

AN ABSTRACT OF THE DISSERTATION OF

Mario D. Ambrosino for the degree of Doctor of Philosophy in Entomology presented on March 13, 2006.

Title: ENHANCING THE PREDATORY POTENTIAL OF HOVERFLIES ON APHIDS IN OREGON BROCCOLI FIELDS WITH FLORAL RESOURCES.

Abstract approved:

Redacted for Privacy

Redacted for Privacy

Four key aspects of the relationship between predatory hoverflies and the aphid pest *Brevicoryne brassicae* L. on broccoli were investigated in the Willamette Valley, Oregon USA: 1) the relationship between aphid density and hoverfly oviposition, 2) the larval voracity of key hoverfly species, 3) the preferences of hoverflies and broccoli pests for candidate insectary plant species, and 4) the role of insectary plantings in enhancing hoverfly oviposition in aphid colonies in broccoli fields.

Hoverfly oviposition at two commercial broccoli field sites increased at aphid densities greater than 50 aphids per plant, but did not peak at the highest aphid densities. A logistic regression model, selected with Akaike's Information Criterion, of the odds of oviposition in relation to aphid density included effects for sampling date and aphid

species (*B. brassicae* and *Myzus persicae* (Sulzer)). The magnitude of the response was similar for *B. brassicae* and *M. persicae*. The oviposition response was greater in the upper part of the plant canopy, and different on individual leaves from that seen on whole plants.

The voracity and development rate of *Scaeva pyrastris* (L.) were greater than those of *Eupeodes fumipennis* (Thomson), and both exceeded *Syrphus opinator* Osten Saken and *Sphaerophoria sulphuripes* (Thomson). Both *E. fumipennis* and *S. opinator* reduced aphid populations to low levels on plants over two weeks, but *E. fumipennis* spent much of the time foraging away from the caged plants.

Alyssum (*Lobularia maritima* (L.) Desv.), coriander (*Coriandrum sativa* L.), buckwheat (*Fagopyrum esculentum* Moench), and phacelia (*Phacelia tanacetifolia* Benth.) were screened for arthropod visitation frequency. The three pest species *Pieris rapae* (L.), *Diabrotica undecimpunctata undecimpunctata* Mannerheim, and *Lygus hesperus* Knight visited phacelia the most frequently, while the hoverfly species visited mostly coriander, which was possibly influenced by competition from other foragers.

Hoverfly oviposition was increased near within-field blocks of alyssum in broccoli fields at the end of the season however, hoverflies arriving at the field had pollen in their guts and were oviparous four to five weeks before their eggs were detected in aphid colonies. This late oviposition may have occurred because threshold densities for oviposition were not reached until this stage.

© Copyright by Mario D. Ambrosino

March 13, 2006

All Rights Reserved

ENHANCING THE PREDATORY POTENTIAL OF HOVERFLIES ON APHIDS IN
OREGON BROCCOLI FIELDS WITH FLORAL RESOURCES.

by
Mario D. Ambrosino

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented March 13, 2006
Commencement June 2006

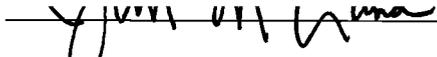
Doctor of Philosophy dissertation of Mario D. Ambrosino presented on March 13, 2006

APPROVED:

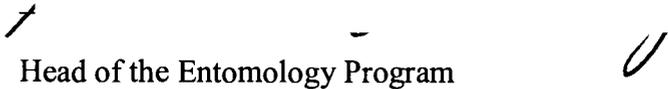
Redacted for Privacy


Major Professor, representing Entomology

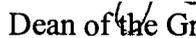
Redacted for Privacy


Co-Major Professor, representing Entomology

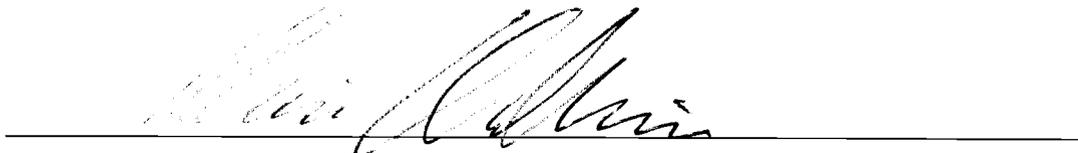
Redacted for Privacy


Head of the Entomology Program

Redacted for Privacy


Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.



Mario D. Ambrosino, Author

ACKNOWLEDGEMENTS

The author wishes to express sincere thanks to his major professors Dr. Paul Jepson and Dr. John Luna for their support and edits. The valuable comments of Dr. Steve Wratten for the planning phase of this project are also greatly appreciated. I would also like to thank the other members of my committee, Dr. Peter McEvoy, Dr. Glenn Fisher, and Dr. Bill Proebsting for their time and assistance with the preliminary examination and other administrative duties.

Thanks are also extended to Dr. Cliff Pereira, Dr. Jennifer Gervais, Dr. Dan Rosenberg, and Dr. Vicente Monleon for their detailed assistance with statistical analyses. Additional advice with statistics and statistical computer programs were provided by Nate Chelgren, Dan Cantlin, Yanli Zhang, Dr. Jon Umble and Dr. Hans Luh.

The field, greenhouse and laboratory assistance of Adam Poole, Amanda Griffith, Lourdes Irwin, and Sarah Cain were crucial for allowing many of these activities to be completed in a timely fashion.

Finally, I would also like to thank many friends, who are too numerous to mention here, for their general support and help.

CONTRIBUTIONS OF AUTHORS

Dr. Paul Jepson and Dr. John Luna assisted with detailed edits to all manuscripts and preliminary planning for the experiments in this project. Dr. Steve Wratten assisted with edits to the third and fourth manuscripts as well as the preliminary planning for this project. Dr. Cliff Pereira performed one of the analyses in the fourth manuscript, and provided edits for that manuscript.

TABLE OF CONTENTS

	<u>Page</u>
GENERAL INTRODUCTION.....	1
OBJECTIVES.....	14
HOVERFLY OVIPOSITION RESPONSE TO APHIDS IN BROCCOLI FIELDS.....	15
Introduction.....	17
Materials and Methods.....	19
Results.....	22
Discussion.....	25
References Cited.....	30
Tables and Figures.....	34
THE VORACITY AND DEVELOPMENT RATES OF FOUR PREDACIOUS HOVERFLY SPECIES (DIPTERA: SYRPHIDAE) FEEDING ON THE CABBAGE APHID, <i>Brevicoryne brassicae</i> L.....	40
Introduction.....	42
Materials and Methods.....	43
Results.....	45
Discussion.....	48
References Cited.....	55
Tables and Figures.....	59
THE RELATIVE FREQUENCIES OF VISITS TO SELECTED INSECTARY PLANTS BY PREDATORY HOVERFLIES (DIPTERA: SYRPHIDAE), AND OTHER BENEFICIAL INSECTS AND HERBIVORES.....	64
Introduction.....	67
Materials and Methods.....	69
Results.....	70
Discussion.....	73
References Cited.....	79
Tables and Figures.....	83
SPATIAL AND TEMPORAL DISTRIBUTION OF PREDATORY HOVERFLIES (DIPTERA: SYRPHIDAE) AND APHIDS (HOMOPTERA: APHIDIDAE) IN A FLOWER-ENHANCED BROCCOLI FIELD.....	87
Introduction.....	89
Materials and Methods.....	91
Results.....	95
Discussion.....	101
References Cited.....	107
Tables and Figures.....	112
OVERALL CONCLUSIONS.....	120
BIBLIOGRAPHY.....	125

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1	Relative percentage of plants with aphids and natural enemies over time.....36
1.2	Mean number of aphids and natural enemies per leaf over time.....37
1.3	Mean number of hoverfly eggs, and relative percentage of leaves or plants with hoverfly eggs in response to aphid intensity per leaf (a), and per plant (b), (with the numeric values included over each category).....38
1.4	Mean number of hoverfly eggs per plant, and relative percentage of plants with hoverfly eggs, per leaf and per plant on leaves and plants with different amounts of either <i>M. persicae</i> or <i>B. brevicoryne</i>39
2.1	Mean numbers (with SE) of <i>B. brassicae</i> on plants in cages with <i>E. fumipennis</i> , <i>S. opinator</i> , or no hoverfly larva.....59
2.2	First laboratory experiment. The daily a) mean larval weight gain, b) mean number of <i>B. brassicae</i> killed and C) cumulative mean number of <i>B. brassicae</i> killed (with standard errors) in enclosures with <i>S. pyrastris</i> , <i>E. fumipennis</i> , or <i>S. opinator</i>60
2.3	Second laboratory experiment. The daily a) mean larval weight gain, b) mean number of <i>B. brassicae</i> killed and C) cumulative mean number of <i>B. brassicae</i> killed (with standard errors) in enclosures with <i>E. fumipennis</i> , <i>S. opinator</i> , or <i>S. sulphuripes</i>61
2.4	Second laboratory experiment. The daily a) mean change in aphid mass, and b) mean cumulative change in aphid mass (with standard errors) in enclosures with <i>E. fumipennis</i> , <i>S. opinator</i> , or <i>S. sulphuripes</i>62
2.5	Second laboratory experiment. The daily a) mean larval weight gain, b) mean number of <i>B. brassicae</i> killed and C) cumulative mean number of <i>B. brassicae</i> killed (with standard errors) in enclosures with <i>E. fumipennis</i> , <i>S. opinator</i> , or these two species competing together in the same enclosure.....63
3.1	Mean number of hoverflies (with SE bars) observed visiting the four flower treatments over all sampling dates at A) the North Site, and B) the South Site. Means within a group of four bars followed by the same letter do not differ ($\alpha = 0.05$) according to the Least Significant Difference test.....85

LIST OF FIGURES (Continued)

<u>Figure</u>		<u>Page</u>
3.2	Mean number of beneficial and pest insects (with SE bars) observed visiting the four flower treatments over all sampling dates at A) the North Site, and B) the South Site. Means within a group of four bars followed by the same letter do not differ ($\alpha = 0.05$) according to the Least Significant Difference test.....	86
4.1	Aerial view of the field with the locations of flower plots and sampling transects.....	114
4.2	The abundance of selected hoverfly species captured in the pan traps.....	115
4.3	The abundance of hoverfly eggs of each type on the broccoli crop plants.....	116
4.4	The proportion of crop plants with cabbage aphids and hoverfly eggs.....	117
4.5	Season-long abundance of hoverfly eggs pooled across species on crop plants at all dates and distances sampled.....	118
4.6	Mean number of hoverfly eggs in the group representing <i>S. sulphuripes</i> and <i>E. fumipennis</i> at each distance class in each field section on the last date that crop plants were sampled.....	119

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.1 Parameter estimates, unconditional standard errors, and odds ratios for variables in the best approximating model to estimate the probability of presence of hoverfly eggs on broccoli plants.....	34
1.2 Distribution of the mean number of aphids, and hoverfly eggs per leaf (with standard errors) among three zones within broccoli plants at both Sites and all dates pooled.....	35
3.1 Factors affecting the selection of different floral resources by hoverflies.....	83
3.2 Relative mean numbers (with standard errors) of all insect groups and species observed visiting flowers over all treatments and sampling dates at each site (units are mean number of individuals/2 min./m ²).....	84
4.1 Predatory hoverfly species present in the broccoli field.....	112
4.2 Mean pollen scores and number of chorionated eggs (with standard errors) for hoverflies captured in yellow pan traps.....	113

ENHANCING THE PREDATORY POTENTIAL OF HOVERFLIES ON APHIDS IN OREGON BROCCOLI FIELDS WITH FLORAL RESOURCES.

GENERAL INTRODUCTION

Conservation biological control entails the management of resources in the environment to enhance the survival, fecundity, longevity and behavior of natural enemies to increase their effectiveness (Landis et al. 2000). The amount of enhancement that is required and the net benefit that can be obtained from these management tactics remains unexplored in many systems.

Conservation biological control had a simple experimental beginning. Van Emden (1963) placed buckets of cut flowers in brassica crops and enhanced parasitoid populations locally. A considerable literature has developed since, which explores the effects of manipulating the crop environment on predator and parasitoid activity. Recent reviews include Gurr et al. (1998), Wratten et al. (1998), and Landis et al. (2000), which describe mechanisms of manipulation that can provide increased shelter for various life stages, alternative hosts and prey, and plant food sources for the adult stages of certain natural enemies. The practice of conservation biological control involves no new natural enemy introductions and focuses upon indigenous species. It needs to be compatible with farming practices to be a component of an IPM system.

Landis et al. (2000) also list five key questions important for implementation: (1) the selection of the most appropriate plant species, (2) the behavioral mechanisms that are influenced by the manipulation, (3) the spatial scale over which the habitat enhancement operates, (4) the potential negative aspects of adding these new plants, such as pest

enhancement, and (5) the degree to which the proposed habitat changes are adopted by land managers. These questions remained unanswered for most cropping systems in North America, including broccoli, which is the focus of this study.

With its relatively rich community of pest arthropods, broccoli is a good candidate for exploring alternative pest management options. Of this pest complex, the cabbage aphid (*Brevicoryne brassicae* L.) and the green peach aphid (*Myzus persicae* Sulzer) present control challenges, partly because of increasing restrictions on the organophosphate and carbamate insecticides that are used to control these phloem-feeding insects.

The enhancement of aphid natural enemy activity represents a potentially viable alternative management strategy for these pests under current broccoli production conditions. The most commonly encountered groups of natural enemies of aphids in these systems include parasitoid wasps, hoverflies (Diptera: Syrphidae), ladybird beetles (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae) and entomopathogenic fungi. Ground-dwelling polyphagous insects and spiders have also been shown to play a role in aphid suppression in other temperate cropping systems.

A small number of projects have investigated the role of natural enemies in local Oregon broccoli systems (McGrath, 2000), as well as in other local brassica crops (McIver, 1984), with varying results. Many species and even whole groups of natural enemies in these systems however, remain uninvestigated. One such group, with potential for contributing to aphid suppression in this system, is that of the hoverflies. Preliminary work in 2000, in local broccoli fields, has shown that several species of predatory hoverflies oviposit within aphid colonies, particularly later in the season. Research in

other locations has demonstrated an ability of hoverflies to be relatively efficient at limiting aphid populations (see review below). Basic information is required on the aphid-limiting potential of indigenous hoverflies, and the degree to which they respond to management and conservation biological control tactics before recommendations can be made about the viability of this type of conservation biological control approach to growers.

Hoverflies as Aphid Predators

Hoverflies have a number of characteristics that make them candidates as important natural enemies of aphids. These include: prey specificity, high mobility to exploit resources and distribute eggs over large areas (Schneider 1948, Chambers 1988, 1991), the ability, in some agroecosystems, to locate and respond to aphid colonies sooner than other aphidophagous predators, including coccinellids (Horn 1981; Dixon 2000), the habit of ovipositing close to aphid colonies (Dixon 1959; Chambers 1988; Dixon 2000), an ability to oviposit at low aphid densities (Chandler 1968b; Chambers 1991; Sadeghi and Gilbert 2000b), high voracity (Kan 1989; Debaraj and Singh 1998), an ability to eat many more aphids than the minimal number required for development (Scott and Barlow 1984, 1990), shorter larval handling times when aphid prey are abundant (Rotheray 1983; Rotheray and Martinat 1984; Barlow and Whittingham 1984), less disruption of aphid colonies than that exhibited by other predators, resulting in slower production of aphid migrants (Michaud and Belliure 2001), and short meal durations and high reproductive rates, allowing them to efficiently exploit short-lived aphid colonies (Ankersmit et al. 1986).

