/05	1472	(66)	930	(48)	634	(30)	827	(46)	**3863**	**(190)**
01/08/05	861	(65)	582	(37)	423	(22)	403	(13)	**2269**	**(137)**
05/08/05	500	(43)	412	(59)	399	(54)	394	(26)	**1705**	**(182)**
Totals	**2866**	**(176)**	**1963**	**(145)**	**1480**	**(108)**	**1644**	**(86)**	**7953**	**(515)**

Table 5.6. Number of all aphidophagous adult syrphids and numbers of gravid females (in brackets) caught in sets of traps and single traps with and without patterns from 15 July to 5 August 2005.

Gravid females	**Mean rank**				**df**	**X^2**	***P***
	No pattern	Outer rim	Centre circle	Cross			
Sets of traps (all gravids)	641.57	593.45	583.49	583.49	3	57.079	*0.000
Single traps (all gravids)	645.64	604.41	578.35	573.61	3	16.398	*0.001
Sets of traps (*E. balteatus*)	134.98	116.93	113.00	114.97	3	23.310	*0.000
Single traps (*E. balteatus*)	140.99	122.20	113.13	105.68	3	11.090	*0.011
Sets of traps (*E. corollae*)	135.60	117.45	115.47	113.48	3	18.642	*0.000
Single traps (*E. corollae*)	127.63	127.78	112.44	114.16	3	4.567	0.206

Table 5.7. Results of Kruskal-Wallis one-way analysis of variance on numbers of gravid syrphids caught in sets of traps and single traps in the field margins of winter wheat crops in 2005. * indicates significant differences between treatments.



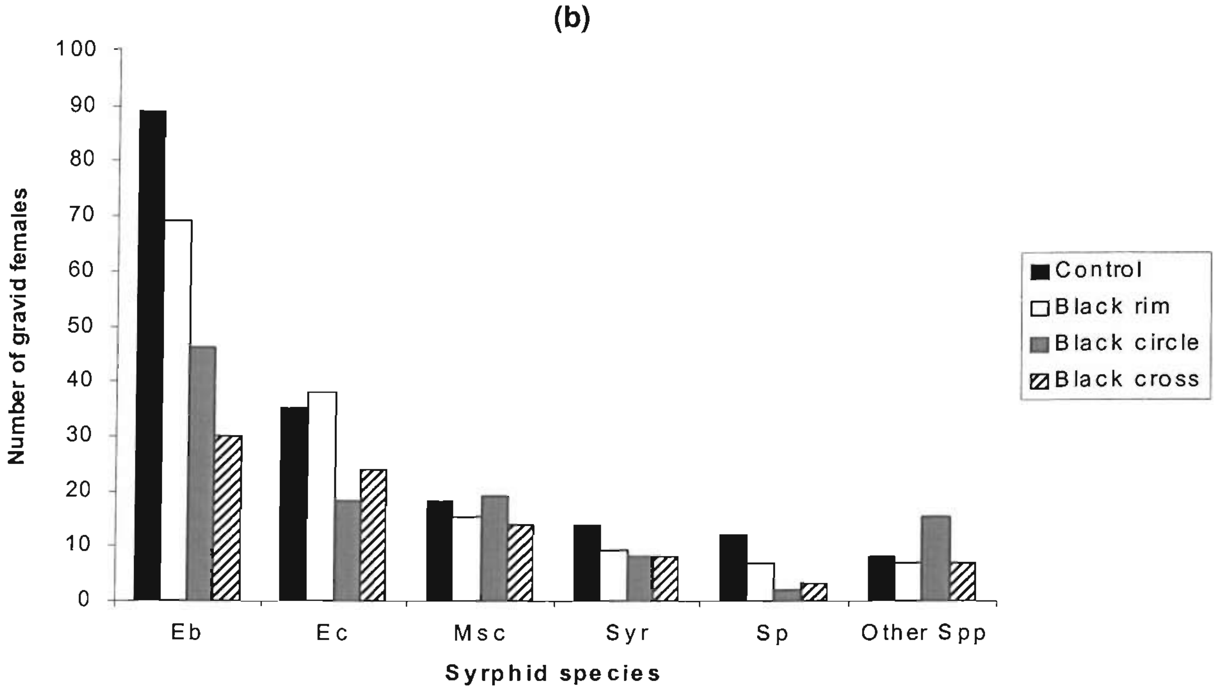


Figure 5.5 (a), (b). Number and species of gravid syrphids caught in sets of traps (a) and single traps (b) with and without patterns over the experimental period in 2005 (Eb = *E. balteatus*; Ec = *E. corollae*; Msc = *Melanostoma scalare*; Syr = *Syrphus ribesii* and *S. vitripennis*, Sp = *Scaeva pyrastri*).

5.18. Discussion

In the field experiment described here, gravid syrphids showed a greater degree of preference for plain trays with no patterns than was apparent in the laboratory tests, where there was little difference in numbers of landings on the three most visited models. However, the paint used in the field was reflective of UV and this could be the reason for increased attraction towards the traps. As was demonstrated in the size experiments, gravid syrphids (as opposed to all adults) seemed to be attracted to large traps that offered the greatest visual cue. It may be that the effect of pattern made the model flower look smaller. However, in the pattern experiment, all adults and gravid females were caught in higher numbers in plain as opposed to patterned traps. It may be simply that the visual stimulus that was supplied by the yellow colouring used in the traps was so effective in directing gravid females towards the traps that at anything that diluted it, or reduced its area made the trap less attractive. This supports the work of several workers (e.g. Kevan & Baker, 1983; Finch, 1991; Sutherland, 1998) who found the colour yellow to be the most important stimulus in attracting syrphids to water traps in the field (see Chapter Two).

As in the height and size experiments, there was a less pronounced preference for one treatment when treatments were presented in isolation and in the case of *E. corollae* almost the same numbers were caught in water traps with a black rim and in plain yellow ones. Preference towards the plain traps was evident in *E. balteatus* (single and sets of traps), but less so in *E. corollae* (sets of traps only).

The next highest ranked treatment was the trap with the black outer rim. However, it was thought that black outer rim made the trap appear smaller than it actually was. Previous work (see Size Discussion) showed that gravid females generally preferred the large traps to the smaller ones. Various workers with other insect groups (e.g. honeybees: Butler, 1951; bumblebees: Manning, 1956) have found that the edge of a disc, which contrasted with its background, received the most visits. It may be that the plain yellow traps used here were preferred to traps with a black outer rim, because these offered the greatest contrast against the background, and a larger area of stimulus.

Traps with a central circle and a black cross were the least preferred patterns. These designs were intended to mimic the markings of real flowers. However, the lines and centre circle probably did not realistically mimic the naturally occurring patterns of real flowers. It has long been established that colour vision in insects is very different to our own. Davies (1993) found that many flowers revealed 'invisible' markings, which could only be seen by insects. When viewed under ultraviolet light, marsh marigolds that appear monotone to humans have light coloured petals and a much darker centre. Hence what we may recognise as a pattern may be perceived very differently by a hoverfly. Chapman *et al.* (1999) found that painted black lines and regularly spaced patterns of black spots had no effect on catch rates of the housefly (*Musca domestica* (L)). Although the situations are not identical, this kind of visual stimulus was not effective in eliciting increased visiting in this experiment either.

Hoverflies may show sensitivity to wavebands across the spectrum, from ultraviolet to yellow (Chittka & Menzel, 1992), although evidence for the existence of true colour vision in hoverflies is limited (Fukushi, 1990). Black markings or darker shades, however, produce little radiation, and may be less attractive to them. Kugler (1950) found that brown centred, older inflorescences of *Senecio jacobaea* (ragwort) were ignored by hoverflies visiting younger yellow flowers. Finch (1991) blackened the interiors of traps and found that the numbers of hoverflies caught became negligible.

There is plenty of evidence to suggest that patterns play a role in attracting honeybees (Zerrahn, 1934; Butler, 1951; Free, 1970) and bumblebees (Kugler, 1943; Manning, 1956) to the nectaries of flowers. However, the anatomy and physiology of the visual systems of hoverflies and honeybees are fundamentally different (Menzel, 1979) and it must not be assumed that patterns are automatically attractive to hoverflies (Stavenga, 1989; Lunau, 1996). O' Carroll *et al.* (1997) found that the neural pathways of hovering insects were unable to detect specific types of pattern such as orientated lines, edges and spots present in numerous flowering species. Similarly, Chittka and Menzel (1992) suggest that the ability to recognise patterns in hoverflies is limited, given the relatively poor spatial resolution of the eye. Although Dinkel and Lanau (2001) observed that *E. tenax* found a small central yellow spot in the centre of a model flower more often and faster if yellow guide lines were present, the effect of guide lines was dependent on the colour yellow.

It is perhaps significant that patterns are more common on zygomorphic flowers with deep nectaries (Kugler, 1930) and that long-tongued insects such as bees (Free, 1970) and butterflies are the most frequent visitors (Kugler, 1963). Syrphid species such as *E. balteatus* have a short, broad proboscis and are most often observed taking pollen from non-patterned flowers with open corollae, such as umbellifers (Gilbert & Jervis (1998). Presumably, the plain traps resembled non-patterned flowers, which may also help explain why these caught more gravid syrphids than the patterned traps.

5.19. General discussion

This work was undertaken in order to design the optimum model flower possible in terms of the number of gravid hoverflies it attracted. Although the experiments were carried out over a relatively short period of time using a limited range of treatments, it was unlikely that the results were compromised overall due to the large number of replicate traps and the sample sizes obtained, particularly in the latter part of July.

The three attributes considered here, (height, size and pattern) were investigated in isolation from each other and no account was taken of the synergistic effects that they may have on syrphid responses. Although the effects of plant and aphid volatiles have been investigated (see Chapter Four), flower shape, surface texture and orientation may also have a role to play. Trap position, field edges, adjacent crops, exposure to wind etc., may also affect the numbers of insects caught.