The effectiveness of predatory hoverflies in limiting aphid population increase has been quantified in different systems with a number of approaches, ranging from field work supported by modeling (Tamaki et al. 1974; Raworth 1984; Winder et al. 1994; Wilson et al. in press) to field exclusion studies (Pollard 1969; Tamaki 1973; Entwistle and Dixon 1989; Chambers 1991; Nunnenmacher et al. 1996), open field studies (Tamaki 1974; Neuenschwander et al. 1975; Chambers et al. 1986; Hasken and Poehling 1995; Tenhumberg and Poehling 1995; Hickman and Wratten 1996), field cage manipulative studies (Tamaki et al. 1974; Tenhumberg 1995), laboratory manipulative studies (Sundby 1966; Ankersmit et al. 1986; Chambers 1986), and different combinations of these (Chambers et al. 1983; Nawrocka 1988). These studies have generally shown that the impact of hoverflies on aphid populations can be substantial, but there are instances of poor control that tend to result from either the late appearance of gravid females or from low hoverfly population densities (Chambers 1988; Tenhumberg and Poehling 1995). A number of these studies are reviewed in detail below (*'Quantification of the potential of hoverflies to reduce aphid populations'*), where some aspects of methodology and design are summarized.

Predatory hoverflies require pollen as a protein source for egg development (Schneider 1948), and nectar for energy. Many non-crop plants can provide these resources, but many farming practices, such as cultivation and herbicide use, reduce or remove these (Landis et al. 2000). Hoverflies demonstrate strong preferences for different flower species (Cowgill 1993b; Colley and Luna 2000), which is probably related to their nutritional requirements and the morphology of their mouthparts (Gilbert 1981). This requirement for nectar and pollen makes flower planting a good candidate

for enhancing hoverfly predatory efficiency. The selection of flowering plants for this purpose requires a detailed knowledge of the phenology and nutritional ecology of local hoverflies.

Habitat Manipulation to Enhance the Predatory Activity of Hoverflies

Hoverfly activity could potentially be enhanced between seasons through mechanisms of increasing the availability of alternative aphid prey and of overwintering shelter, but these mechanisms may not act quickly enough for the decision time frame of a crop manager. The obligate feeding on nectar and pollen of hoverflies confers a strong behavioral disposition to locate these resources early in hoverfly adult development, and enhancement of floral resources may increase local activity within the growing season. This enhancement of activity by manipulated floral resources could act on some or all of a hierarchical set of behavioral responses from long-range attraction, to short-range attraction and arrestment, more frequent return rates with greater hoverfly retention, increased survivorship, increased prey-finding ability (reduced 'commute' time between floral and aphid resources), increased fecundity and increased impact on aphid populations. If these processes occur over the same spatial and temporal frame as that of crop pest management decision-making, the manipulation of these floral resources could represent an effective conservation biological control tactic.

While it is clear that many species of predacious hoverflies in different geographic areas are attracted to, and feed on, floral resources of many types (MacLeod 1992; Cowgill 1993; Lovei et al. 1993; Colley and Luna 2000), there is insufficient information on the extent to which manipulating and conserving floral resources may

enhance the biological control potential of hoverflies. Trials investigating the use of this strategy have looked at the spatial relationship of certain of the behavioral responses described above to both natural and manipulated floral resources in cropping systems. A greater overall attraction of hoverfly adults to whole crop fields containing borders of floral resources has been demonstrated in experiments comparing fields with and without these resources. For example, Rupert & Molthan (1991), demonstrated increased aphidophagous syrphid densities (species not given) in winter wheat fields with herb rich borders (> 60 spp.), compared with fields that had been treated with herbicides. Similarly, Hickman and Wratten (1996) trapped greater numbers of aphidophagous Syrphidae in winter wheat fields with borders sown with *Phacelia tanacetifolia*. A similar study in UK winter wheat, however failed to detect any differences (Holland et al. 1994).

Within the crop field area, increased densities of adult hoverflies have been detected closer to floral resources. For example, Harwood et al. (1992) trapped greater numbers of aphidophagous hoverflies (including *Eristalis* spp.) near to borders sown with wild flower mixtures, compared with unmanaged borders in winter wheat fields. Lovei et al. (1992, 1993, 1994, 1997) have demonstrated higher densities of trapped adult aphidophagous syrphids (including native New Zealand *Melanostoma* spp.) close to strips planted with a number of flower species, including *P. tanacetifolia* and *Coriandrum sativum*. White et al. (1995), trapped higher numbers of adult syrphids close to *P. tanacetifolia* strips in cabbage fields. Sutherland et al. (2001) however, found in trapping and census counts of adult syrphids, that some species (e.g. *Episyrphus balteatus*) are strongly associated with field boundaries, rather than within field flower

blocks. They postulated that field boundaries provide a number of additional resources, including non-crop aphid species and lekking sites.

In addition to the correlative studies mentioned above, actual *retention* of hoverflies attracted by flowers has only been investigated on a few occasions with varying results. A study of paint-marked individuals (MacLeod 1999) showed a certain dominant species of that system (*Episyrphus balteatus*) to stay mostly around a patch of mixed flowers and disperse more slowly from borders rich in floral resources. Another study of a rubidium-labeled patch of mixed flowers (Long et al. 1998) demonstrated an equal number of hoverflies at different distances in a zone 30 meters from the flowers. In other labeling studies looking at the pollen content of guts in flies sampled at different distances from added floral patches, Lovei et al. (1994, 1997) showed that hoverflies containing the phacelia pollen, started to become less abundant at sampling points over 20 to 30 meters away from the flower patches. While these studies provide important information on the attraction, retention and dispersal of hoverflies around floral resources, there is still very little information on hoverfly foraging dynamics after visiting flowers, and how this has related to their ability to find, oviposit near to and have an impact upon, aphids.

Another indicator of the spatial effect of flowers on hoverfly activity is that of *oviposition* on crop plants at different distances from floral resources. Dixon (1959) provided an early example of a *temporal* correlation of oviposition at aphid colonies with the presence of flowers on the same plants. One of the first demonstrations of a *spatial* correlation of increased oviposition on plants with aphids near to flowers was seen in a cole crop/cabbage aphid system with floral borders (van Emden 1965). Other early

studies (Chandler 1968a; Pollard 1971; Chambers 1987) were not able to detect such a spatial effect of oviposition with proximity to flowers, but all of the examples above had low replication and few sampling points.

The clearest demonstration of increased oviposition at sampling points near floral resources is reported by Hickman et al. (1996), where oviposition was enhanced in fields in England with *P. tanacetifolia* -planted borders, compared with flowerless fields at distances up to 100 m from flowers. Other studies in winter wheat looking at the spatial effect of flowering strips have initially shown greater densities hoverfly eggs (species not given) (Sengongca and Frings, 1988) or larvae (species not given) (Hausammann, 1996) in treatments that did not contain flowers. More detailed analysis however revealed that aphid densities were higher in these treatments, and that when the aphid density effect was excluded the numbers of hoverfly eggs or larvae *per aphid* were significantly greater near to the flower treatments. The concurrent attraction of hoverflies to both flowers and aphids in crop fields in these studies and others (eg. Chambers 1991; Tenhumberg and Poehling 1995) points to the need for an experimental design that accounts for the effect that both of these factors have on hoverfly attraction and distribution (see '*Quantification of the Field-Scale Effect of Added Flowering Plants*' below).

A final indicator of the effect of flowers on hoverfly activity is the potential indirect *impact on aphid populations* and crop yield. This indirect impact has been demonstrated in a few instances in replicated trials. Sengongca and Frings (1988) found lower aphid numbers and higher yields within sugar beet fields containing *P. tanacetifolia* strips than in fields without the floral strips. Hoverflies were attributed to be the main aphid mortality factor responsible for this difference. In a cereal system

study looking at the effect of field border strips of *P. tanacetifolia*, Hickman and Wratten (1996) found aphid populations to be significantly lower in the fields with flowers during the second half of the cropping season. Combined with the results of greater hoverfly oviposition in the treated fields, it was again suggested that hoverflies were the main mortality factor responsible for this difference. In a cereal system with sown borders of four species of flowering weeds, Hausammann (1996) found that aphids were reduced in fields with flowers.

Quantification of the Potential of Hoverflies to Reduce Aphid Populations

While it is necessary for the assessment of biological control potential to understand the spatial dynamics of how hoverflies are attracted to and use floral resources, information on how various hoverfly species could possibly impact aphid colonies on individual plants is also needed. Many of the field studies of hoverfly effectiveness in limiting aphid populations mentioned above, have demonstrated the potential of hoverflies, but the variability of this impact shows that further studies on hoverfly effectiveness are needed (Poehling 1991; Tenhumberg and Poehling 1995). Field cage exclusion studies in systems with hoverflies have given some information on the predatory potential of hoverflies when correlated with their abundance in the field, but this technique has not allowed the reliable separation of effects resulting from hoverfly activity from that of other predators present (Hagen et al. 1999), or of effects that these predators have on each other (Hindayana et al. 2001). Studies quantifying the impact of hoverflies have also looked at the timing of aphid population decline relative to the presence of hoverfly larvae, but other aphid-limiting factors have often not been

accounted for in these observational studies. These additional factors include emigration of alatae, changes in host plant physiology and the impact of weather and photoperiod conditions (Chambers 1988).

Those studies most clearly quantifying the impact of hoverflies (see Table in Appendix 1) have also used data on aphid mortality rates from manipulative studies in the laboratory or on caged field plants, in conjunction with field-collected data on relative densities of hoverflies and other predators and their prey (Tamaki 1974; Neuenschwander et al. 1975; Chambers et al. 1983; Chambers and Adams 1986; Tenhumberg 1995; Nawrocka 1988; Tenhumberg and Poehling 1991; Nunnenmacher et al. 1996). From this approach (i.e. using manipulative experiments to supplement field-obtained data) it can then be calculated whether the aphid mortality seen in a given field is within the capacity demonstrated by measurements of adult density, oviposition and consumption rate, from the laboratory or cage studies. When using results from manipulative cage or laboratory studies as an indicator of the predatory capacity of a given hoverfly species, it is important to make conditions in the manipulative experiment as close as possible to those in the field situation that is being modeled. Otherwise, the predatory capacity may be overestimated if conditions of microclimate or prey availability are enhanced greatly beyond that seen in the field.

Hoverfly Oviposition

Investigations of the spatial aspects of hoverfly resource use should include an analysis of the concurrent attraction of ovipositing females to aphid patches. The effects of spatial arrangement, size, and patterns of aggregation of aphids should also ideally, be

taken into account. Similarly, investigations of the potential capacity of hoverflies to limit aphid populations should also include an analysis of their ability to find, choose between and oviposit near aphid patches in order to assess the numerical response component of the hoverfly response.

There is now a large body of literature on the oviposition behavior of aphidophagous hoverflies. Sadeghi and Gilbert (2000b) have published the most recent review. Variations in behavior have been demonstrated among species to different cues important for oviposition including: aphid number, aphid colony type, aphid species and honeydew. There is a lack of information on other factors that are of potential importance, including, host plant characteristics (Chandler 1968d), the arrangement of aphid colonies on plants (Chandler 1968e) or the effect of conspecific hoverfly eggs already present (Scholz and Poehling 2000; Belliure and Michaud 2001). Many studies have shown increased oviposition near larger aphid colonies (Dixon 1959; Chandler 1968b; Bargaen et al. 1998; Scholz and Poehling 2000; Belliure and Michaud 2001), or near spots on plants that present cues such as honeydew (Buddenberg and Powell 1992; Scholz and Poehling 2000). Other studies have however shown an increase of oviposition on smaller, younger colonies in some instances (Kan 1988a,b), or even on bare leaves for those species predisposed to eat both arthropod and plant matter (Chandler 1968d). The relative importance of these olfactory, tactile and visual cues is still poorly understood.

Other factors affecting the oviposition response to aphid numbers include those inherent within hoverfly individuals. They include age (Chandler 1967; Sadeghi and Gilbert 2000b) and egg load (Sadeghi and Gilbert 2000a). Individual flies of the species

Episyrphus balteatus (DeGeer) have also demonstrated varying preferences for different aphid prey species (Sadeghi and Gilbert 1999).

In two local field trials conducted in the 2000 season (unpublished data) looking at number of hoverfly eggs per aphid on leaves and whole plants in commercial broccoli fields, hoverfly eggs appeared in the later half of the season, mostly on plants with greater than 50 aphids. Additionally, the hoverfly egg/aphid ratio was greater for cabbage aphid than other aphid species present, especially those on the upper portions of the mature broccoli plants. The pattern of hoverfly oviposition relative to the distribution of different aphid species over the plant is being analyzed further from this data set.

The Relative Attractiveness of Floral Resources and the Effect of these Resources on Hoverfly Individuals

It has long been recognized that hoverflies use floral resources selectively, although the degree of selectivity varies between species (Haslett 1989). For those available flowers that a community of hoverflies can access, it is not clear whether they are selecting between these resources based on cues from flower color, flower form, nectar and pollen amount, or nectar and pollen quality, exogenous factors such as competition (Morse 1981), or, various combinations of these factors (Sutherland et al. 1999). Even if there are multiple reasons why a hoverfly individual chooses one flower type over another, differential visitation and feeding patterns observed within the local hoverfly assemblage at specific flower types can still serve as an indicator of floral resources most likely to enhance hoverfly predatory activity, if the sample size of observations is large enough (Jervis and Kidd 1996). While candidate floral resources

under consideration for the enhancement of biological control in agroecosystems must ultimately be screened for a wide range of attributes such as potential hazard as pest hosts or weeds, as well as agronomic and economic compatibility (Gurr et al. 1998), their relative attractiveness to the key local natural enemy species should be a prime initial consideration. The relative attractiveness of select species of flowering plants to the hoverfly community has been demonstrated on other continents (Cowgill 1993; Lovei et al. 1993), as well as for the local hoverfly community that is being analyzed in the current project (Colley and Luna 2000; unpublished 2000 report included at end of this proposal). Those species of flowering plants most attractive to predacious hoverflies and least attractive to arthropod herbivores will be used as the priority species for future work.

While feeding at the flowers of a given variety or species of flowering plant is a strong indication of the potential of these plants to enhance biological control, it is not sufficient evidence. For this reason, authors such as Jervis and Kidd (1996) have suggested that functional response experiments are needed to determine the exact effects of nectar and pollen on the health and performance of natural enemy individuals. Fecundity and longevity should be looked at initially, but the ideal ultimate comparison of the relative benefit of different flower types would be to include effects on searching efficiency also (Jervis and Kidd 1996).

OBJECTIVES

The objectives of this research were to:

1. Evaluate the prey-finding and oviposition behavior of adult hoverflies.
2. Evaluate the developmental rates and abilities of hoverflies to limit populations of *B. brassicae* in controlled cage and field experiments.
3. Evaluate the relative attractiveness of selected insectary plants to hoverflies and other key pest and natural enemy species in the broccoli crop system.
4. Quantify the field-scale effect that added flowering plants have on the attraction and oviposition activities of hoverflies, as well as on the abundance of other arthropod natural enemies and herbivores in broccoli.

MANUSCRIPT 1

HOVERFLY OVIPOSITION RESPONSE TO APHIDS IN BROCCOLI FIELDS

AUTHORS:

M.D. Ambrosino, P.C. Jepson, J.M. Luna

JOURNAL:

To be submitted to:

Entomologia Experimentalis et Applicata

Blackwell Publishing Ltd.