In all experiments, *E. balteatus* was the main species caught, with *E. corollae* the second most common. The majority of gravid *E balteatus* and *E. corollae* were collected from traps at the end of July/beginning of August, which appears to a peak period for these species of hoverfly (e.g. Rotheray, 1980; Sutherland, 1998; Gilbert, 2005) (Appendix).

It appears from the results of these experiments that gravid females, including those of the two most common species are preferentially attracted towards large, non patterned traps at a height of 30 cm. This height is probably related to the preferred height for oviposition of the main species and was the same for traps placed in the tramlines in the crop as for the highly visible traps in the field margins.

The only experiment where there appeared to be differences between overall hoverfly response and that of gravid females, was in the size experiments. It appeared that though small trays seemed more attractive to males and/or immature females, that the larger trays were more attractive to gravid females. Possible reasons for this are discussed above, however it emphasises the importance of isolating and identifying the responses of the target group in an investigation such as this one. As any potential enhancement of biocontrol by hoverflies requires gravid females, it is suggested that within the range tested, large targets are likely to be more useful than small ones in optimising visitation and therefore potential oviposition and biocontrol of aphids. However, the results only applied to the range of sizes used. If larger still models were used, it is possible that they might be even more attractive or alternatively that there is an optimum size beyond which attractiveness does not increase.

It also appeared that none of the patterns tested increased the attractiveness of model flowers to *E. balteatus,* or to gravid syrphids generally. It has been argued above that the markings used in this experiment may not have resembled those of real flowers to syrphid perception. It is an area where further research might prove fruitful. Possibilities include looking at the effect of ultraviolet reflecting markings. Highly broken outlines, such as those found on petals, or clusters of dots might also elicit more visits. However, in the absence of evidence to the contrary, plain yellow trays appeared to be the most effective stimulus in attracting gravid syrphids.

Although it cannot be assumed with certainty that yellow targets without water in them are perceived in the same way, and will have the same attractiveness relative to each other, as yellow water traps, it seems likely that this is the case.

There was some evidence that for all the attributes tested the response to single isolated treatments was less rigid than that to treatments that were put out in sets. This is what would be expected. Traps (or sets of traps were put out at intervals of 25m and although the fluorescent yellow paint made them highly visible, at this distance it would only be possible for a hoverfly to see one at a time. Given no choice it might be expected that a hoverfly seeking a flower to visit would land on a promising looking source. However, when preference was shown, it was for the same options as when treatments were presented in close proximity, and therefore the possibility that model flowers might be used singly does not affect the choice of characteristics for an optimum model.

Yellow traps to attract and catch gravid hoverflies were a useful way of comparing the floral characteristics investigated in this chapter. The fact that 2005 was a year when hoverfly numbers were very high (see Appendix) was opportune. Over the course of the experimental period, many thousands of hoverflies were caught. However, the method was labour intensive in that it took a great deal of time to collect, count, identify and dissect females to identify those that were gravid. Although it would have been ideal to have used bait plants to measure oviposition within the vicinity of yellow targets (see Chapter Two), due to the large number of different experiments going on at the time, this was not possible. It would also have been an impossible method to use when treatments were presented in sets. However, this work was important in that it concentrated on identifying gravid syrphids in trap catches in order to decide how best to attract them to agricultural land.

5.20. Conclusions

It appeared that from the range of options investigated in this chapter, that the optimum model flower should be without pattern, 25cms in diameter and positioned 30cms above the ground. A pilot experiment to test a model with these, and other characteristics identified in earlier chapters, is described in Chapter Six.

CHAPTER 6

THE EFFICACY OF THE OPTIMUM MODEL FLOWER ON OVIPOSITION BY APHIDOPHAGOUS SYRPHIDS

6.1. Introduction

In previous chapters it was demonstrated that oviposition on nearby bait plants by aphidophagous syrphids occurred in the presence of model flowers without food resources (see Chapter 2) and, at least for those tested, that the presence of a volatile was not significantly associated with an increase in oviposition (see Chapter 4). Within the parameters set in the experiments carried out, analysis of trap catches also suggested that gravid females were attracted to targets painted with fluorescent yellow paint with an ultraviolet component (See Chapter 3) and to targets that were large (25 cm diameter), non-patterned and placed 30 cm above ground level.

Lack of time meant that a full scale field based experiment to test this 'optimum' model was not possible. However, a pilot experiment was carried out in the grounds of the University of Southampton with the aim of assessing the extent to which a model flower with the attributes described above might enhance oviposition on nearby bait plants compared to oviposition on bait plants at control positions with no model flowers.

6.2. Methods and Materials

Experimental site

Experiments were carried out in the grounds of Boldrewood, University of Southampton, UK in 2007. The site (see Fig. 6.1) consisted mainly of open grassed areas lined with mature broadleaved tree species such beech (*Fagus sylvatica*), poplar (*Populus nigra* (L)), sycamore (*Acer pseudoplatanus*), horse chestnut (*Aesculus hippocastanum* (L)) and evergreens such as holly (*Ilex* *aquifolium* (L)), yew (*Taxus baccata* (L)), pine (*Pinus nigra* (Arn)), sequoia (*Sequoiadendron giganteum* (Lindl)) and spuce (*Picia* spp.). The site boundaries were interspersed with laurel (*Prunus laurocerasus* (L)) and privet (*Ligustrum* spp.) hedgerows and shrubs. The few weedy plant species that were present in the plant beds near the greenhouse were unknown. A main road ran parallel to one side of the site.

Preparation of bait plants

Standardised pots (diameters 70cm) of ten one-week old spring barley plants (*Hordeum vulgare* (L.) (var. 'Gleam') previously infested with the wheat aphid *Rhopalosiphum padi* supplied by Mambotox (University of Southampton Science Park, Chilworth, UK) were used as bait plants for the first experiment. Further standardised bait plants, which were used when the experiment was repeated, were grown in a glasshouse at 15-18^{o}C with 16h day length, in peat-based compost using the same batch of seed (supplied by Mambotox) as the plants in the first experiment and in pots of the same size. Approximately 15 seeds were scattered in each pot and after germination these were thinned out to leave 10 seedlings in each pot. As soon as the plants emerged they were infested with *R. padi* by placing two cut seedlings from previously infested plants (supplied by Mambotox) on top of each pot. The cut seedlings were removed after 48h. The plants were put out in the University grounds approximately one week after sowing.

Model flowers

Model flowers consisted of ten flowerpot trays (diameters 25cm) painted with Plasti-Kote P142S fluorescent yellow ultraviolet reflecting paint (see Chapter 2 Methods section for details of preparation). A hole was drilled in the centre of each tray, which was then mounted 30cms above the ground on a bamboo cane inserted into the soil with a mallet (Fig. 6.1). Three bait plants were selected at random and equally spaced on the ground approximately 16cm from the centre of each model flower or control (no plant tray) (Fig. 6.1).

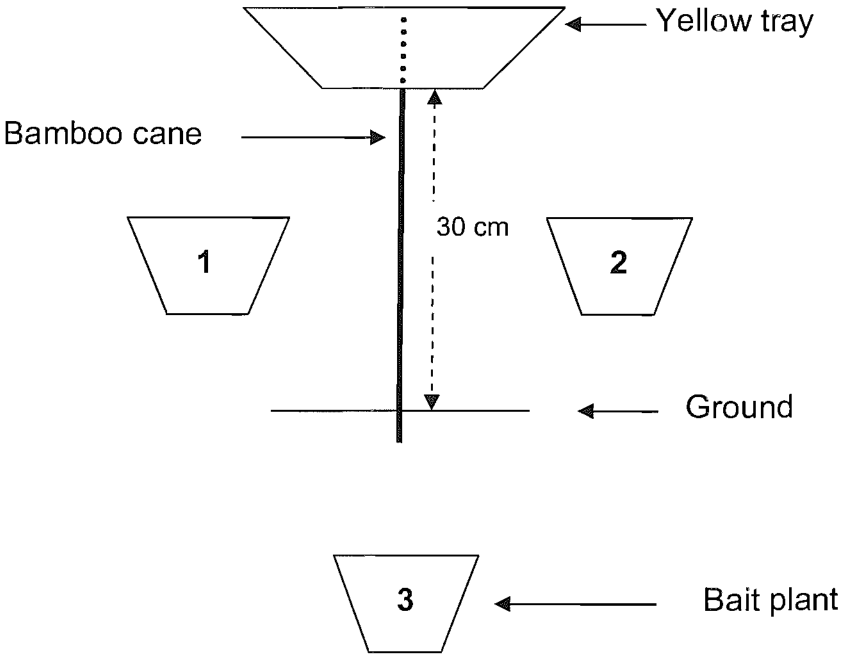


Figure 6.1. Simplified diagram illustrating the height of the model flower and the general arrangement of the three bait plants which were set out on the ground around it (not to scale) in 2007. Controls were without yellow trays.

10 model flower and 10 control positions were set out alternately at intervals of 25 metres along the perimeter of the University grounds (see Fig 6.2). The first two positions were in flower beds bordering on the glasshouses at Boldrewood (Fig. 6.2). All other positions were either under trees or beside hedges with the stake supporting the model flower or marking the control position 60 cm from the trunk, or from the base of the hedge. See Fig. 6.2 legend for details of tree and hedge species. After 24 h all bait plants were collected and white plastic markers used to identify the position that they had occupied. The positions of model flowers and controls were reversed and new bait plants were put out using the white markers to ensure that they occupied exactly the same positions as those set out the previous day. The white markers were then removed. After 24 h the second set of bait plants were

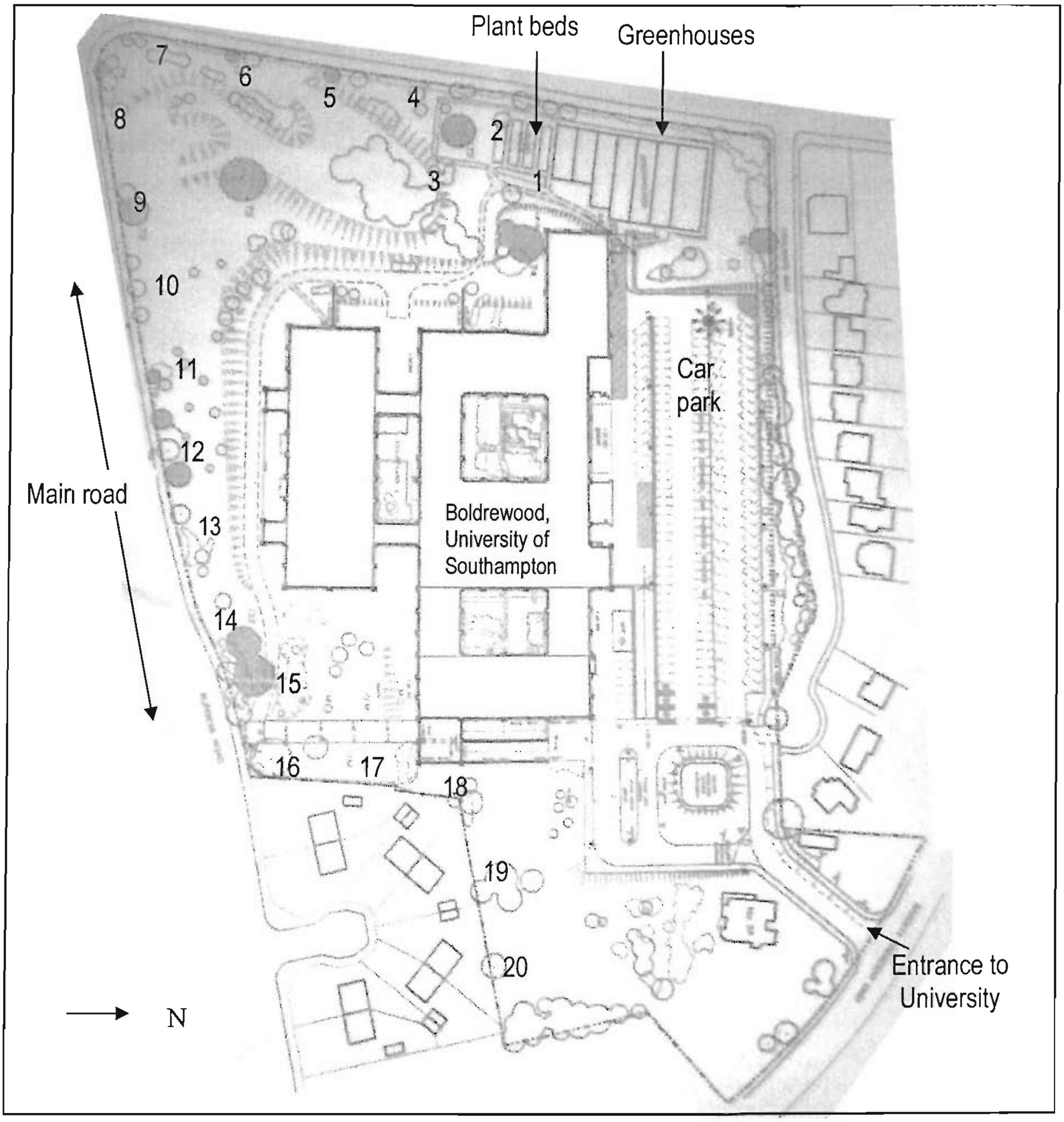
collected. Once a set of bait plants was collected, the total number of syrphid eggs found at each model flower and control position was recorded and as far as possible the eggs were identified to species. The experiment was repeated the following week. As bait plants were only put out on days with similar fine sunny weather, the second set of bait plants in the repeat experiment was put out 24 h after the first set was collected. During the repeat experiment there was disruption at some positions due to grass cutting activities and eggs laid at these positions have been omitted from the analyses.

Analysis

A Mann-Whitney *U* test was carried out to compare the total number of eggs found in the vicinity of model flowers and at control positions. Due to disruptions at positions 9, 10, 13 and 14 during the second (11 and 13 August) experimental period, these were excluded from the analysis.

As it was thought that position might have an effect on the number of eggs laid, a Kruskal-Wallis test was carried out to compare the numbers of eggs found on bait plants in the different positions. All statistical analyses were performed using SPSS11.

Fig. 6.2. Digital photograph (Scale 1:1000) of site map (Drawing No. (11) 05; Job No. 3359; 27.01.00) showing the approximate positions where bait plants were set out. Model flowers and control positions alternated and on day two of each experiment, new bait plants were set out with the positions of the previous day reversed. See text for details.



Position of treatments

1 = Plant bed (weedy species)
2 = Plant bed (weedy species)
3 = Pine tree
4 = Sycamore tree
5 = Holly hedge
6 = Cypress tree
7 = Privet hedge
8 = Yew tree
9 = Cypress tree
10 = Pine tree
11 = Pine tree
12 = Horse chestnut tree
13 = Pine tree
14 = Pine tree
15 = Sequoia tree
16 = Mature beech tree
17 = Laurel hedgerow
18 = Laurel hedgerow
19 = Cypress tree
20 = Spruce tree

6.3. Results

Numbers of eggs

A total of 1384 syrphids eggs were found on bait plants near the control and model flowers positions over the experimental period. Of these, 529 were found at control positions and 845 at model flower positions (see Table 6.1). Except for five eggs (species unknown) these were all visually assessed as *E. balteatus*. Table 6.1 shows the number of eggs found on bait plants at each position. For each experimental period, and for each individual collection period, a higher total of eggs was counted on bait plants in the vicinity of model flowers than on those at control positions.

Differences between the overall numbers of syrphid eggs on bait plants at control and model flower positions over the experimental period were significant (Mann-Whitney test; $P < 0.05$; Table 6.2) with more eggs laid on bait plants near model flowers than on control bait plants.

Fig. 6.3 shows the total numbers of eggs found at each position when model flowers were present and when they were absent. At 13 out of the 16 positions where no disruption took place, a higher number of eggs were laid on bait plants when model flowers were present than when they were absent. The number of eggs laid varied, with the highest numbers found at positions one (178) and two (169) and the lowest (2) found at position 13 (Table 6.1). There were no significant differences between numbers of eggs found at the different positions (Kruskal-Wallis test; $X^2 = 16.554$; df = 15; $P > 0.05$).

Position	3 and 4 August		11 and 13 August		
	MF	C	MF	C	ALL
1. Edge of flower bed	70	58	50	0	178
2. Edge of flower bed	60	53	31	25	169
3. Under pine tree	8	18	0	0	26
4. Under sycamore	29	3	1	0	33
5. Beside holly edge	39	26	11	0	76
6. Under cypress	32	11	0	8	51
7. Beside privet hedge	76	42	10	0	128
8. Under pine tree	42	84	0	0	126
9. Under pine tree	10	0	-	-	10
10. Open position	31	34	-	-	65
11. Open position	23	4	0	0	27
12. Open position	15	0	3	0	18
13. Under pine tree	1	1	-	-	2
14. Under pine tree	29	20	-	-	49
15. Under sequoia	38	5	0	0	43
16. Under beech tree	13	24	10	0	47
17. By laurel	68	29	5	6	108
18. By laurel	75	39	2	3	119
19. Open position	51	21	5	7	84
20. Open position	2	8	15	0	25
Totals					
	384	276	81	36	
	328	204	62	13	
All	**712**	**480**	**143**	**49**	**1384**

Table 6.1. Number of eggs found on bait plants near model flowers and at control positions at each date. MF = eggs laid by model flowers; C = eggs laid at control positions; non-underlined numbers refer to eggs collected on 3 or 11 August; underlined numbers refer to eggs collected on 4 or 13 August. Eggs laid at positions 10, 11, 13 and 14 on 11 or 13th August have been excluded from the analysis because bait plants at these positions were disrupted during the experimental period.

	Mean Rank		***U***	***P***
	Control	**Treatment**		
Overall result	31.53	41.47	469.00	*0.042

Table 6.2. Results of Mann-Whitney tests on numbers of syrphid eggs oviposited on bait plants at control and model flower positions. Four sets of bait plants were put out on 3 and 4 August 2007 and on 11 and 13 August. * indicates significant differences between treatments.