9600 Garsington Road

Oxford OX4 2DQ, UK

HOVERFLY OVIPOSITION RESPONSE TO APHIDS IN BROCCOLI FIELDS

Abstract

The oviposition response of predacious hoverflies (Diptera: Syrphidae) to *Brevicoryne brassicae* L. and *Myzus persicae* (Sulzer) in commercial broccoli fields was investigated at two sites over the course of the growing season. The oviposition responses to these aphid species on different parts of the broccoli plant canopy were also examined. There were no hoverfly eggs on broccoli plants without aphids, eggs were very low on plants with less than 50 aphids, and no peak in oviposition relative to aphid numbers on plants were observed. The oviposition response at the scale of individual leaves was different from the plant scale in that there was some oviposition on individual broccoli leaves without aphids, and no hoverfly eggs were seen on leaves that had more than 400 aphids. The data from the broccoli plant canopy were divided in three sections vertically, 'upper', 'middle' and 'lower'. *B. brassicae* was more abundant in the two higher canopy sections, while *M. persicae* was mostly in the lower section. At this scale of canopy section, the rate of hoverfly oviposition per aphid was higher in the upper section than in the two other sections. *B. brassicae* were more abundant than *M. persicae* at the plant scale, but the only difference in oviposition response seen was some plants without *M. persicae* had hoverfly eggs. Modeling of this response with logistic regression showed that the numbers of each aphid species, as well as day in the season influenced the presence of hoverfly eggs.

Keywords.

Hoverflies, Syrphidae, oviposition, numerical response, broccoli, aphids

Introduction

Many species of predatory hoverflies (Diptera: Syrphidae) are recognized as important natural enemies that can have a significant impact on aphid populations (Chambers 1988). Hoverflies have high reproductive rates and voracity, allowing them to exploit short-lived aphid colonies efficiently (Ankersmit et al. 1986), high mobility, enabling them to distribute eggs over large areas (Schneider 1948; Chambers 1988, 1991), and an ability to oviposit at aphid colonies earlier in the season than other aphidophaga (Hagen and van den Bosch 1968; Horn 1981; Dixon 2000). Adults oviposit close to aphid colonies (Chambers 1988; Dixon 2000), even at relatively low aphid densities (Chandler 1968b; Kan 1988a,b; Chambers 1991; Sadeghi and Gilbert 2000b).

The ability to detect, and oviposit near to, aphid colonies plays a major role in the predatory effectiveness of hoverflies. Species may vary in their preferences to oviposit near aphid colonies of different sizes (Dixon 1959; Chandler 1968b; Kan 1988b; Bargaen et al. 1998; Scholz and Poehling 2000; Belliure and Michaud 2001), and some may select leaves with other cues such as honeydew (Buddenberg and Powell 1992; Scholz and Poehling 2000), bare leaves (Chandler 1968d), or even aphid free plants next to plants that aphids have colonized (Chandler 1968d). This variation could reflect adaptations that reduce competition among species (Chandler 1968b). Other ovipositional cues of potential importance to hoverflies include aphid colony type (Kan 1988a,b) aphid species (Sadeghi and Gilbert 2000b), the arrangement of aphids on the host plant (Chandler 1968c), host plant characteristics (Chandler 1968b,d), and the presence of conspecifics or other hoverfly eggs (Scholz and Poehling 2000; Belliure and Michaud 2001).

The oviposition responses of hoverflies can also vary among individuals of the same species (Sadeghi and Gilbert 1999). Factors inherent to the hoverfly individual that affect oviposition response include fly age (Chandler 1967; Sadeghi and Gilbert 2000b), cumulative experience and 'stimulus satiation' (Chandler 1967), and egg load over time (Sadeghi and Gilbert 2000a).

A high rate of prey search is considered to be one of the most desirable attributes of biological control agents (Kidd and Jervis 1996; Murdoch and Briggs 1996; van Driesche and Bellows 1996). It is especially important for assessing the biocontrol potential of predacious hoverflies, because the relatively sessile nature of the larvae does not allow them to exploit aphid hosts on different plants. The adults' ability to find and oviposit within the future foraging range of its progeny is therefore a critical determinant of potential biocontrol performance. Due to difficulties observing the foraging and oviposition behaviors of rapidly moving and highly dispersive organisms such as hoverflies, much of the information on hoverfly prey search and oviposition response has been generated from controlled environment studies. However, it is also necessary to characterize their search efficiency for different sizes, types and arrangements of prey patches that typically occur in the field.

The cabbage aphid (*Brevicoryne brassicae* L.) is a major contaminant pest of broccoli grown for processing in the Willamette Valley of Oregon. Predacious hoverflies have been shown to be one of the main natural enemy groups, but they are generally not found on plants in brassica crop fields until *B. brassicae* have colonized a large percentage of plants (van Emden 1965; Oatman & Platner 1969; Wnuk and Wojciechowicz 1993; Ambrosino 2006; Nieto et al. 2006). The green peach aphid

(*Myzus persicae* (Sulzer)) is also common on brassica crops such as broccoli, but in lower numbers than *B. brassicae* and does not usually cause contamination problems. Little is known about the field-scale hoverfly oviposition response to these aphid species on individual leaves or plants over the course of the broccoli season. We examined how hoverflies respond to aphids on commercial broccoli plantings, compared with other natural enemies over the course of a full cropping season at two sites. We determined the likelihood that eggs would be laid on plants with different densities of different aphid species, and investigated the oviposition response to each aphid species on three different sections of the broccoli plant canopy.

Materials and Methods

Field Sites.

Data were collected from two broccoli fields in the Willamette Valley in Oregon. The North Site was planted on 27 April in a 15 ha field near Corvallis, OR bordered by corn, strawberry, and grass seed crops on each of three sides, and mature hazelnuts on the fourth side. This field was sprayed with Spinosad, a selective lepidopteran pesticide 34 days after transplanting and imadacloprid, 61 days after transplanting. The South Site was a 14 ha field near Eugene, OR, about 90 km south of the North Site. This field was planted on 13 May and bordered by grass seed crops on two sides, young hazelnut trees on a third side, and a squash field on the fourth side. This field was sprayed with Spinosad two times, 19 days and 48 days after transplanting. Two 15 x 66 m sections of broccoli in each field were left unsprayed for arthropod sampling.

Sampling Procedure.

In each of the four unsprayed sampling areas at the two sites, every leaf on 50 randomly selected broccoli plants was examined for the presence of hoverfly eggs and larvae, *B. brassicae*, *M. persicae*, potato aphid (*Macrosiphum euphorbiae* (Thomas)), and other aphid natural enemies such as predacious cecidomyiid midge larvae and eggs (Diptera: Cecidomyiidae), parasitized aphid mummies, spiders, lady beetles (Coleoptera: Coccinellidae), and lacewings (Neuroptera). Sampling began in each field when plants were at the 5-leaf stage, and was repeated every four to six days in each field until harvest (about 10 weeks later).

At the 10-leaf stage of broccoli plant development, data from each leaf of each plant were allocated to either 'upper' (leaves closest to the broccoli head under 6 cm² each), 'middle' (leaves next closest to head over 6 cm² each), or 'lower' (leaves closest to ground which had started to wither) leaf developmental classes. Aphids within each colony encountered were identified to species and divided into three classes of developmental stage: adult alatae, adult apterae and immature. A representative sample of each type of natural enemy egg and larval type encountered was returned to the laboratory and reared to the adult stage for identification. On the last two sampling dates of the season, the plant sample size in each plot was reduced from 50 plants per section to 30 plants and then to 15 plants to accommodate the increasing number of leaves. At harvest, 100 broccoli heads were randomly selected and harvested from each unsprayed sampling area. Each head was examined for arthropods for five minutes by destructive sampling into pieces smaller than 1 cm³.

Analysis.

Prior to the analysis, models were constructed to represent hypotheses about the most likely combinations of factors relating to the presence of hoverfly eggs on plants. A set of 17 models were chosen to represent the relative effects of sampling date, field site, *B. brassicae* and *M. persicae*. The goodness of fit of these models to the data was determined using logistic regression in PROC GENMOD of SAS (Allison 1999; SAS Institute 2000). To first see if the global model provided a reasonable first approximation of the data, a Hosmer and Lemeshow goodness of fit test (SAS Institute 2000) was used to test for lack of fit of a global model. Correlations between variables were examined using Pearson correlation coefficients. To determine if different aphid species, field sites, date and/or certain combinations of these factors best explained of hoverfly oviposition on plants, a small-sample variant of Akaike's information criterion (AIC_c) was used to rank this set of biologically relevant models according to their ability to approximate the information in the data (Burnham and Anderson 2002). The relative importance of each model was also assessed by looking at Akaike weights, defined as the relative likelihood of each model (Burnham and Anderson 2002). A maximum rescaled adjusted r^2 value (Allison 1999) was calculated for the highest ranking model in the set. An unconditional standard error that incorporated uncertainty associated both with the estimation of a parameter and with model selection was computed for each parameter estimate (Burnham and Anderson 2003). Ninety-five percent confidence intervals for the variables included in the best model(s) were calculated using the Estimate ± 1.96 (unconditional SE).

The differences in aphid presence and hoverfly oviposition among the three broccoli leaf zone developmental classes were also investigated. Differences in aphid and egg distribution by zone were not subjected to statistical analysis because these data

were nested within the analyses that were undertaken on the per-plant data, and because the zone classification system was subjective, and not based on leaf developmental or physiological status.

Results

Hoverfly response over time at each site compared to the other natural enemies.

The most common natural enemies were spiders, hoverflies, cecidomyiid flies and parasitoid wasps. All of these groups except the spiders started to arrive to the broccoli plants only one to two weeks before harvest at both sites (Fig. 1.1). The eggs, larvae and adults of lady beetles and green lacewings were also present on some broccoli plants towards the end of the season, but only sporadically and in much lower numbers than the other natural enemies (data not shown). Hoverfly larvae were not commonly observed with the non-destructive plant sampling method used. Over six different hoverfly egg chorion morphotypes were observed, but most of these eggs that were observed and collected were not identified to species. For the portion of eggs that were reared to the adult stage and identified, the species consisted of *Eupeodes fumipennis* (Thomson), *Sphaerophoria sulphuripes* (Thomson), *Platycheirus stegnus* (Say) and *Syrphus opinator* Osten Sacken.

Although the relative percentage of plants with aphids and natural enemy groups were similar at each site over the course of the broccoli season (Fig 1.1), the mean number of aphids per leaf was much higher at the North Site just before harvest, and the mean number of hoverflies, cecidomyiids and aphid mummies at the North Site was approximately twice as high as the South Site at this time (Fig. 1.2). While the relative

percentage of plants with *B. brassicae* and *M. persicae* were also similar at the end of the season just before harvest, the mean numbers of *B. brassicae* per plant were five to six times higher than the mean number of *M. persicae*. Only a few individuals of *M. euphorbiae* were found on the broccoli plants throughout the course of the study. The hoverfly oviposition response was investigated further by looking at the response to *B. brassicae* and *M. persicae* on different parts of the plant at the two sites over time.

Hoverfly response to each aphid species at each site.

Both the mean number of hoverfly eggs per leaf, and the relative percentage of leaves with hoverfly eggs gradually increased with increasing aphid numbers (Fig. 1.3a). There was some oviposition on leaves without aphids, but no hoverfly eggs were seen on leaves that were in an aphid class of more than 400 aphids (Fig. 1.3a). While similar relationships between egg number and aphid densities on whole plants were seen (Fig. 1.3b), plants without aphids did not have any eggs, and there was a bigger jump in both hoverfly egg numbers as well as the relative percentage of plants with hoverfly eggs for plants with 51-100 aphids and then again for plants with 201-300 aphids. There was very little oviposition on plants with fewer than 50 aphids, and no reduction in either the mean egg numbers or relative percentage of plants with eggs was seen on the plants with highest numbers of aphids (Fig. 1.3b). Given that egg laying on an individual leaf may be affected by aphid cues (including odor, honeydew and visual cues) from neighboring leaves, further analysis of the hoverfly egg/aphid density relationship was conducted on the whole plant data.

The frequency distribution of egg number per plant in different classes of aphid number per plant was not the same for each aphid species. The mean number of hoverfly

eggs and the relative percentage of plants with hoverfly eggs increased with increasing numbers of *B. brassicae* (Fig 1.4), in a pattern similar to that seen for all aphids (Fig. 1.3b). This relationship was not seen with *M. persicae* however, as plants with no *M. persicae* had some hoverfly eggs (Fig. 1.4).

Prior to the selection of models from the set of hypothetical models chosen to represent the relative effects of sampling date, field site, *B. brassicae* and *M. persicae*, the global model in this set was tested for lack of fit to see if it provided a reasonable first approximation of the data. There was no evidence of a lack of fit for the global model ($P = 0.44$, Hosmer and Lemeshow test), and there were no strong correlations between any of the explanatory variables. The model containing the effects *B. brassicae*, *M. persicae* and sampling date without interactions was the best approximating model based on AIC_c , comprising over 73% of the confidence set. The next best approximating model, the model containing each of the four explanatory variables without interactions, was only slightly competitive since the weight of the best model was over 3 times greater than this one. The remaining 15 models appeared to poorly approximate the data, as indicated by their relatively high AIC_c values and relatively low AIC_c weights (data not shown). These results suggest that the most likely parsimonious model for describing the factors relating to the presence of hoverfly eggs on plants was the one containing only these three variables.

When the data were fit to the best model, the maximum rescaled adjusted r^2 value was 0.40, indicating that this model described the data only moderately well. Parameter estimates for each of the variables in this highest-ranked model are shown in Table 1.1. The presence of hoverfly eggs was strongly associated with *B. brassicae* ($p < 0.0001$), *M.*

persicae ($p = 0.0008$), and sampling date ($p < 0.0001$). It is estimated that the relative odds of hoverfly eggs being present on a plant increased 1.3% (i.e. odds ratio = 1.013) for each additional *B. brassicae* individual (95% C.I.: 0.8 - 1.9), 1.9% for each additional *M. persicae* individual (95% C.I.: 0.8 - 3.0), and 10.3% for each additional date in the broccoli season (95% C.I.: 5.6 - 15.1).

The distribution of each aphid species and hoverfly eggs in three different zones within the plant.

M. persicae were generally less abundant than *B. brassicae* on whole plants, and tended to be on the leaves in the 'lower' zone at the base of the plants at both sites on all dates (Table 1.2). The greatest numbers of *B. brassicae* were found in the 'middle' zone, with smaller, but similar numbers found in the 'upper' zone (Table 1.2). Although the mean number of hoverfly eggs in the upper zone was lower than that seen for the other two zones, the ratio of hoverfly eggs to total aphids in this zone was twice as high as the ratio in the other two zones (Table 1.2). The inspection of broccoli heads at harvest yielded very few aphids and no hoverfly eggs (data not shown).

Discussion

Model selection and parameter estimates indicated that the data were consistent with the hypotheses that hoverfly egg numbers on a plant were associated with *B. brassicae*, *M. persicae*, and sampling date. Even though there were more aphids and hoverfly eggs on the broccoli plants at the North Site, the magnitude of the hoverfly egg response to aphids was similar at both sites. The fitted logistic regression model does not specify the aphid density at which hoverfly oviposition was first seen, but there were no

hoverfly eggs on plants without aphids, and both the mean number of eggs and the relative percentage of plants with eggs were very low on plants with less than 50 aphids.