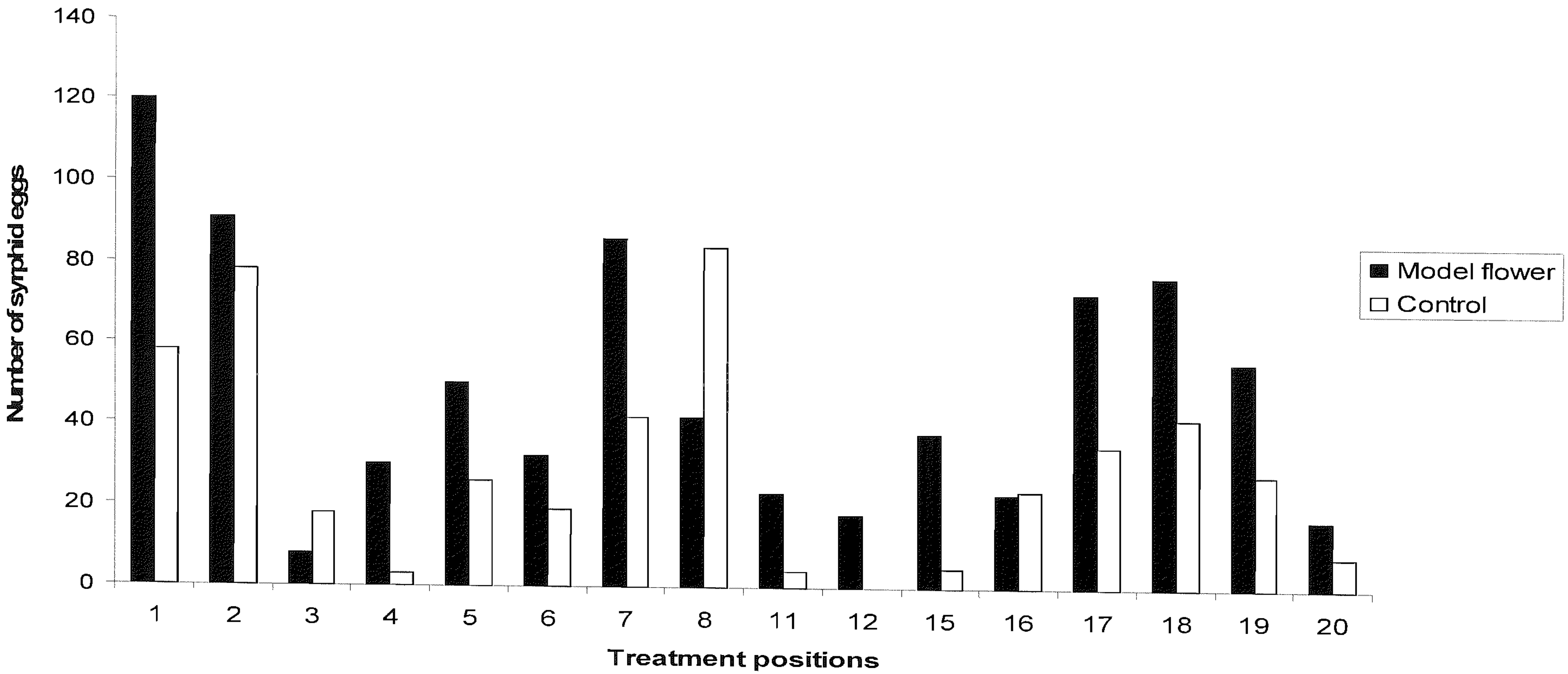


Figure 6.3. Number of syrphids eggs on bait plants at model flower and control positions in 2007 (1 = weed bed; 2 = plant bed; 3 = mature pine; 4 = sycamore; 5 = holly hedge; 6 = cypresses; 7 = privet hedge; 8 = mature yew; 11 = mature pine; 12 = mature horse chestnut; 15 = giant sequoia; 16 = mature beech tree; 17 = laurel hedge; 18 = laurel hedge; 19 = cypress; 20 = spruce. Positions 9, 10, 13 and 14 were excluded due to disruptions in the second collection period.

6.4. Discussion

It would have been preferable if the model flower used in this work could have been tested in the margins of the cereal fields where the preliminary work was carried out and on a much larger scale and with more repetition. It would also have been preferable to have started the experiment earlier in the year and to have increased the repetition. This was not possible, partly because of very poor weather conditions in July 2007 and partly because of time constraints.

However, the results of this pilot experiment, with overall more oviposition found near model flowers than at control positions, do suggest that the presence of model flowers with the features identified as most attractive from the work described in previous chapters, enhance syrphid oviposition in their vicinity.

The results also suggest that there was a decline in the gravid female population during the course of the work; at all positions fewer eggs were laid during the second than during the first experimental period. Although no trapping was carried out in 2007, this suggests that the pattern of occurrence of gravid females, with peak occurrences in early August, was followed by a decline as identified by a number of workers (e.g. Rotheray, 1980; Sutherland, 1998; Gilbert, 2005) (see Appendix). This same pattern was found in previous years and may be connected with the gradual decline in syrphid populations associated with the change in environmental conditions and the migratory strategies of *E. balteatus* (Svensson & Janzon (1984).

Had the experiment been carried out in the margins of cereal fields, the amount of variation between the different positions at which model flowers and controls were placed would be expected to be much less. Although there might be natural flowers or hedges in field margins, as in some of the positions used in this experiment, the Boldrewood area as a whole was much more shaded and variable than a farm environment, with the majority of positions under trees. As each position was used consecutively as both a control and model flower position, the possibility that variations in oviposition resulting from environmental differences between positions affected the results was reduced to a minimum. However, the complexity of the site and the interacting effects of landscape context and habitat quality made interpretation of the results more difficult. It is therefore suggested that in further experiments where oviposition near model flowers and controls is to be compared, then experiments should be carried out in a much less complex environment.

Trees provide shelter, overwintering sites and food resources, which has a positive effect on species diversity and the development of syrphid populations (Salveter, 1998). It might therefore have been expected that the species composition of the population of gravid females, as reflected in the species composition of the eggs laid, would be more diverse from that found in a farm environment. In fact almost all eggs, on bait plants in flower beds, under trees or by hedgerows, were identified as being laid by *E. balteatus*. This is perhaps not surprising. Agricultural landscapes near woodland have been associated with significantly higher numbers of *E. balteatus* in and around farm fields (Marshall & West, 2007). This also suggests that in orchards, where aphid pests can cause economic damage to flowers, fruitlets or fruits directly (Solomon *et al.,* 2000; Rossi *et al.,* 2006), model flowers may be of great value in attracting gravid *E. balteatus*. However, model flowers will be of little value if the spraying regime common in commercial orchards is in use. Knowledge of the phenology of *E. balteatus* may be one solution in determining spray timings and regimes.

E. balteatus also demonstrates a very positive habitat association with hedgerows (Sutherland *et al.,* 1999), presumably in response to aphid resources and shelter. Hoverflies generally are known to use hedgerows as movement corridors between feeding and oviposition sites. The importance of hedgerows in maintaining hoverfly populations has been emphasised by a number of workers (e.g. Janzen, 1967; Kevan & Baker, 1983; Sutherland *et al.,* 1999). Janzen (1967), for example, noted a reduction in predator populations in areas where hedgerows had been removed to create larger fields. Syrphids may accumulate in the lea of the hedge (Lewis, 1969a), which offers the best protection from wind movements.

Except for the plant beds, all positions in this experiment were distant from flowering plants. Although immature hoverflies depend on pollen and nectar for reproductive success (e.g. Schneider, 1948; Salveter, 1998) and therefore require flowers as sources of food, it was found during this project that the amount of oviposition near model flowers was not affected by the presence or absence of food (see Chapter Three). The fact that in this experiment at nearly all positions more eggs were found on bait plants associated with model flowers, which contained no food resources, reinforced these findings. However, it seems likely that the presence of natural flowers enhanced the effect of the models as more eggs were found at the two flower bed positions than at any of the others. This agrees with the work of Schneider (2006) who suggested that syrphids prefer areas with flowers for oviposition and that landscapes without floral resources may hamper their ecological and economical efficiency. It seems likely that the visual stimulus of flowering plants enhanced the stimulus provided by the model flowers alone to attract more gravid females. It is not known whether any of these females used the natural flowers as a food resource, but as more eggs were found by model flowers than by controls, even in the flower beds, it may well be the case that a combination of model and natural flowers would be most effective for enhancing oviposition in crops.

In designing the model used in this experiment, some floral characteristics (e.g. morphology) were not investigated at all and for those that were investigated it was only possible to test a few variations of a particular characteristic. It would also be useful to look at the effects of using multiples of model flowers compared to single flowers.

Further work is needed to continue to find the optimum model flower and the optimum way of using it. However the results do suggest strongly that the use of model flowers does increase syrphid oviposition by *E. balteatus* at least in their vicinity and therefore is of potential use in enhancing biological control of aphids by syrphid larvae.

CHAPTER 7

GENERAL DISCUSSION

The aim of this project was to investigate the effects of standardised model flowers on oviposition in their vicinity by aphidophagous hoverflies. The question of whether the presence of flowers near a crop increases hoverfly oviposition near at hand remains controversial and the amount of variation associated with testing this using real flowers, adds to the difficulty of producing a definitive answer. Therefore, in order to minimise the variation associated with the use of natural occurring flowers, simple standardised model flowers, that could be exactly replicated, were used instead. These were put in field margins close to winter wheat crops and natural flowers near the models were removed. It was decided that the important attributes that the model should have were high visual impact, as visual stimuli are very important in flower recognition and choice by hoverflies (e.g. Kevan & Baker, 1983) and food resources, as hoverflies are flower feeders. The decision to use fluorescent yellow painted flowerpot trays as the 'flowers' was based on their success, when filled with water, in trapping hoverflies in the field (see Appendix), where they were seen to contain food rewards. The visual impact of the models was intensified by setting them out in groups of three and presenting them on stakes at different heights. Honey and pollen were added to the trays and oviposition levels by flowers and controls were assessed using standardised bait plants infested with aphids. No aphids were found in the crop itself, so another source of possible variation was eliminated.

Chapter two describes the testing of this model. In 2002, when the testing began, the numbers of hoverflies including gravid females (See Table 1. Appendix), were the lowest of all the years of this project. Despite low levels of oviposition overall, it was found that more eggs were laid on bait plants near model flowers than at control positions with no flowers. Although it cannot be assumed that the same results would have been seen if it had been possible to standardise real flowers to the same extent, and use them instead of models, it provides strong supporting evidence that adding flowers to a crop environment is likely to increase hoverfly oviposition locally. At this time, it was not known whether or not the attraction to the yellow model flowers might increase if a different yellow paint was used. This was explored in Chapter Three.

From a follow up experiment in 2002 and 2003, another year when number of hoverflies were low (see Appendix), by comparing the relative importance of the model's attributes (colour, honey and pollen) it was found that more eggs were laid near yellow than near unpainted models, and that the presence or absence of pollen and/or honey made no difference to the numbers of egg laid on the bait plants, even when the visual stimulus provided by a bright 'yellow' flower was absent. This was an unexpected result as it had been assumed that most visits to flowers by hoverflies would be made because they were hungry and that in the absence of food, they would fly away and search for it elsewhere. Subsequent laboratory work found that for gravid *E. balteatus* flies which had been starved for 24 h laid as many eggs, and landed on yellow targets no more often, than flies which before the experiment had been given uninterrupted access to food. This suggested that, for gravid females of this species at least, yellow targets are attractive, and ovipositional stimuli are responded to, regardless of their hunger state. However, poplar pollen and honey from unknown sources were used as food rewards in both field and laboratory experiments. Most of the eggs collected during this project (and most of the hoverflies trapped) were *E. balteatus,* and as discussed (Chapter 2), these foods are unlikely to be optimal for this species. It is possible that the use of different food resources might have made the traps more attractive. To clarify this point it would be useful to carry out further lab and field experiments using food rewards from plant species known to be attractive to *E balteatus* in particular.

A practical point is that if yellow targets alone could be used to attract gravid hoverflies to the crop. This would potentially be a very cheap and simple way of enhancing the biological control of aphids in the crop. From a farmer's point of view, plain yellow targets without food resources require little labour and are easy to maintain.

During the course of this project, oviposition levels were only investigated near targets sited in the field margins. Although significant differences in the numbers of eggs laid between treatments were found at a distance of 10m from the targets, it was not known how far this effect extended. Model flowers may be of more value if placed both in the field margins and in the crop. The best distance to leave between targets and their effectiveness in attracting gravid syrphids to all areas of the crop still needs to be assessed.

A related area requiring investigation concerns the question of where the hoverflies that were attracted to the targets actually came from. It is possible that even targets in the field margins only concentrate populations of hoverflies that are already in the vicinity and do not attract them from outside the crop. Given the extreme mobility of hoverflies (e.g. Schneider, 1966; Svensson & Janzon, 1984; Cowgill, 1991) this seems unlikely. However, it is possible that local clusters of hoverflies were formed near the targets used in this project, leading to their redistribution within the field and possibly depleting areas of the field distant from the targets. If gravid females were attracted away from the field centre (see Laubertie *et al.,* 2006), where they play an important role in natural pest control, this could actually lead to a drop in biological control of aphids rather than an enhancement of it. Time was not available to investigate this during the course of this project but further work using mark and recapture techniques to track the movements of gravid hoverflies might help to elucidate this.

This work only looked at gravid females. In a much wider context, the absence of food resources might be a limiting factor, as pollen is needed by immature adults so that they become sexually mature. Further work using model flowers and natural flowers would be required to confirm this.

The remainder of the project focused on improving the model to make it as attractive as possible. Of the flower attributes (colour, pollen, nectar) used here, colour appeared to be of paramount importance in eliciting the response that was seen and it was decided not to add food to any further models. Different aspects of the model flower such as colour (Chapter Three), the effects of adding aphid and plant-derived volatiles (Chapter Four) and size, height and pattern preferences of gravid female hoverflies (Chapter five) were explored. Finally, a model flower with 'optimum' characteristics was tested in the grounds of the University of Southampton (Chapter Six).

It was established (Chapter Three) that ultraviolet reflecting fluorescent yellow was more attractive to *E. balteatus* and to gravid syrphids generally, than non-fluorescent yellows or fluorescent yellow trays without the ultraviolet component. However, *E. balteatus* and *E. corollae* responded differently to the two ultraviolet reflecting trays. Such differences could be the result of genetic variation (Sadeghi & Gilbert, 2000), which may be a mechanism for resource partitioning and the avoidance of competition for resources (Haslett, 1989a). However, different hoverfly species may show preferential attraction to different coloured flowers (Colley & Luna, 2000). Although this work did not look at the effect of other colours on behaviour, the yellow paint used was accurately defined by spectral reflectance curves to match those of real flowers that are known to attract *E. balteatus* and *E. corollae* (Chambers & Adams, 1986: Pike *et al.*, 1991). However, other fluorescent ultraviolet reflecting colours may be as attractive, but these were not investigated. Older *E. balteatus* may show a pronounced response to green and yellow/greens as they age and it would be worth investigating oviposition responses to these colours in future trials. Another idea would be to use plant 'tags' as visual stimulants in the hope that these might attract gravid syrphids. The idea is that the yellow upper surface (possibly coated with wax) would act as a visual cue. The underside of the 'leaf' could be coloured green and impregnated with honeydew to stimulate oviposition.

Investigations were carried out to find out whether an aphid-derived volatile, nepetalactone and a plant-derived volatile, *cis*-jasmone enhanced the design of the model flower (Chapter Four). Information on the effects of nepetalactone on hoverflies was extremely limited (e.g. Sutherland, 1998), but there is some evidence (e.g. Powell & Glinwood, 2003; Wadhams *et al.,* 2004; Birkett & Pickett, 2004) to suggest that the pheromone may enhance parasitoid activity. This work demonstrated that nepetalactone, on its own, in different concentrations, or in conjunction with model flowers did not enhance syrphid oviposition on nearby bait plants or further into the crop. Release of the pheromone by female aphid migrants in the autumn may indicate a reduction in food supply for aphidophagous syrphid larvae. Indeed, nepetalactone appeared to be an oviposition deterrent, and not an attractant as noted by several workers (e.g. Hardie *et al,* 1994; Lilley *et al.,* 1994; Powell & Glinwood, 1998) in parasitoids. Although Sutherland (1998) recorded strong electrophysiological activity to nepetalactone in *E .balteatus,* little is known about the receptors responsible for the apparent repellent response (Peterson & Coats, 2001). If nepetalactone is to be used in the integrated control of crop pests, then any decision on its use would have to consider the possibility that it might diminish syrphid activity in the crop.

The role of *cis*-jasmone in enhancing the oviposition behaviour of parasitoids has been evaluated (e.g. Powell *et al.*, 1991; Pickett *et al.,* 1992; Hardie *et al.*, 1994; Lilley *et al.*, 1994), but no studies have been undertaken to assess its efficacy on aphidophagous syrphids. In 2004, there was a trend for oviposition to be enhanced on bait plants near *cis*-jasmone, although a follow up experiment the following year produced no evidence to suggest that gravid females were attracted to yellow water trays near the volatile. Flaws in the experimental design meant that rainy weather affected dispersal of the volatile. There is also evidence to suggest that the effects of *cis*-jasmone are long-lived (Bruce *et al.,* 2003) and it is possible that plants within the vicinity of *cis*-jasmone acted as a sink for the volatile, which affected responses when trap positions were changed. The importance of designing an experiment that is unaffected by environmental conditions and the persistent effect of *cis*-jasmone was highlighted by this. It was not possible to come to any conclusions on the possible usefulness of *cis*-jasmone as an attractant for gravid hoverflies as time did not permit further work to be carried out. However, it certainly seems likely that flower feeders such as hoverflies would be attracted by flower volatiles and there is evidence for this. Laubertie *et al.* (2006), for example, found that the addition of rose water to yellow water traps significantly increased the number of hoverflies caught. Although *cis*-jasmone is insoluble in water, alternative formulations may offer opportunities for further investigation.

The work described in Chapter Five used yellow water trap data to examine preference for height, size and pattern of model flower targets. As it was gravid females that were being targeted, and it could not be assumed that their behaviour and preferences would be the same as immature females and males, trapped females were dissected to see if they were gravid. In most cases, gravid females exhibited the same preferences as did all adults grouped together. However, this was not the case for size preference where gravid females preferred the large traps, while adults as a whole appeared to prefer the small ones. This may be because small flowers represent better food rewards which are possibly less important to gravid females. However all the trays used were bigger and brighter than natural flowers that would be encountered by a hoverfly in the UK, and it cannot be assumed that the response to them would be the same. This preference for small traps was not maintained in the last part of the experiment when three small, two medium and one large trap were presented together in a set. In this arrangement the large traps were most attractive to all adults combined as well as to gravid females. This may have been a consequence of a change in behaviour associated with increasing age.

For height, size and pattern experiments treatments were presented in groups and in isolation. Preferences tended to be less clearly defined when traps were presented singly. This was expected as no choice was offered. However, the preferred treatments were the same when treatments were isolated from each other as when they were singly placed. It was important to know this because if yellow model flower targets are to be used to enhance hoverfly oviposition in a crop, the model used would presumably be an optimum one and the element of choice would be removed.

Overall it was established that traps at a height of 30 cm, (possibly related to favourite oviposition levels) the largest size (25 cm diameter) used and a target with no pattern were the preferred options. These features were incorporated into an 'optimum' model which was tested in the grounds of Southampton University (Chapter Six). Volatiles were left out of the model because of the lack of any evidence that they would be effective. Model flowers were without food resources as it was established (Chapter Two) that oviposition occurred in their absence.

Overall, significantly more eggs were found on bait plants near model flowers than on bait plants near controls. It was also found that more eggs, though the difference was not significant, were laid in positions where model and natural flowers were close together. Presumably this was because of the increased visual stimulus produced. Natural flowers are important as a source of food for hoverflies and this suggests that if natural and model flowers were combined in e.g. a field margin, the effect of the model might be enhanced as well as food and shelter being provided for hoverflies and other natural enemies of pest species.

Despite the complexity of the site, and the short time period over which the experiment was carried out and the fact that this was a small-scale experiment, the model flower 'worked'. However further refining of the model and further testing in a crop environment is important.

During years 2001-5 yellow water trap data were collected to monitor local syrphid populations during the period of this project (Appendix). This phenology study was useful in that it provided information concerning the occurrence of gravid females of hoverfly species important in the biological control of aphids such as *E. balteatus*. This species was the most abundant throughout the project with *E. corollae* also well represented. This suggests that targeting *E. balteatus,* the most important hoverfly for the control of aphids on agricultural land (Chambers *et al*., 1986) where there are different preferences between hoverfly species for e.g. colour, is a sensible option.

As was found by Owen (1991), there were huge fluctuations in numbers of hoverflies between years. In 2001 and 2005 numbers trapped were two orders of magnitude higher than in the years in between. Unfortunately these

(2002-4) were the main years in which experiments that involved measuring oviposition were carried out. These figures emphasise the fact that pest control that relies on biological agents is never going to be entirely predictable. However in all years, no matter what the overall population levels, the peak period for gravid females was consistently at the end of July or the beginning of August. This suggests that there is potential in using targets in crops that mature later in the year and are susceptible to aphid attack.

The work has consistently produced evidence that model flowers do attract gravid hoverflies and that their presence leads to increased syrphid oviposition in their vicinity. Importantly, the work has shown that a visual cue and an aphid stimulus elicit an oviposition response whether or not food resources are available. A model based on optimum height, size, pattern and colour was tested in the field and proved effective. This could be of great interest to farmers and growers. Model flowers may attract hoverflies to fruit orchards, nursery gardens, horticultural industries and crop fields, where aphids can cause economic damage to herbs, flowers and ground crops such as spinach, cabbage and broccoli throughout the growing season.