The within-plant distribution of greater *M. persicae* on lower leaves and greater *B. brassicae* on upper leaves has been seen on broccoli plants in other studies (Trumble, 1981), but these distributions can change with changing nitrogen levels in different leaves as the plants age (Petherbridge and Mellor 1936), or possibly with the absence of competing aphid species (Nieto et al. 2003). Although the mean numbers of aphids and hoverfly eggs per leaf were higher in the 'middle' and 'lower' zones of the broccoli plants, the ratio of eggs to aphids was higher in the 'upper' zone. A similar pattern has been seen with a higher rate of parasitism in *B. brassicae* in the upper leaves of Brussels sprouts plants (George 1957). The higher rate of hoverfly oviposition per aphid seen in the 'upper' zone of the broccoli plants in this study could have either been a result of the fact that this zone of the plant was more accessible for foraging hoverfly females, especially after the canopy had closed within rows, or that the densities of aphids were so high in the other two zones that the oviposition response had already peaked in those zones. There was no evidence of a peak in hoverfly oviposition for a certain number of aphids at the level of the plant, but the lack of oviposition on individual leaves with the highest numbers of aphids suggests that such a peak could also exist at the level of plant zone.

This lack of hoverfly oviposition on leaves with similarly high numbers of aphids per leaf found in this study has been seen for other hoverfly and aphid species on the compound leaves of pea plants in the field (Kan 1988b). This has been attributed to a 'buy futures' tactic of ovipositing hoverflies whereby the foraging gravid females are

selecting aphid colony sizes based on the future potential value of short-lived aphid colonies rather than their immediate value (Kan 1988b). There was no evidence of a peak in hoverfly oviposition at higher aphid numbers at the plant level however. The oviposition response to lower aphid numbers was similar at both the plant and leaf levels, except for a low percentage of leaves with no aphids on which oviposition occurred. Other factors besides aphid numbers that have been shown to influence hoverfly oviposition at the scale of individual leaves, such as honeydew, aphid colony type and arrangement, or cues from other predators and conspecifics were not analyzed in this study.

Even though the frequency distributions of egg number per plant for plants in different classes of aphid number was not the same for each aphid species, the highest ranked parsimonious model showed that egg numbers on a plant were associated with both *B. brassicae* and *M. persicae* to a similar degree, but this model described the data only moderately well. Although selectivity in oviposition near certain aphid species over other species has been observed for hoverflies (Sadeghi and Gilbert 2000b; Sadeghi 2002), these results can be more variable under field conditions (eg. the costs of being a generalist are not as high when high quality prey patches are less abundant), and selective oviposition is sometimes not seen for other aphidophaga (Frechette et al. 2006). Potential differences in the selectivity of oviposition response to these two aphid species may not have been observable in this study for a few different reasons. First, the complex of hoverfly species ovipositing on broccoli in these fields included at least 4 different species, and variable prey search and oviposition behaviors among these species could have obscured any observable oviposition preferences that any one of them may have

had. Secondly, the plant-scale analysis, although important for assessing the ability of hoverflies to distribute eggs among plants in a crop field, pools many of the potential oviposition cues mentioned above that could emanate from each species, also obscuring any oviposition preferences. Thirdly, although prey aphid species selection is largely accomplished by the ovipositing female hoverflies that can forage among different aphid species on different plants, the two main aphids species in this study are both commonly found together on the same plant or even on the same leaf in many brassica crops, and it is conceivable that the foraging larvae also have a role in the selection between these two species as they move around and among the leaves on a given plant.

The timing and levels of hoverflies relative to cecidomyiids, parasitoid mummies and ladybird beetles at colonies of *B. brassicae* and *M. persicae* on brassica plants match those seen in other studies (Petherbridge and Mellor 1936; Banks 1952; George 1957). The strong associations between hoverfly eggs and the two aphid species are consistent with the idea that the complex of hoverfly species present in these fields had a high rate of prey search, but this response was not soon enough to reduce *B. brassicae* infestations to economically acceptable levels. *M. persicae* was present on a large percentage of the plants at harvest, but they were present in relatively low numbers, and mostly on the lower leaves. With this density and distribution, they do not commonly contaminate the broccoli heads as do *B. brassicae*, but their presence may be beneficial in that individuals of this species contribute oviposition cues to hoverflies and other natural enemies that can attack both of these aphid species.

Acknowledgements

We thank Stahlbush Island Farms Inc. for access to the broccoli fields. Drs. J.A. Gervais and D.K. Rosenberg (Oregon State University) provided statistical assistance, and A. Poole assisted with field sampling. This study was funded by the Western Region Sustainable Agriculture, Research and Education program of the United States Department of Agriculture.

References Cited

- Allison, P. D. 1999. Logistic Regression Using the SAS System. SAS Institute, Cary, North Carolina, USA.
- Ambrosino, M. D. 2006. Enhancing the predatory potential of hoverflies on aphids in Oregon broccoli fields with floral resources. Ph.D. Thesis. Oregon State University.
- Ankersmit, G. W., H. Dijkman, N.J. Keuning, H. Mertens, A. Sins & H.M. Tacoma. 1986. *Episyrphus balteatus* as a predator of the aphid *Sitobion avenae* on winter wheat. *Entomo. exp. appl.* 42: 271-277.
- Banks, C. J. 1952. The natural enemies of aphids. *Rep. Rothamstead Exp. Sta.*: 116-117.
- Bargen, H., K. Saudhof, and H. M. Poehling. 1998. Prey finding by larvae and adult females of *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata* 87: 245-254.
- Belliure, B., and J. P. Michaud. 2001. Biology and behavior of *Pseudodorus clavatus* (Diptera: Syrphidae), an important predator of citrus aphids. *Annals of the Entomological Society of America* 94: 91-96.
- Budenberg, W. J., and W. Powell. 1992. The role of honeydew as an ovipositional stimulant for two species of syrphids. *Entomologia Experimentalis et Applicata* 64: 57-61.
- Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information Theoretic Approach. Springer Verlag, New York. 488 pp.
- Chambers, R. J. 1988. Syrphidae, pp. 259-270, Chapter 9.2.3. *In* A. K. Minks, and Harrewijn, P. [eds.], *Aphids: their biology, natural enemies, and control*. Elsevier.
- Chambers, R. J. 1991. Oviposition by aphidophagous hoverflies (Diptera: Syrphidae) in relation to aphid density and distribution in winter wheat., pp. 115-121. *In* L.E.A. Polgar [ed.], *Behaviour and impact of aphidophaga: proceedings of the 4th meeting of the IOBC "Ecology of Aphidophaga"*. SPB Academic Publishing, The Hague, The Netherlands.
- Chandler, A. E. F. 1968a. Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). *Annals of Applied Biology* 61: 402-414.
- Chandler, A. E. F. 1968b. Some host-plant factors affecting oviposition by aphidophagous Syrphidae (Diptera). *Annals of Applied Biology* 61: 415-423.

- Chandler, A. E. F. 1968c. The relationship between aphid infestations and oviposition by aphidophagous Syrphidae (Diptera). *Annals of Applied Biology* 61: 425-34.
- Chandler, A. E. F. 1968d. Height preferences for oviposition of aphidophagous Syrphidae (Diptera). *Entomophaga* 13: 187-195.
- Chandler, A. E. F. 1967. Oviposition responses by aphidophagous Syrphidae (Diptera). *Nature* 213: 736.
- Debaraj, Y., and T. K. Singh. 1998. Studies on some aspects of prey-predator interaction with reference to cabbage aphid, *Brevicoryne brassicae* (Linnaeus) and its predatory insects. *Journal of Advanced Zoology* 19: 50-54.
- Dixon, A. F. G. 2000. *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge University Press, 257pp., Cambridge.
- Dixon, T. J. 1959. Studies on oviposition behaviour of Syrphidae (Diptera). *Trans. R. Ent. Soc. Lond.* III: 57-80.
- Fréchette, B., A. F. G. Dixon, C. Alauzet, N. Boughenou, and J. L. Hemptinne. 2006. Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey? *Entomologia Experimentalis et Applicata* 118: 121-127.
- George, K. S. 1957. Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). *Bulletin of Entomological Research* 48: 619-629.
- Hagen, K. S., and R. van den Bosch. 1968. Impact of pathogens, parasites and predators on aphids. *Annual Review of Entomology* 13: 325-284.
- Horn, D. J. 1981. Effect of weedy backgrounds on colonization of collards by green peach aphid, *Myzus persicae*, and its major predators. *Environmental Entomology* 10: 285-289.
- Kan, E. 1988a. Assessment of aphid colonies by hoverflies. I Maple aphids and *E. balteatus* (Diptera: Syrphidae). *Journal of Ethology* 6: 39-48.
- Kan, E. 1988b. Assessment of aphid colonies by hoverflies. II Pea aphids and 3 syrphid species: *Betasyrphus serarius*, *Metasyrphus frequens* and *Syrphus vitripennis* (Diptera: Syrphidae). *Journal of Ethology* 6: 135-142.
- Kidd, N., and M. Jervis. 1996. Population dynamics, pp. 293-374. *In* M. Jervis and N. Kidd [eds.], *Insect Natural Enemies*. Chapman and Hall, London.

- Murdoch, W. W., and C. J. Briggs. 1996. Theory for biological control: recent developments. *Ecology* 77: 2001-2013.
- Nieto, D. J., C. Shennan, W. H. Settle, R. O'malley, S. Bros, and J. Y. Honda. 2006. How Natural Enemies and Cabbage Aphid (*Brevicoryne brassicae* L.) Population Dynamics Affect Organic Broccoli Harvest. *Environmental Entomology* 35: 94-101.
- Oatman, E. R., and G. R. Platner. 1969. An ecological study of insect populations on cabbage in southern California. *Hilgardia* 40: 1-40.
- Petherbridge, F. R., and J. E. M. Mellor. 1936. Observations on the life history and control of the cabbage aphid, *Brevicoryne brassicae* L. *Annals of Applied Biology* 23: 329-241.
- Sadeghi, H. 2002. The relationship between oviposition preference and larval performance in an Aphidophagous hover fly, *Syrphus ribesii* L. (Diptera: Syrphidae). *Journal of Agricultural Science and Technology* 4: 1-10.
- Sadeghi, H., and F. Gilbert. 2000a. The effect of egg load and host deprivation on oviposition behaviour in aphidophagous hoverflies. *Ecological Entomology* 69: 101-108.
- Sadeghi, H., and F. Gilbert. 2000b. Oviposition preferences of aphidophagous hoverflies. *Ecological Entomology* 69: 91-100.
- Sadeghi, H., and F. Gilbert. 1999. Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. *Oecologia* 118: 405-411.
- SAS Institute, 2000. SAS version 8. SAS Institute, Cary, NC.
- Schneider, F. 1948. Beitrag zur Kenntnis der Generationsverhältnisse und Diapause räuberischer Schwebfliegen (Syrphidae, Dipt.). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 21: 249-285.
- Scholz, D., and H. M. Poehling. 2000. Oviposition site selection of *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata* 94: 149-158.
- Trumble, J. T. 1982. Within-plant distribution and sampling of aphids (Homoptera: Aphididae) on broccoli in Southern California. *J. Econ. Ento.* 75: 587-592.
- Van Driesche, R. G., and T. S. Bellows, Jr. 1996. *Biological Control*. Chapman and Hall, New York.

- van Emden, H. 1965. The effect of uncultivated land on the distribution of cabbage aphid (*Brevicoryne brassicae*) on an adjacent crop. *Journal of Applied Ecology* 2: 171-196.
- Wnuk, A., and E. Wojciechowicz. 1993. Syrphid predators (Diptera, Syrphidae) occurring in colonies of the cabbage aphid, *Brevicoryne brassicae* (L.), on cabbage and cauliflower. *Polskie Pismo Entomologiczne* 62: 215-229.

Table 1.1. Parameter estimates, unconditional standard errors, and odds ratios for variables in the best approximating model to estimate the probability of presence of hoverfly eggs on broccoli plants.

Variable	Estimate	SE	Odds ratio [§] (95% CI)
CA*	0.013	0.003	1.013 (1.008 to 1.019)
GPA [†]	0.019	0.006	1.019 (1.008 to 1.030)
Date	0.103	0.024	1.103 (1.056 to 1.151)

[§] Odds ratio calculated as e^b

* 'CA' = cabbage aphid, *B. brevicoryne*

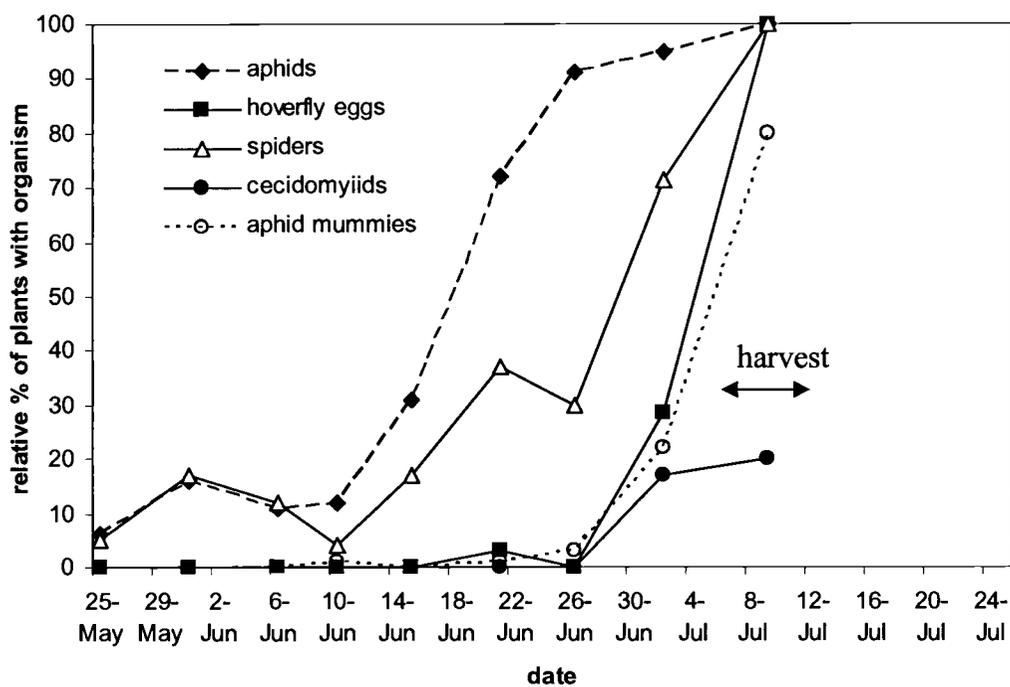
[†] 'GPA' = green peach aphid, *M. persicae*

Table 1.2. Distribution of the mean number of aphids, and hoverfly eggs per leaf (with standard errors) among three zones within broccoli plants at both Sites and all dates pooled.

Organism	Plant Zone		
	Upper	Middle	Lower
<i>B. brassicae</i>	0.92 (0.29)	2.49 (0.96)	0.99 (0.39)
<i>M. persicae</i>	0.00 (0.00)	0.15 (0.03)	0.83 (0.22)
Hoverfly eggs	0.01 (0.01)	0.03 (0.01)	0.02 (0.01)
Ratio eggs/aphids	0.023	0.011	0.011

Figure 1.1. Relative percentage of plants with aphids and natural enemies over time.