However there still remain many questions to answer. Apart from those addressed earlier in this discussion, areas in which further research could be carried out include:

1. Many features of model flowers e.g. morphology, were not considered in the design of the model flower and would be worth investigating. Another area that could be explored would be to look at the angle at which model flowers are presented. In female Hessian flies, for example, Harris *et al.* (1993) demonstrated that vertical shapes were more attractive than shapes presented horizontally. Surface texture and other tactile cues may also improve the design of the model flower. It is also possible that the motion of floral parts may enhance visibility. This could be accomplished by placing model

flowers on flexible ‘stems’. Further work on the effects of adding volatiles to the model are also needed.

2. How far apart do model flowers need to be, where should they be sited and should they be presented singly or in groups?

3. This study did not investigate the impact of model flowers on the dynamics of aphid populations in the crop and therefore the economic effects of using this method to enhance oviposition by aphidophagous hoverflies still needs to be assessed.

Appendix

Analysis of yellow water trap data from 2001-2005.

The data (from yellow water traps) included here was collected during the course of this project, from a large garden (2001 - 2002) and from the farm where the main experiments were carried out (2003 - 2005).

Garden site

The garden was a 2-acre site at Carriers Crossing, Salisbury, Wiltshire (OS Grid ref. SU 338 125) (Fig.1) which provided habitats abundant in floral resources, the main species being *Senecio monroi* (ragwort), *Campanulla* spp. (bariegata), *Sedam kamtschaticum* (stonecrop), *Lamium album* (white dead nettle), *Papaver orientale* (poppy) and *Lavandula angustifolia* (lavender). Other plant species included *Vicia faba* (broad bean), *Phaseolus coccineus* (runner bean), *Peucedanum* graveolens (dill), *Mentha spicata* (mint), *Ocimum basilicum* (basil), *Salvia officinalis* (sage), *Thymus vulgaris* (thyme), *Festuca elatior, F. ovina* (meadow fescues) and *Anthoxanthum odoratum, Lolium perenne* (grasses). The site also had an assortment of *Fagus sylvatica* (beech), *Alnus glutinosa* (Alder) and *Corylus avellana* (hazel) species.

To the north, east and west of the site, water meadows were managed by Country Stewardship. To the south, mature maple lined the boundary fence. Behind this, a large field was under winter wheat. The whole area was designated a Special Site of Scientific Interest.

Field sites 2003 -2005

In 2003, 2004 and 2005, syrphids were collected from four winter wheat fields (between 14 & 16-ha) (harvested 16th August) located at Uggford Farm, Wilton, Salisbury, Wiltshire, UK. Field boundaries for each site consisted primarily of hawthorn hedgerows (*Crataegus monogyna*), hazel (*Corylus avellana*), beech

(*Fagus sylvatica*) and alder (*Alnus glutinosa*) interspersed with common chalkland grasses such as cocksfoot (*Dactylis glomerata*) and broome (*Bromus erectus*). In the open spaces, the main flowering species were hogweed (*Heracleum sphondylium*), white dead nettle (*L. album*), hedge mustard (*Sisymbrium officinale*), field scabious (*Knautia arvensis*) and sheepsbit scabious (*Jasione* montana) and red and white clovers *(Trifolium pratense, T. repens*). A farm track ran parallel to one side of each field.

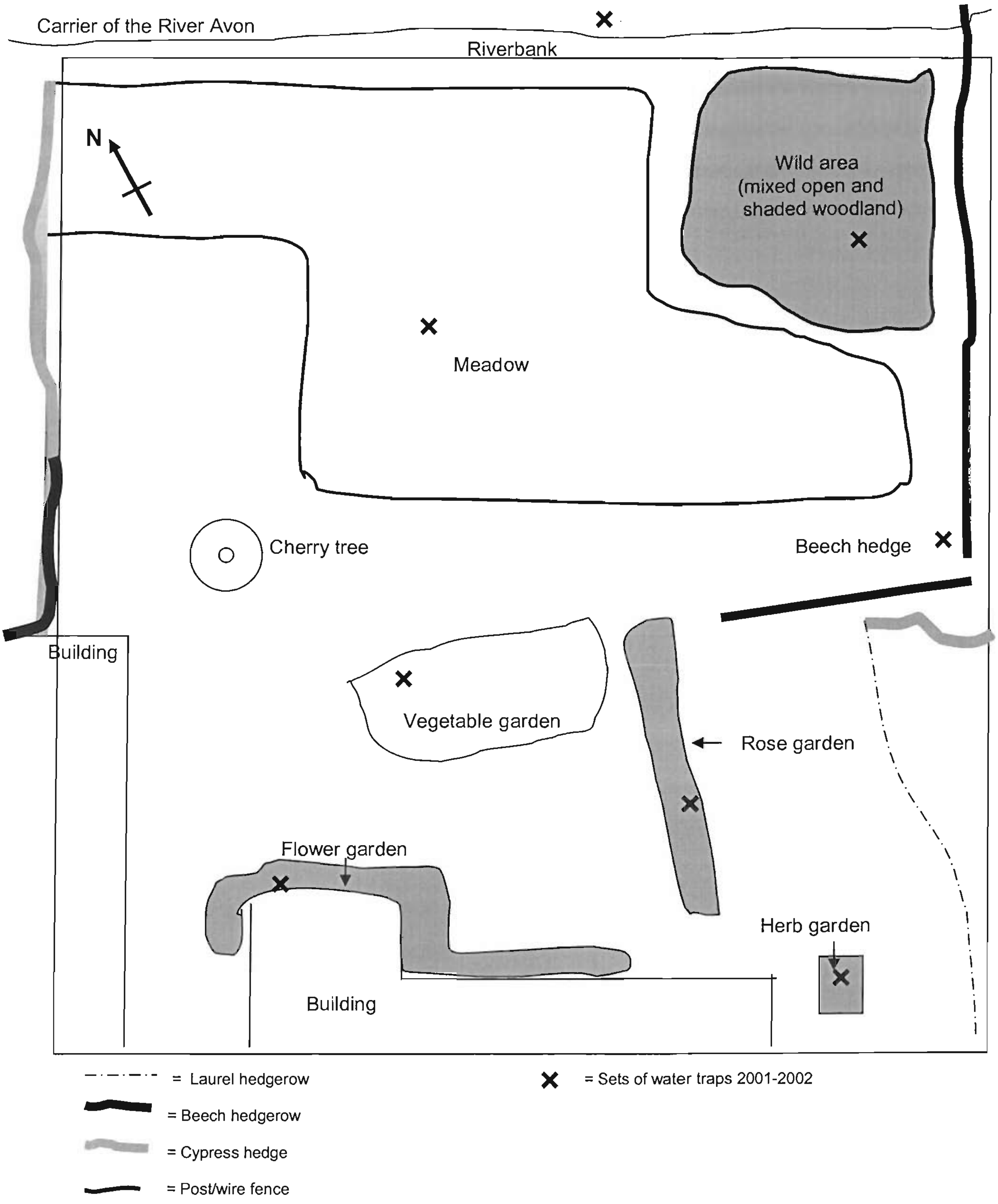


Figure 1. Sketch map of the site at Carriers Crossing, Salisbury, Wiltshire (not to scale).

The treatments

In each year, the type of trap used was a 19 cm diameter x 2cm deep flowerpot tray pre-sprayed with fluorescent yellow enamel paint. (see Chapter 2, Methods section for details of trap preparation). Traps contained tap water and a few drops of ordinary household detergent (this enabled the insects to drown quickly). Traps were emptied, cleaned and reset at intervals (see below for details).

2001/2

Traps were treated with Glocote 1263 (Goo-Var Ltd., high visibility). Sets of five traps (total 40) were placed on the ground in a straight line with 45 cm between in eight different parts of the garden (see Fig.1). The minimum distance between sets of traps was 25 metres. Traps were left for seven days and then emptied. In 2001, collections of hoverflies were made from 8 July to 15 September and in 2002, from 26 May to 25 August.

2003-5

In each of the years 2003 to 2005, 15 traps were treated with Plasti-Kote 142S fluorescent yellow enamel paint. Single traps were placed on the ground at 25 metre intervals in the field margins of three winter wheat fields (five in each field). Traps were left out for 48h before emptying. Collections of hoverflies were made from 8 July to 11 August (2003), 21 May to 27 August (2004) and from 9 July to 11 August (2005).

2.2.4. Identification

Syrphid catches were transferred to 70% alcohol in labelled plastic vials and then identified to species and sex using keys from Stubbs & Falk (2000). Female syrphids were dissected, and any eggs counted. Flies were placed on a glass slide and the head and thorax removed with a scalpel under a dissecting microscope (x60). The ventral surface of the abdomen was then freed from the underlying membranes (Gilbert, 1993) using a curved pin. A drop of water was added to prevent drying before exuding the abdominal contents with forceps.

Meteorological data

Meteorological station weather data for Wiltshire was obtained for the years 2001 – 2005 (Met. Office: 2001 – 2005).

Analysis

As the numbers of traps, and collection periods differed between years, data were analysed as the number of aphidophagous syrphids and gravid females caught per trap per day. Only data from traps emptied from 12 July to 11 August were included in the analysis since very few syrphids, and only three gravid females, were trapped before or after these dates.

Results

Numbers and species of syrphids

Table 1 shows the number of all adult aphidophagous syrphids and the number and percentages of gravid females caught per trap per day over the period of analysis in each year and Figures 2 a-d show the actual numbers of males, females and gravid females counted on for each collection period. The main species trapped was *E. balteatus* (79% of all adults and 72% of all gravid females). The next most represented species was *E. corollae* (8% of all adults and 13% of gravid females). This general pattern applied to each year over which collecting took place (Fig 2 a – d). Other species trapped included *Syrphus ribesii, S. vitripennis, Scaeva pyrastri, Platycheirus* species, *Sphaerophoria scripta, Chrysotoxum bicinctum* (L.) and *Xanthandrus comtus* (Harris) species. Overall, more females were caught than males (Figs 2. a and c).