(a) North Site



(b) South Site

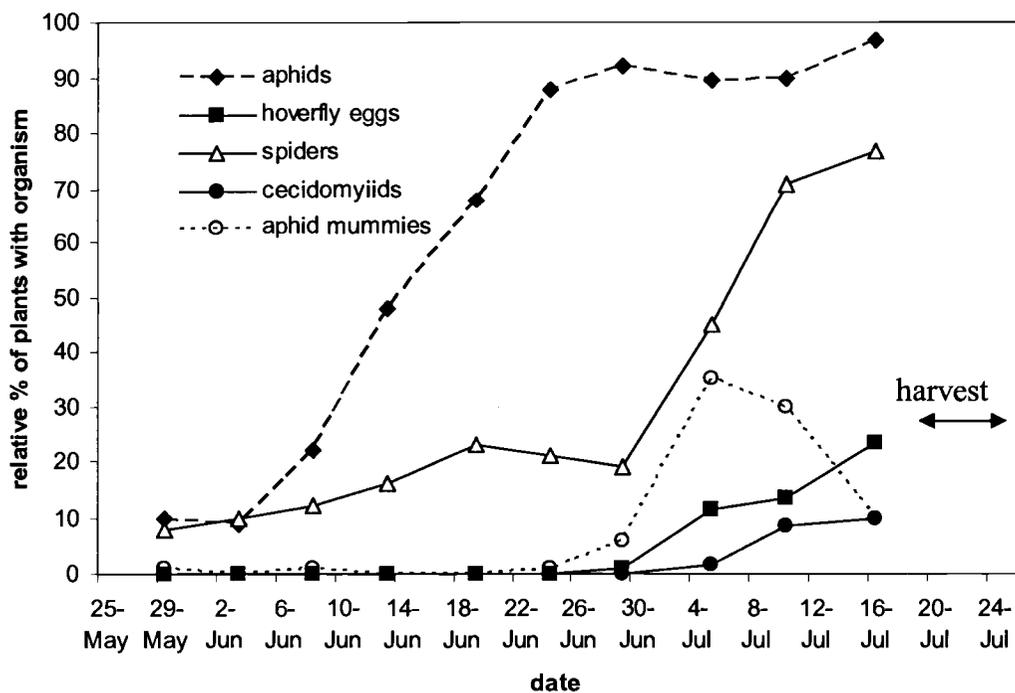
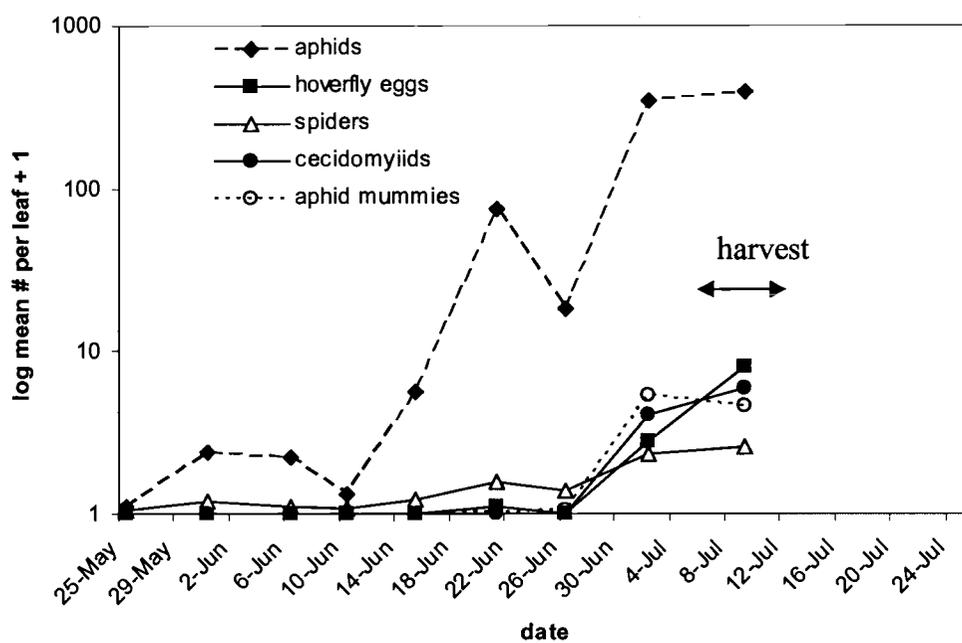


Figure 1.2. Mean number of aphids and natural enemies per leaf over time.

(a) North Site



(b) South Site

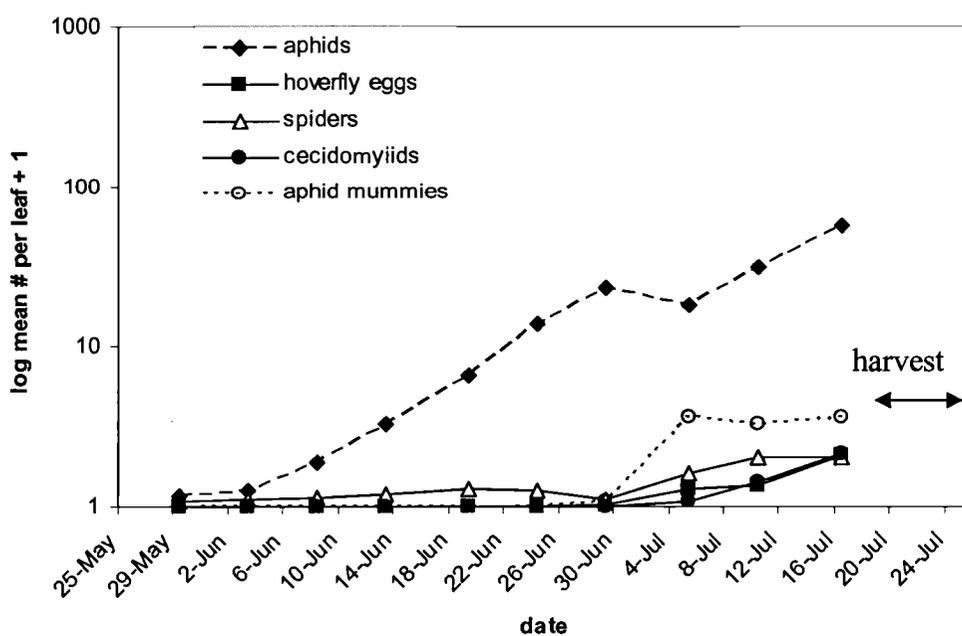


Figure 1.3. Mean number of hoverfly eggs, and relative percentage of leaves or plants with hoverfly eggs in response to aphid intensity per leaf (a), and per plant (b), (with the numeric values included over each category).

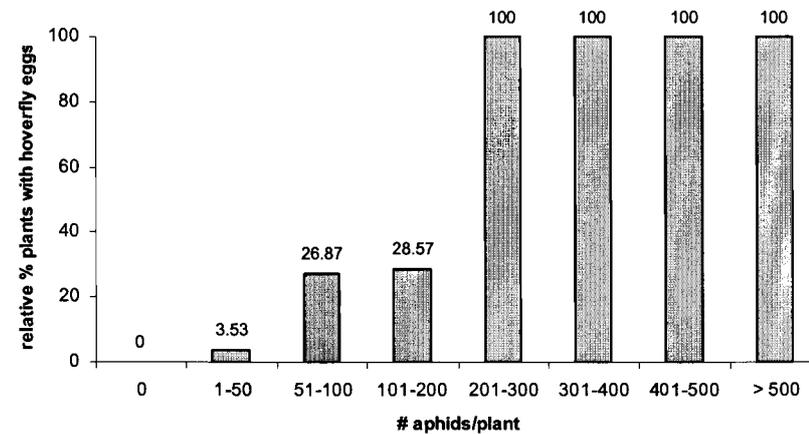
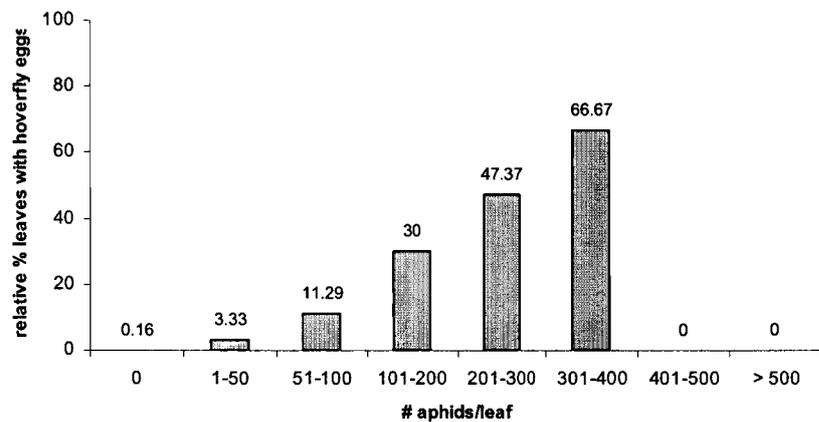
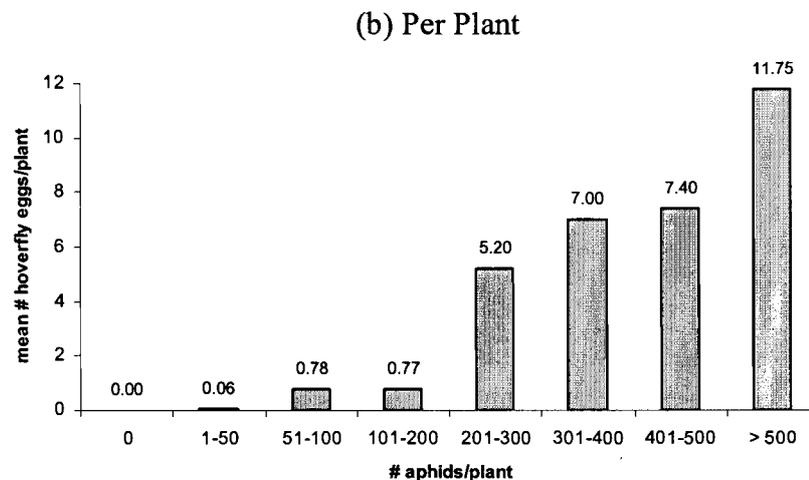
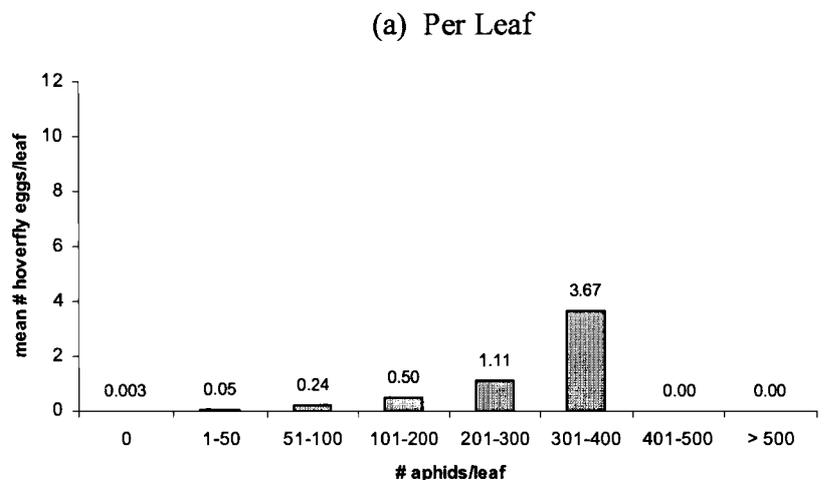
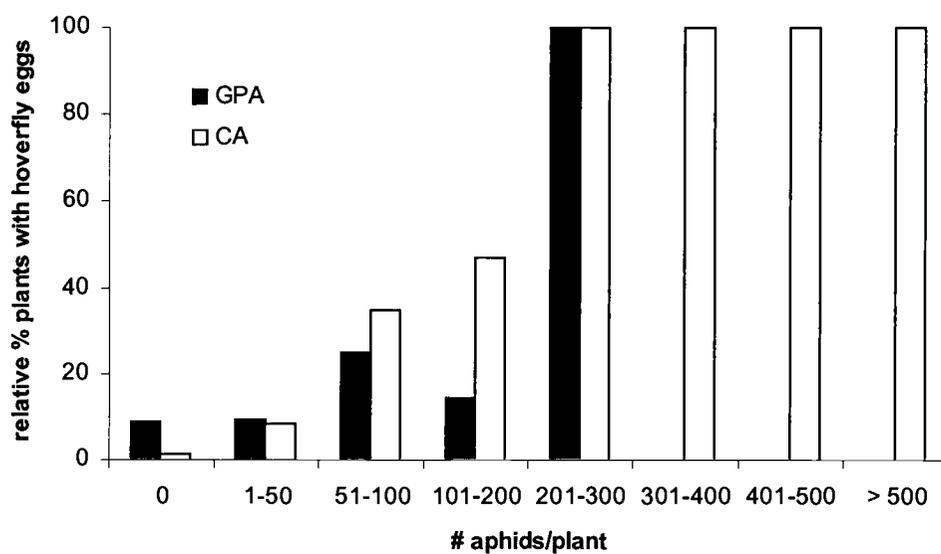
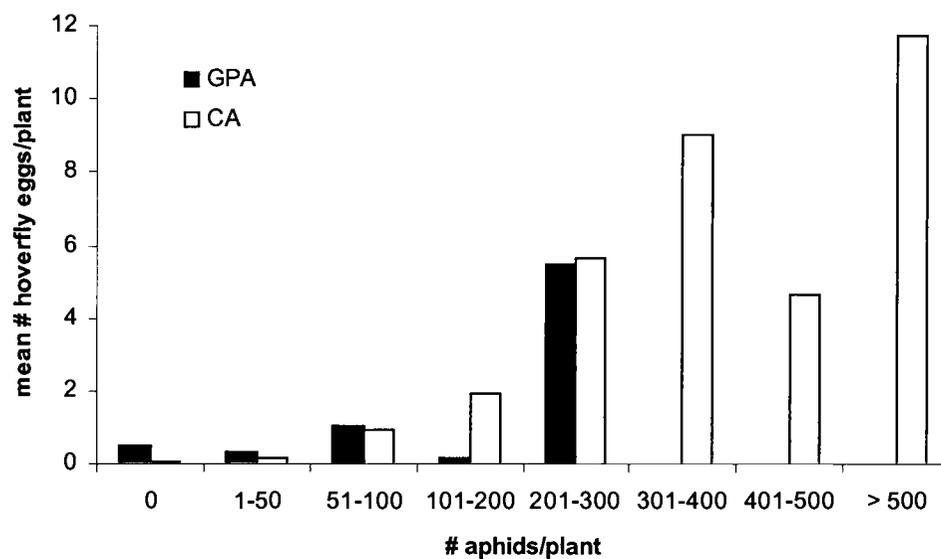


Figure 1.4. Mean number of hoverfly eggs per plant, and relative percentage of plants with hoverfly eggs, per leaf and per plant on leaves and plants with different amounts of either *M. persicae* or *B. brevicoryne*.



MANUSCRIPT 2

**THE VORACITY AND DEVELOPMENT RATES OF FOUR PREDACIOUS HOVERFLY SPECIES
(DIPTERA: SYRPHIDAE) FEEDING ON THE CABBAGE APHID, *BREVICORYNE BRASSICAE* L.**

AUTHORS:

M.D. Ambrosino, P.C. Jepson, J.M. Luna

JOURNAL:

To be submitted to:

Journal of Economic Entomology

Entomological Society of America

10001 Derekwood Lane, Suite 100

Lanham MD, 20706-4876

THE VORACITY AND DEVELOPMENT RATES OF FOUR PREDACIOUS HOVERFLY SPECIES (DIPTERA: SYRPHIDAE) FEEDING ON THE CABBAGE APHID, *BREVICORYNE BRASSICAE* L.

Abstract

The voracity and larval development rates of *Eupeodes fumipennis* (Thomson), *Syrphus opinator* Osten Sacken, *Scaeva pyrastris* (L.), and *Sphaerophoria sulphuripes* (Thomson) fed on *Brevicoryne brassicae* L. were compared in glasshouse and laboratory conditions on plant and artificial substrates. The mean number of *B. brassicae* killed and the development rate of *S. pyrastris* in laboratory arenas were higher than those for *E. fumipennis*, which, in turn were higher than *S. opinator* and *S. sulphuripes*. With the exception of a few individuals, the latter two species did not develop successfully into puparia after 32 days when fed *B. brassicae*. Both *E. fumipennis* and *S. opinator* could reduce *B. brassicae* populations on plants in cages in the glasshouse. *E. fumipennis*, unlike *S. opinator* spent much of the time foraging off of the plants away from the aphids. The four hoverfly species are the most common species found in colonies of *B. brassicae* on broccoli plants in the Willamette Valley in Oregon, and the implications of these findings for *B. brassicae* management are discussed.

Keywords

Hoverflies, Syrphidae, voracity, broccoli, aphids

Introduction

Hoverflies have been shown to be important aphid predators in many agricultural systems (Chambers 1988). Larval feeding rate is one of the major determinants of their effectiveness (Tamaki 1974; Ankersmit 1986). Characteristics that give hoverfly larvae a relatively strong ability to exploit and limit short-lived aphid populations include high reproductive rates, rapid development (Ankersmit et al. 1986; Sood et al. 1994), and the larval behavior of superfluous killing of more aphid prey than is necessary for development and future optimal fecundity when aphids are abundant (Scott and Barlow 1984). The ability of hoverfly larvae to capture and kill prey can vary however, depending on plant structure (Bansch 1966), diel periodicity (Ankersmit 1986), temperature (Soleyman-Nezhadiyan and Laughlin 1998), relative humidity (Lal and Haque 1955) and degree of starvation or satiation (Rotheray and Martinat 1984; Scott and Barlow 1990; Rojo et al. 1996).

Hoverflies are commonly the most important natural enemy group attacking the cabbage aphid (*Brevicoryne brassicae* L.) (Petherbridge and Mellor 1936; George 1957; van Emden 1963; Hughes 1963). *B. brassicae* is the main contaminant pest of broccoli in the Willamette Valley of Oregon. This species of aphid is attacked by a rich complex of natural enemies in broccoli fields in this area, including predacious cecidomyiid midges (Diptera: Cecidomyiidae), parasitoid wasps, spiders, lady beetles (Coleoptera: Coccinellidae), and lacewings (Neuroptera), but predacious hoverflies (Diptera: Syrphidae) are the most consistent and abundant natural enemy group appearing at colonies of this aphid (Ambrosino 2006). The most common hoverfly species which oviposit at *B. brassicae* colonies in commercial broccoli fields are *Eupeodes fumipennis*

(Thomson), *Syrphus opinator* Osten Sacken and *Sphaerophoria sulphuripes* (refer to ms2, ms3), while *Scaeva pyrastris* (L.) is one of the most common species appearing at colonies of *B. brassicae* on broccoli in garden plots at the beginning and end of the broccoli growing season in this area (M.D.A. pers. obs.). The relative capacities of these hoverfly species to limit *B. brassicae* populations are unknown, and this study aimed to quantify relative larval development rates and voracities to contribute to ranking of these species as biological control agents to be exploited in *B. brassicae* management.

Materials and Methods

Hoverfly colonies. Multi-generation colonies of each of the species commonly seen attacking *B. brassicae* in this area were established over the course of 2001 and 2002 to obtain the large numbers of even-aged and naïve hoverfly larvae necessary for experimentation. Adults were collected from the field and placed within 1m³ cages containing flowers, hazelnut pollen, honey, sugar water and broccoli seedlings with *B. brassicae* for mating and oviposition. Plants with hoverfly eggs were then transferred to smaller cages with additional aphids.

Experimental design. The consumption rates of *B. brassicae* by four hoverfly species was assessed both on plants in cages in the greenhouse and in the absence of a plant substrate in a controlled laboratory environment. The greenhouse cages consisted of a four-leaved broccoli seedling (var. 'Munchkin') in a 10 cm pot placed in a 20 liter plastic container with a mesh cover. Cage temperatures were 20±4°C with an RH range of 70±10% and a 16h:8h L:D cycle. A total of 50 mid-sized *B. brassicae* were placed in

three 1.5 cm diameter clip cages on the three lower leaves and allowed to settle overnight. A single first instar hoverfly larva was then placed on the fourth leaf and the number of aphids was counted at 24 hour intervals. Larvae of the hoverfly species *E. fumipennis* and *S. opinator* were included in these investigations, which were replicated six times, and included a control with no larvae.

For the laboratory trials, two day old first instar hoverfly larvae were placed in 10 cm diameter Petri dish arenas with counted and weighed amounts of *B. brassicae*. Arenas containing each hoverfly species were replicated ten times. The arenas were covered, but not sealed to the outer environment of $22\pm 1^{\circ}\text{C}$, $75\pm 5\%$ RH, and a 16h:8d L:D cycle. A new batch of aphids was added each day to each arena. To determine the appropriate amount of aphids to add each day, the minimum and maximum amounts of aphids consumed per day by these hoverfly species were quantified in preliminary experiments where differing amounts of aphids were offered. The changes in aphid mass and aphid mortality in the absence of predators was found to be negligible.

The first laboratory experiment compared the daily mean and cumulative numbers of *B. brassicae* killed, mean hoverfly larval development time, and the mean change in hoverfly larva mass among *E. fumipennis*, *S. opinator*, and *S. pyrastris*. The second laboratory experiment compared *E. fumipennis*, *S. opinator*, and *S. sulphuripes* as above, and included measurements of aphid mass as well. This experiment also included a treatment with single individuals of *E. fumipennis* and *S. opinator* within in the same arena with aphids to seek evidence of larval competition that might affect rates of larval development and aphid consumption rates.

Results

Larvae of both *E. fumipennis* and *S. opinator* appeared to reduce the aphid populations on the caged plants over two weeks compared to the control, and the magnitude of aphid reduction was not different between these two species on any given date (Fig. 2.1). The *E. fumipennis* larvae moved off the plant and crawled around the cage in most of the cages, while the *S. opinator* larvae mostly remained sedentary on the plants. Given the artificial nature of the cage environment and the substrates present it is not possible to conclude if this behavior represented between-plant excursions, or if it was an unanticipated effect of cage micro-climate or conditions. Subsequent experiments compared the aphid consumption rates and larval development per unit time among hoverfly species in a more controlled environment in the laboratory to establish maximum feeding rates for these species.

In addition to controlling for physical substrate, light cycle, temperature and RH in the laboratory experiment, the objective comparison of the larval voracities and developmental rates among these species also required a preliminary determination of the maximum and minimum amounts of *B. brassicae* that each species could consume. For each of the hoverfly species, the minimum mass of *B. brassicae* per day necessary to keep them alive and allow them to develop to the puparial stage was approximately equal to the mass of the hoverfly larva, while the maximum amount they could feed on each day without running out of aphids was approximately three times the mass of the larva. This later amount was used to ensure that the hoverfly larvae were not limited for aphid food.

In the first laboratory experiment, the mean larval development time (+/- SE) from two day old first instar larvae to puparium was 10.5 days (± 1.5) for *E. fumipennis*, 10.0 days (± 0.0) for *S. pyrastris*. None of the *S. opinator* larvae developed into puparia during the 14 days of the trial. The mean gain in larval mass per day was highest for *S. pyrastris*, and lowest for *S. opinator* for the length of the experiment, especially during the second week (Fig. 2.2a). The mean number of *B. brassicae* killed per day (Fig. 2.2b), as well as for the mean cumulative number of *B. brassicae* killed over time (Fig. 2.2c) were highest for *S. pyrastris*, followed by *E. fumipennis* and finally *S. opinator*. The mean total number of *B. brassicae* killed by *E. fumipennis* was similar to that for *S. pyrastris*, but one day later, and the mean total number killed by *S. opinator* was only about 75% of the total for the other two species after 14 days (Fig. 2.3c). The length of the second laboratory experiment was extended to one month to observe the relatively slow developmental rates and voracity for *S. opinator*.

In the second laboratory experiment, the mean larval development time (+/- SE) from two day old first instars to puparium for *E. fumipennis* was 10.4 days (± 0.4). Three individuals of *S. sulphuripes* developed into puparia with a mean time of 26.3 days (± 2.4), and no individuals of *S. opinator* developed into puparia during the 32 days of the experiment. The mean gain in larval mass per day for *E. fumipennis* was much greater than that for both *S. opinator* and *S. sulphuripes*, and the rate for *S. opinator* was slightly higher than that for *S. sulphuripes* for most of the experiment (Fig. 2.3a). The developmental rates for *E. fumipennis* and *S. opinator* were similar to those in the first laboratory experiment (Figs. 2.2a, 2.3a). The mean number of *B. brassicae* killed per day was also much greater for *E. fumipennis* than the other two species, which were similar to

each other (Fig. 2.3b). The mean cumulative number of *B. brassicae* killed per unit time showed a similar trend among the three species (Fig. 2.3c). The mean number of aphids killed per day and the mean cumulative number of aphids killed per day by *E. fumipennis* and *S. opinator* in the first two weeks were similar to that seen in the first laboratory experiment (Figs. 2.2c, 2.3c), but the mean cumulative number of aphids killed by *S. opinator* gradually increased to a level similar to that seen for *E. fumipennis* when the *S. opinator* were allowed to feed on the aphids for the additional two weeks (Fig. 2.3c).

The number of aphids killed per day by a hoverfly larva can vary greatly depending on the size distribution of aphids used, and the mean change in mass of *B. brassicae* per day was quantified to provide a standardized measurement of consumption. The trends of differences seen among species for the mean number of aphids killed per day and the mean cumulative number of aphids killed per day were similar to the mean change in aphid mass per day and the mean cumulative change in aphid mass per day (Fig. 2.4).

The second laboratory experiment also included a treatment with one individual each of *E. fumipennis* and *S. opinator* in the same arena. The rates of larval development were similar for each species in the first five days of the experiment when compared to arenas without competing hoverfly individuals, but all of the *S. opinator* individuals were dead by the sixth day when included with *E. fumipennis* (Fig. 2.5a). The mean larval development time (+/- SE) of *E. fumipennis* under competition was 9.8 days (± 0.3). The mean number of *B. brassicae* killed per day in these arenas appeared to be greater than that seen for *E. fumipennis* in arenas without *S. opinator* (Fig. 2.5b), but the mean

cumulative number of *B. brassicae* eventually killed did not appear to be different from arenas without *S. opinator* (Fig. 2.5c).

Discussion

The rates of larval development and aphid consumption were consistently higher for *S. pyrastris* than those of *E. fumipennis*, and these rates for *E. fumipennis* were substantially higher than those of both *S. opinator* and *S. sulphuripes*. The slow larval development and low voracity rates of *S. opinator* and *S. sulphuripes* could not be distinguished between. *S. pyrastris* has been shown to be the most voracious hoverfly species of *B. brassicae* in cauliflower fields (Makhmoor and Verma 1987), but this hoverfly species is usually seen attacking *B. brassicae* in smaller garden plots of brassica plants and not in larger crop fields in the Willamette Valley of Oregon. The other three hoverfly species in this study are the most common species seen on broccoli plants in larger broccoli crop fields in this area (Ambrosino 2006), as well as being the three most common predatory hoverfly species foraging on floral resources next to these crop fields (Ambrosino et al. 2006). The unsuccessful development and lower voracity of *S. opinator* and *S. sulphuripes* on *B. brassicae* could be an indication that they prefer other aphid species, such as *Myzus persicae* (Sulzer), which are also present on most broccoli plants in this region. When starved, hoverfly larvae reappropriate some of the available energy from production to maintenance, and the developmental time becomes extended (Barlow 1979). Alternatively, the larvae of these two species appear to be more sedentary and have thinner cuticles than that of *E. fumipennis*, and may have been limited by certain artificial conditions in the experimental arenas. A final possibility for the

prolonged development of these two species could be a facultative diapause, which has been seen in the larvae of many hoverfly species (Schneider 1948; Dzioczek 2005), but the experimental conditions were held constant and not performed at a time of year where such a response would be expected.

Although only a few individuals of *S. sulphuripes* and no individuals of *S. opinator* successfully developed into puparia, they remained alive and fed on *B. brassicae* for up to one month. The larvae of these two species appeared to develop very slowly, but they continued to kill aphids, and the mean cumulative number of *B. brassicae* killed and the mean cumulative change in *B. brassicae* mass eventually reached higher levels than that seen for *E. fumipennis* after a period of three to four weeks. This indicates that these two species may also be important for limiting *B. brassicae* colonies on broccoli plants if they arrive early enough or when there are few *E. fumipennis* present. Some hoverfly species have a preference for aphid host prey of certain sizes (Agarwala et al. 1989), and non-preferred prey can be killed by a larva, but not accepted for feeding, (Meyling 2003). The aphid mass consumed was considered to be a better measure of voracity than the number of aphids killed. Conversion equations were not used to calculate aphid mass because these can be inaccurate (Laska 1984). The trends in mean change in aphid mass were very similar to the mean change in aphids killed for each species, probably because similar aphid size distributions were used throughout the investigation.

When *E. fumipennis* and *S. opinator* individuals were placed in the same arena with unlimited amounts of *B. brassicae*, the rate of development of *E. fumipennis* was slightly faster, but the cumulative amount of *B. brassicae* killed was slightly less than that

for arenas containing only *E. fumipennis*. While the rate of development for *S. opinator* larvae competing with *E. fumipennis* was also slightly more rapid during the first few days when compared to that seen in arenas containing only *S. opinator*, the mortality was much higher. This effect of more rapid development but greater mortality under controlled conditions of interspecific competition has been seen for other hoverfly species (Hagvar 1972). Eggs of *E. fumipennis* and *S. opinator* are commonly found together in close proximity on broccoli plants, and it is possible that some competition occurs among hoverfly species on certain parts of the plant. Where competition for *B. brassicae* from other hoverfly species does occur, it could reduce the *per capita* consumption rates of *E. fumipennis* even if *B. brassicae* resources were unlimited. Competition for *B. brassicae* between hoverflies and other aphidophaga has also been demonstrated, and the degree of competition also depends on the timing of arrival (Kindlmann and Ruzicka 1992).

It is also possible that these hoverfly species and other aphidophaga could prey upon each other, with the outcomes of such encounters depending on which species happens to be largest at the time of the encounter (Hindayana 2001), and relative densities of hoverfly larvae and aphids (Branquart et al. 1997). The dead *S. opinator* in the arenas did not appear different from *S. opinator* that had died of other causes in other treatments, and so they may not have been preyed upon by *E. fumipennis*. In the broccoli fields in this area, the natural enemies that would most likely have higher order effects on hoverfly eggs and larvae, and therefore reduce their aphid-limiting potential, would most likely be spiders and parasitoid wasps that are specialists for hoverflies, although the parasitoids do not always greatly reduce larval voracity (Tinkeu et al. 1998). Any

reduction in aphid-limiting potential of hoverflies that might occur from the activity of predators would likely be greater than reductions that might occur from competition for aphids among hoverfly species or other aphidophaga.