There were very big fluctuations between years in numbers of syrphids trapped (Table 1) Total numbers of gravid females trapped in individual years varied from nine in 2003 (0.06 per trap per day) nine in 2004 (0.06) and 14 in 2002 (0.01) to

280 (1.87) in 2005 and 608 (0.43) in 2001 (Fig. 2 b and d). The same pattern was seen for all adults combined (Fig. 2 a and c).

Percentages of gravid females in each collection varied, but the highest numbers of gravids, and for adult syrphids overall, were always found in trap catches emptied at the end of July or the beginning of August.

2.3.2. Weather conditions

July 2001 was a dull month with near normal rainfall and temperature. August temperatures approached 32°C with most areas receiving more sunshine than average. Conditions in 2002 were wet throughout July and early August with higher than average rainfall. In July and August 2003 temperatures were above average and conditions were very warm and sunny across all parts of the UK. In July 2004, Wiltshire and the UK generally, received above average rainfall. August was a very wet month and mean temperatures were only one or two degrees higher than average? In 2005, rainfall varied across the south in July and August, although mean temperatures were above average.

Year	**12 July**			**21 July**			**29 July**			**6 August**			**13 August**		
	All	Gravid	%	All	Gravid	%	All	Gravid	%	All	Gravid	%	All	Gravid	%
2001	0.400	0.021	5.2	2.200	0.329	4.9	13.411	0.704	5.2	5.107	0.990	19.4	0.736	0.011	17.5
2002	0.050	0.007	14.0	0.043	0.011	25.6	0.200	0.018	9.0	0.082	0.004	4.9	0.096	0.011	11.5
	12 July			21 July			29 July			6 August			13 August		
	All	Gravid	%	All	Gravid	%l	All	Gravid	%	All	Gravid	%	All	Gravid	%
2003	0.867	0.033	3.8	0.433	0.000	0.0	0.700	0.133	19.0	0.200	0.067	33.5	0.233	0.067	28.8
2004	0.133	0.067	50.0	0.133	0.067	50.0	0.233	0.033	14.2	0.400	0.100	25.0	0.333	0.033	9.1
2005	1.600	0.333	20.8	13.000	0.200	15.4	120.800	6.633	5.5	16.670	1.433	8.6	12.467	0.733	5.9

Table 1. Numbers of all aphidophagous syrphid and gravid females caught per day per trap from traps emptied between 12 July and 11 August in each year. Percentages refer to the percentage of gravid females in the catch. Data for 2001 and 2 were derived from the combined contents of 40 traps, arranged in sets of five, and data for 2003-5 were derived from 15 traps set out singly.

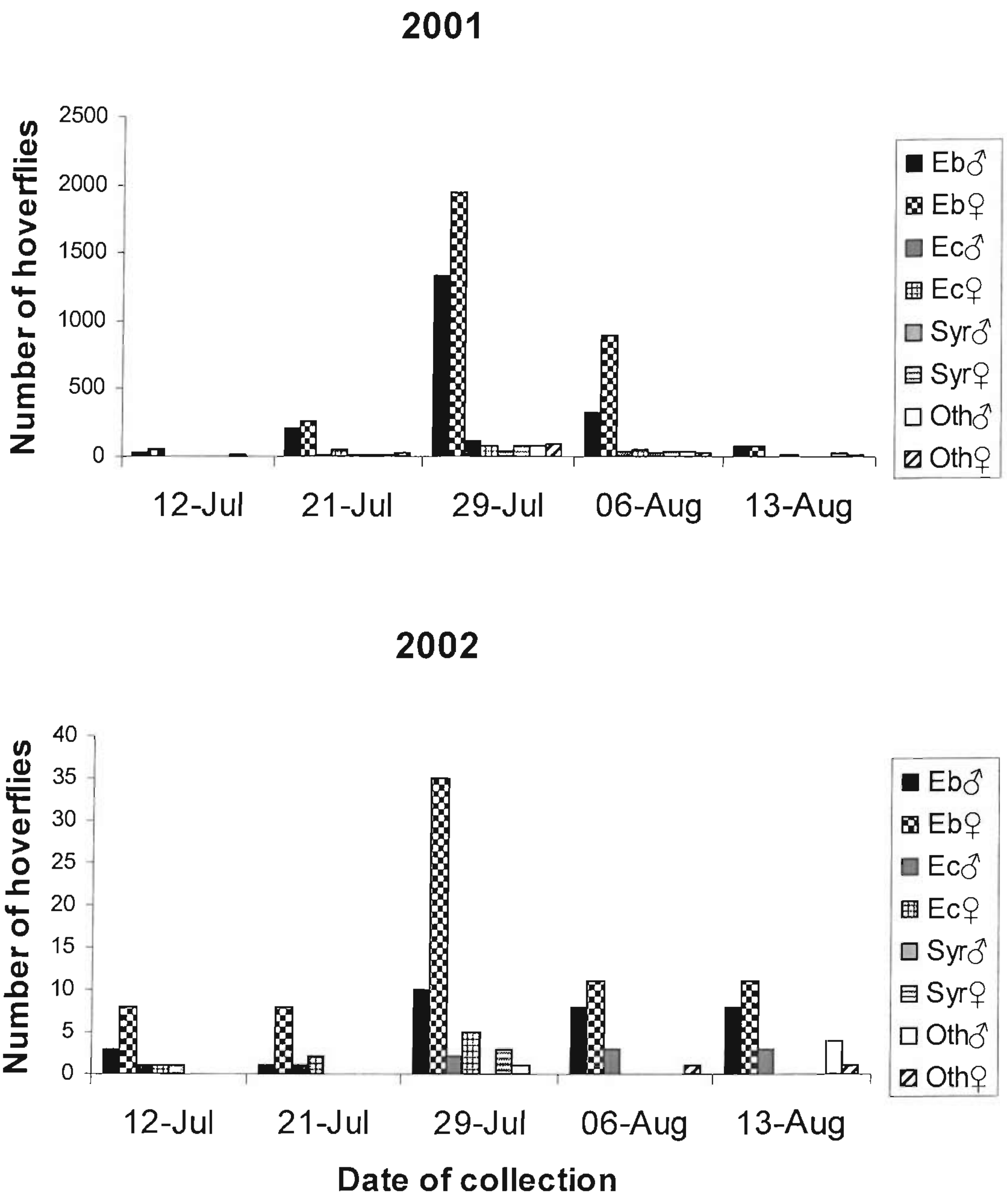


Figure 2a. Total numbers of male and female aphidophagous syrphids caught in traps in 2001 and 2002. Each bar represents the combined contents of 40 yellow water traps over a collecting period of seven days.

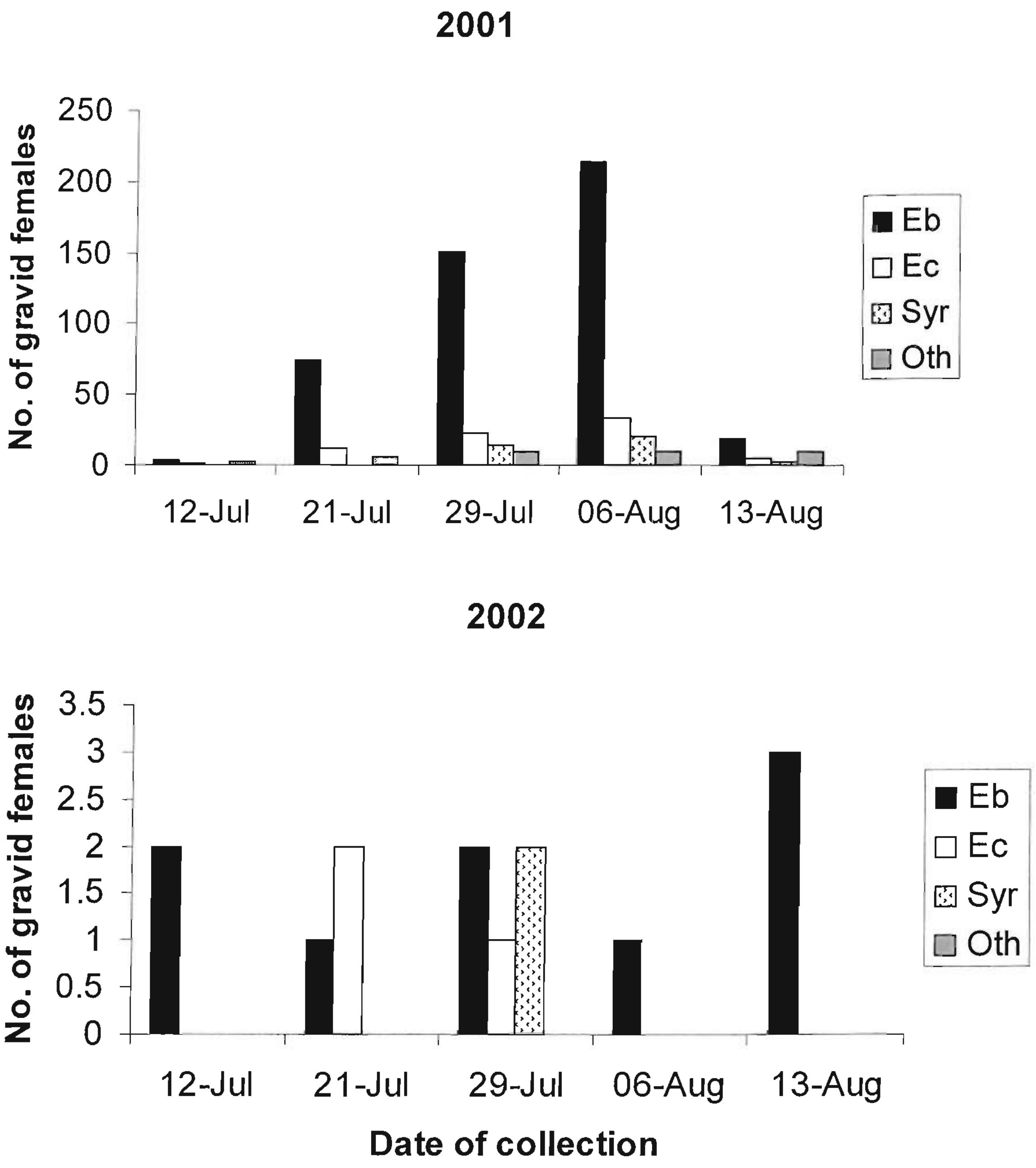


Figure 2.b. Numbers of gravid female aphidophagous syrphids trapped in 2001 and 2002. Each bar represents the combined contents of 40 yellow water traps over a collecting period of seven days.