Even though *E. fumipennis* larvae displayed a greater aphid-limiting potential than *S. opinator* in the laboratory arenas, this effect was not seen on plants in cages in the glasshouse. Although the first instar of some species of hoverfly larvae exhibit a directed search toward aphid prey (Bargen et al. 1998), in their initial search, larvae generally exhibit relatively random foraging patterns guided primarily by photo- and geo-tactic cues, as opposed to more directed patterns guided by visual or olfactory cues from the prey (Bansch 1966; Chambers 1988). Once cues for larval arrestment are sufficient (Rotheray 1983), hoverfly larvae can display either sit and wait or active foraging strategies (Gries 1986). Certain hoverfly species will migrate off individual plants in voracity experiments when aphid numbers get low (Chambers 1986), but many of the *E. fumipennis* larvae in this study left the plants on the first day when aphids were most abundant and many of the individuals were found foraging on the insides of the cages. Although an attempt was made to simulate the likely spatial foraging range of hoverfly larvae that occur in the field, it is possible that the plants in the cages did not provide the substrate that *E. fumipennis* prefers for foraging (eg. wide plant stems or dense canopy) and they migrated to find such substrates. The larvae were spending less time overall close to the aphids on the plants and their ability to kill aphids per unit time was enhanced in the smaller space of laboratory arenas relative to *S. opinator*, which displayed a similar sedentary behavior on both the caged plant and laboratory arena substrates. The effect of increased voracity in smaller enclosures that results from scale-

dependant attack rates has been seen for other hoverfly species with mobile larvae (Barlow 1979).

The predatory efficiency of hoverfly larvae can vary based on environmental factors. An initial attempt was made in this study to mimic the conditions that could represent those seen at *B. brassicae* colonies on broccoli plants. The mobile foraging behavior of the larvae of *E. fumipennis* made assessment of their voracity on plants in cages difficult, and so smaller arenas were used to provide more objective voracity comparisons among species. Care has to be taken in the design of these arenas, since the type of functional response observed can be a result of experimental design (van Alphen and Jervis 1996). Aside from alterations in the rates of attack, development and voracity of hoverfly larvae, their preferences for aphid prey species can also be altered by the type of laboratory arena when prey that are difficult to find or catch on a plant become more suitable in the lab (Sadeghi and Gilbert 2000). As long as prey densities, patch sizes and encounter rates offered in the experimental settings are carefully chosen to be within the range of those found in nature, then the information provided by voracity experiments can be used for valid comparisons (van Alphen and Jervis 1996).

This study evaluated the most important hoverfly species that appear on broccoli by comparing the maximum potential voracities among them. The functional response is useful for calculating the number of aphids killed per day by different stages or sizes of predator as well as for characterizing the response at low prey densities, but it is only one of the responses that influence predator efficiency, and it can vary based on the experimental design or the time interval used (van Alphen and Jervis 1996). The functional response of the different sizes and instars of each species to different aphid

densities was not calculated in this study because only a small number of larvae were available from the hoverfly colonies of each species at any given time. The use of maximum potential voracity was sufficient to assess the potential of each of these species for limiting colonies of *B. brassicae* on plants. The mean number of *B. brassicae* killed per day, the total cumulative voracity, and the larval developmental rates were higher in this study than that seen for the voracity and development of other species (Debaraj and Singh 1998), which could be a result of real differences in the capacity of the species, or the fact that unlimited amounts of *B. brassicae* were not provided to those species in other studies. It is important to remember that the values determined for each species determined in the lab are useful for comparing the species, but are likely the highest possible values, since other important aspects of killing efficiency, such as search time, capture efficiency and handling time (Hagvar 1974) are diminished in small enclosures. The actual aphid limiting potential of these species is probably closer to that seen in the glasshouse cages. It appears that *E. fumipennis* is the most active natural enemy attacking *B. brassicae* in commercial broccoli fields, but it would also be useful to further investigate the life history traits of *S. pyrastris* to find out why it is not exploiting aphid resources available to it in commercial broccoli fields.

Acknowledgements

This study was funded by the Western Region Sustainable Agriculture, Research and Education program of the United States Department of Agriculture. We would like to thank Amanda Griffith for help with the hoverfly and aphid colonies, and Dr. Piotr Bebas for help with translations.

References Cited

- Agarwala, B. K., A. K. Bhaumik, and F. S. Gilbert. 1989. Relative development and voracity of six species of aphidophagous syrphids in cruciferous crops. *Proceedings of the Indian Academy of Sciences, Animal Sciences* 98: 267-274.
- Ambrosino, M. D., Luna, J. M., Jepson, P. C., and Wratten S. D., 2005. The relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects and herbivores. *Env. Entomol.*, In Press.
- Ambrosino, M. D. 2006. Enhancing the predatory potential of hoverflies on aphids in Oregon broccoli fields with floral resources. Ph.D. Thesis. Oregon State University.
- Ankersmit, G. W., H. Dijkman, N.J. Keuning, H. Mertens, A. Sins & H.M. Tacoma. 1986. *Episyrphus balteatus* as a predator of the aphid *Sitobion avenae* on winter wheat. *Entomol. Exp. Appl.* 42: 271-277.
- Bansch, R. 1966. On prey-seeking behaviour of aphidophagous insects., pp. 123-128. *In* I. Hodek [ed.], *Proc. Prague Symposium Ecology of Aphidophagous Insects*. Academia, Prague.
- Bargen, H., K. Saudhof, and H. M. Poehling. 1998. Prey finding by larvae and adult females of *Episyrphus balteatus*. *Entomol. Exp. Appl.* 87: 245-254.
- Barlow, C. A. 1979. Energy utilization by larvae of the flower fly, *Syrphus corollae* (Fabr.) (Dipt., Syrphidae). *Can. Entomol.* 111: 897-904.
- Branquart, E., J. L. Hemptinne, C. Bauffe, and L. Benfekih. 1997. Cannibalism in *Episyrphus balteatus* (Dipt.: Syrphidae). *Entomophaga* 42: 145-152.
- Chambers, R. J. 1986. Preliminary experiments on the potential of hoverflies (Diptera: Syrphidae) for the control of aphids under glass. *Entomophaga*: 197-204.
- Chambers, R. J. 1988. Syrphidae, pp. 259-270, Chapter 9.2.3. *In* A. K. Minks, and Harrewijn, P. [eds.], *Aphids: their biology, natural enemies, and control*. Elsevier.
- Debaraj, Y., and T. K. Singh. 1998. Studies on some aspects of prey-predator interaction with reference to cabbage aphid, *Brevicoryne brassicae* (L.) and its predatory insects. *Journal of Advanced Zoology* 19: 50-54.
- Dziock, F. 2005. Evolution of prey specialization in aphidophagous syrphids of the genera *Melanostoma* and *Platycheirus* (Diptera : Syrphidae) - 1. Body size, development and prey traits. *Eur. J. Entomol.* 102: 413-421.

- George, K. S. 1957. Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). Bull. Entomol. Res. 48: 619-629.
- Hagvar, E. B. 1972. The effect of intra- and interspecific larval competition for food (*Myzus persicae*) on the development at 20 C of *Syrphus ribesii* and *Syrphus corollae* [Diptera: Syrphidae]. Entomophaga 17: 71-77.
- Hagvar, E. B. 1974. Effectiveness of larvae of *Syrphus ribesii* and *S. Corollae* (Diptera: Syrphidae) as predators on *Myzus persicae* (Homoptera: Aphididae). Entomophaga 19: 123-134.
- Hindayana, D., R. Meyhofer, D. Scholz, and H. M. Poehling. 2001. Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. Biol. Control.: 236-246.
- Huges, R. D. 1963. Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). J. Anim. Ecol. 32: 393-424.
- Kindlmann, P., and Z. Ruzicka. 1992. Possible consequences of a specific interaction between predators and parasites of aphids. Ecol. Model. 61: 253-265.
- Lal, R., and E. Haque. 1955. Effect of nutrition under controlled conditions of temperature and humidity on longevity and fecundity of *Sphaerophoria scutellaris* (Fabr.) (Syrphidae, Diptera) - efficacy of its maggots as aphid predators. Indian J. Entomol. 17: 317-325.
- Laska, P. 1984. A method of comparing the role of aphid parasitoids and predators exemplified by the cabbage aphid, *Brevicoryne brassicae*. Acta Entomol Bohemoslov. Praha : Ceskoslovenska akademie ved 81: 81-89.
- Makhmoor, H. D., and A. K. Verma. 1987. Bionomics of major aphidophagous syrphids occurring in mid-hill regions of Himachal Pradesh. Journal of Biological Control 1: 23-31.
- Meyling, N. V., A. Enkegaard, and H. Brødsgaard. 2003. Two *Anthocoris* bugs as predators of glasshouse aphids – voracity and prey preference. Entomol. Exp. Appl. 108: 59-70.
- Petherbridge, F. R., and J. E. M. Mellor. 1936. Observations on the life history and control of the cabbage aphid, *Brevicoryne brassicae* L. Annal. Appl. Biol. 23: 329-241.

- Rojo, S., K. R. Hopper, and M. A. Marcos Garcia. 1996. Fitness of the hover flies *Episyrphus balteatus* and *Eupeodes corollae* faced with limited larval prey. *Entomol. Exp. Appl.* 81: 53-59.
- Rotheray, G. E., and Martinat, P. 1984. Searching behaviour in relation to starvation of *Syrphus ribesii*. *Entomol. Exp. Appl.* 13: 194-207.
- Sadeghi, H. 2002. The relationship between oviposition preference and larval performance in an Aphidophagous hover fly, *Syrphus ribesii* L. (Diptera: Syrphidae). *J. Agric. Sci. Technol.* 4: 1-10.
- Sadeghi, H., and F. Gilbert. 1999. Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. *Oecologia* 118: 405-411.
- Schneider, F. 1948. Beitrag zur Kenntnis der Generationsverhältnisse und Diapause räuberischer Schwebfliegen (Syrphidae, Dipt.). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 21: 249-285.
- Scott, S. M., and C. A. Barlow. 1984. Effect of prey availability during development on the reproductive output of *Metasyrphus corollae* (Diptera: Syrphidae). *Environ. Entomol.* 13: 669-674.
- Scott, S. M., and C. A. Barlow. 1990. Effect of hunger on the allocation of time among pea plants by the larvae of an aphidophagous hover fly, *Eupeodes corollae* (Dipt.: Syrphidae). *Entomophaga* 35: 163-172.
- Soleyman Nezhadiyan, E., and R. Laughlin. 1998. Voracity of larvae, rate of development in eggs, larvae and pupae, and flight seasons of adults of the hoverflies *Melangyna viridiceps* Macquart and *Symosyrphus grandicornis* Macquart (Diptera: Syrphidae). *Aust. J. Entomol.* 37: 243-248.
- Sood, A. K., K. C. Sharma, K. L. Kakar, C. Usha, and U. Chauhan. 1994. Use of intrinsic rate of increase in the evaluation of biocontrol potential of a syrphid predator *Eupeodes frequens* Matsumura (Diptera : Syrphidae) of the chrysanthemum aphid *Macrosiphoniella sanborni* (Gillette) (Homoptera : Aphididae). *Annal. Entomol.* 12: 39-42.
- Tamaki, G. 1974. Life system analysis of the autumn population of *Myzus persicae* on peach trees. *Environ. Entomol.* 3: 221-226
- Tinkeu, L. N., G. Delabye, D. Stilmant, and T. Hance. 1998. Phenology of parasitism and its influence on the predatory efficiency of larvae of *Episyrphus balteatus* (Diptera: Syrphidae). *Integrated control in cereal crops IOBC Bulletin* 21: 133-139.

- van Alphen, J. J. M., and M. A. Jervis. 1996. Foraging Behaviour, pp. 1-62. *In* M. Jervis and N. Kidd [eds.], *Insect Natural Enemies*. Chapman and Hall, London.
- van Emden, H. F. 1963. A field technique for comparing the intensity of mortality factors acting on the cabbage aphid, *Brevicoryne brassicae* (L.) (Hem.: Aphididae), in different areas of a crop. *Entomol. Exp. Appl.* 6: 53-62.
- Wnuk, A., and E. Wojciechowicz. 1993. Syrphid predators (Diptera, Syrphidae) occurring in colonies of the cabbage aphid, *Brevicoryne brassicae* (L.), on cabbage and cauliflower. *Polskie Pismo Entomologiczne* 62: 215-22.

Figure 2.1. Mean numbers (with SE) of *B. brassicae* on plants in cages with *E. fumipennis*, *S. opinator*, or no hoverfly larva.

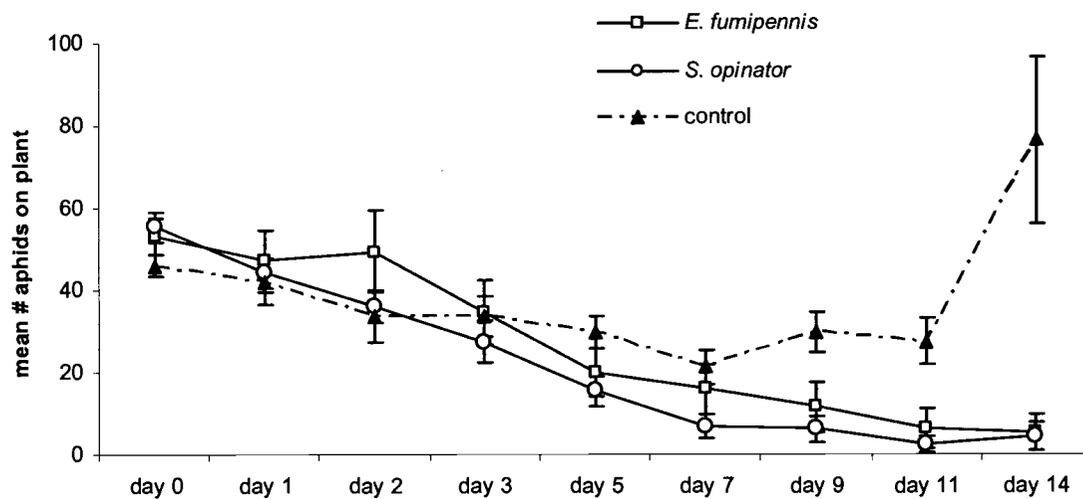


Figure 2.2. First laboratory experiment. The daily a) mean larval weight gain, b) mean number of *B. brassicae* killed and C) cumulative mean number of *B. brassicae* killed (with standard errors) in enclosures with *S. pyrastris*, *E. fumipennis*, or *S. opinator*.