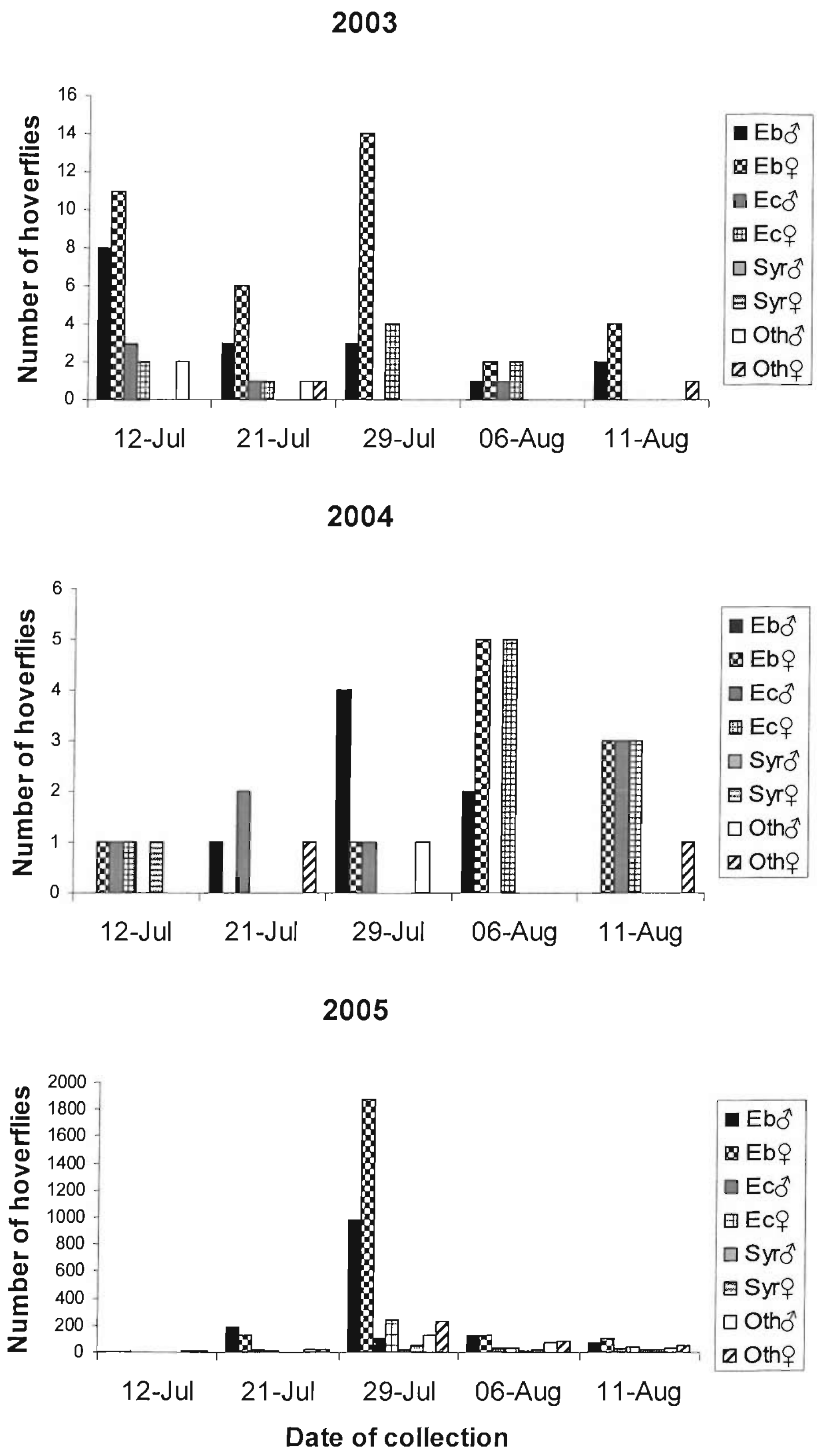


Figure 2.c. Total numbers of male and female aphidophagous syrphids caught in traps in 2003-2005. Each bar represents the combined contents of 15 yellow water traps over a collecting period of two days.

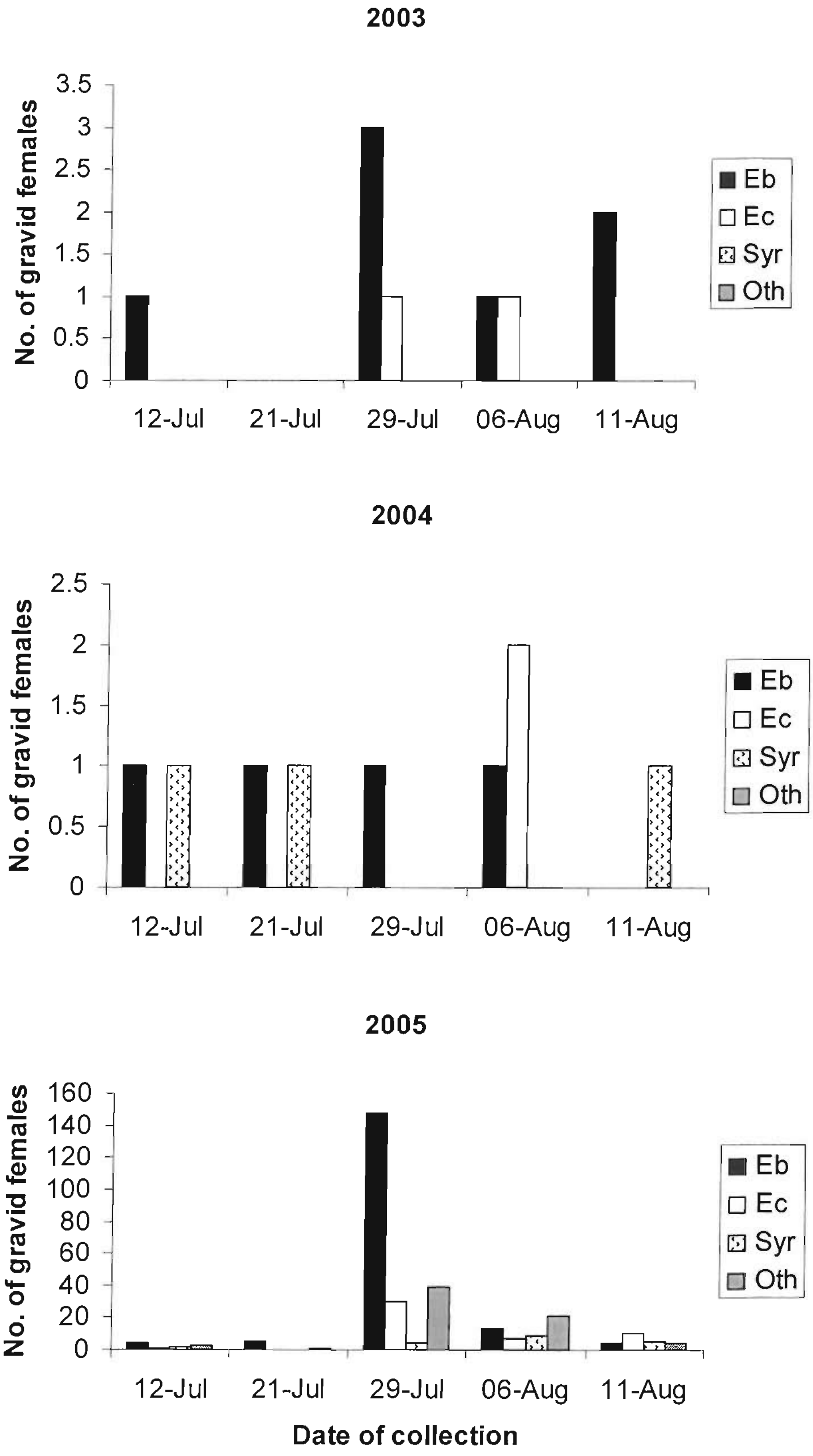


Figure 2.d. Numbers of gravid female aphidophagous syrphids trapped between 2003 and 2005. Each bar represents the combined contents of 15 yellow water traps over a collecting period of two days.

Conclusions

In each year, a similar pattern was seen in that *E. balteatus* was overwhelmingly the most abundant gravid species throughout the trapping period. This suggests that tailoring attractants to this species in particular where there are inter-species preferences in terms of colour or other factors such as height or size of targets is likely to achieve the best overall results in terms of enhanced biocontrol of aphids.

From this work, and the work of others described above, potentially, the most effective period to put out model flower targets to attract gravid females to enhance biocontrol of aphids by syrphid larvae would be in late July and early August when peak occurrences are seen. This is too late to coincide with the period when the main cereal crops in U.K. are susceptible to aphids and crops targeted would need to be those that mature later in the season. The effectiveness of doing this would also be dependent on weather conditions remaining suitable for the successful hatching and maturation of the larvae. Exploitation of aphid colonies before host-plant quality declines and weather conditions change is important if biological control is to be achieved (van Emden *et al.,* 1969).

However as there is much evidence that syrphid larvae are effective predators of aphids in cereal crops in the U.K., with *E. balteatus* the most dominant predator in aphid colonies on wheat in midsummer (Sadeghi & Gilbert, 2000), targeting gravid females from early summer onwards for crops where aphids may be a problem during this period would be recommended, despite the fact that few or none were trapped at the relevant times in this project.

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