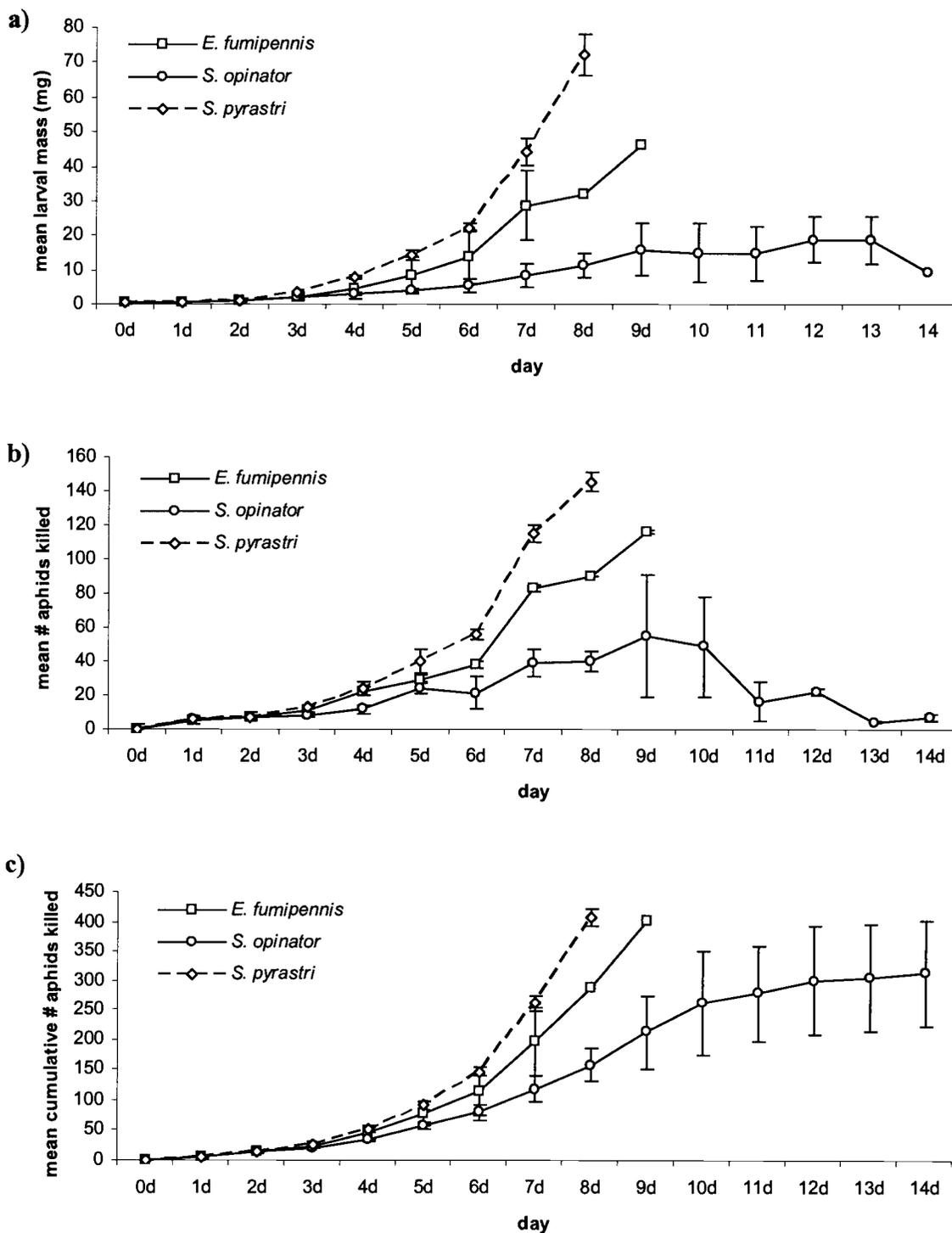


Figure 2.3. Second laboratory experiment. The daily a) mean larval weight gain, b) mean number of *B. brassicae* killed and C) cumulative mean number of *B. brassicae* killed (with standard errors) in enclosures with *E. fumipennis*, *S. opinator*, or *S. sulphuripes*.

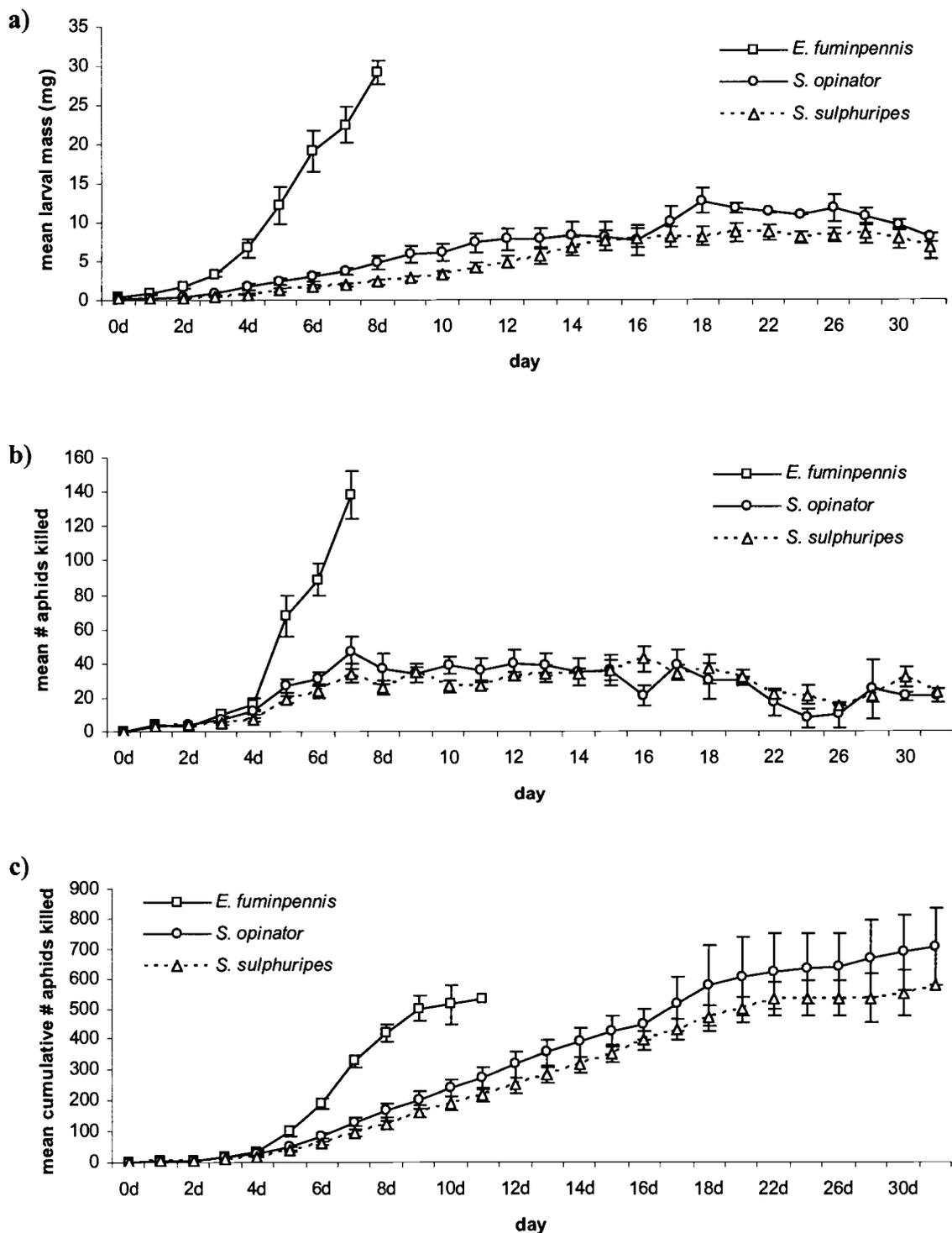
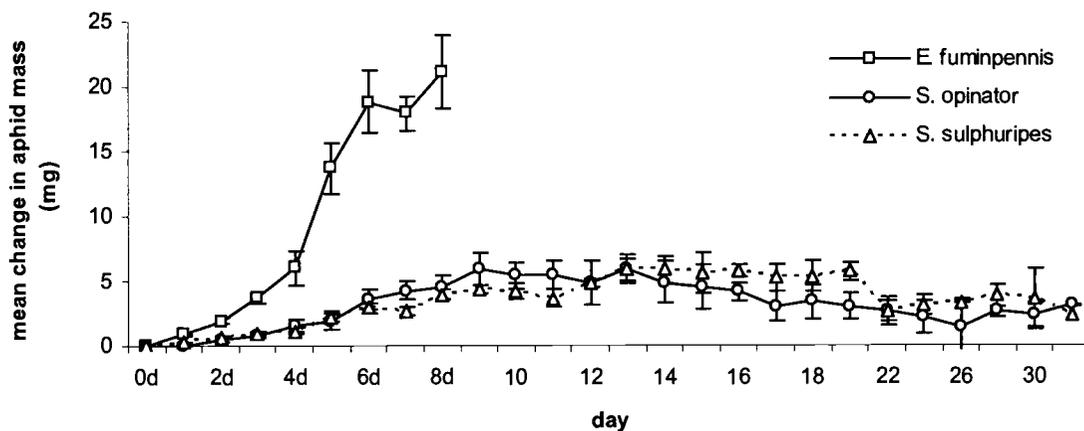


Figure 2.4. Second laboratory experiment. The daily a) mean change in aphid mass, and b) mean cumulative change in aphid mass (with standard errors) in enclosures with *E. fumipennis*, *S. opinator*, or *S. sulphuripes*.

a)



b)

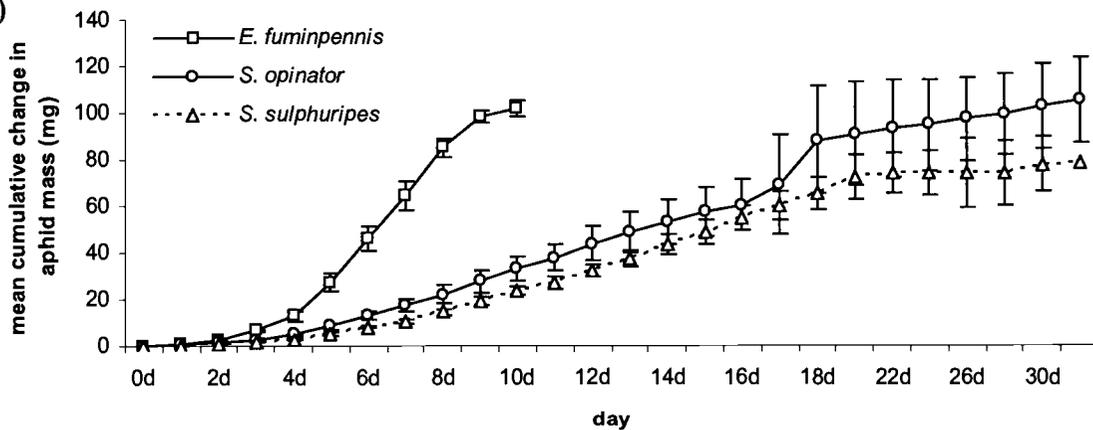
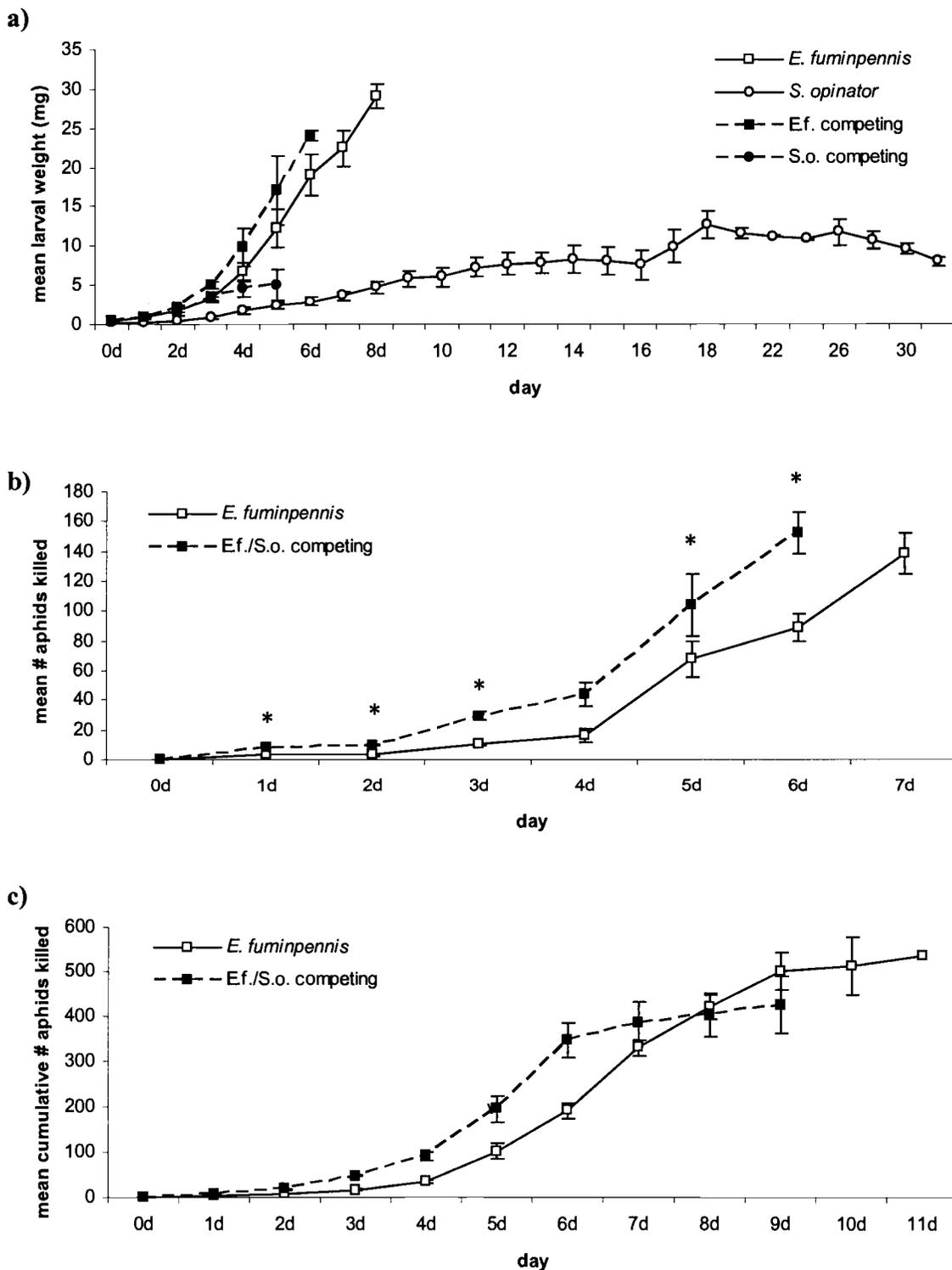


Figure 2.5. Second laboratory experiment. The daily a) mean larval weight gain, b) mean number of *B. brassicae* killed and C) cumulative mean number of *B. brassicae* killed (with standard errors) in enclosures with *E. fumipennis*, *S. opinator*, or these two species competing together in the same enclosure. (Points with an asterisk are significantly greater than the other mean at $\alpha = 0.05$).



MANUSCRIPT 3

**THE RELATIVE FREQUENCIES OF VISITS TO SELECTED INSECTARY PLANTS BY
PREDATORY HOVERFLIES (DIPTERA: SYRPHIDAE), OTHER BENEFICIAL INSECTS AND
HERBIVORES**

AUTHORS:

M.D. Ambrosino, J.M. Luna, P.C. Jepson, and S.D. Wratten

JOURNAL:

In press:

Environmental Entomology

Entomological Society of America

10001 Derekwood Lane, Suite 100

Lanham MD, 20706-4876

**THE RELATIVE FREQUENCIES OF VISITS TO SELECTED INSECTARY PLANTS BY
PREDATORY HOVERFLIES (DIPTERA: SYRPHIDAE), OTHER BENEFICIAL INSECTS AND
HERBIVORES**

Abstract

The use of insectary plants in agroecosystems to provide floral resources for enhancing natural enemy activity is an increasingly used practice, but candidate flowering plant species are not always screened for their attractiveness to key arthropods in the system being studied. In the work presented here, the relative attractiveness of four species of insectary plants to beneficial and pest insect species was assessed by observing the relative frequencies of flower visits to replicated blocks of the insectary flowers in two Oregon broccoli fields. The four plant species tested were alyssum (*Lobularia maritima* (L.) Desv.), coriander (*Coriandrum sativa* L.), buckwheat (*Fagopyrum esculentum* Moench), and phacelia (*Phacelia tanacetifolia* Benth.). Predatory hoverflies (Syrphidae) were identified to species, where possible, due to their previously observed importance as aphid predators in broccoli fields in the study area. The other beneficial insect groups observed were in the families Apidae, Coccinellidae, Tachinidae and Vespidae, and the three main pest species were western tarnished plant bug (*Lygus hesperus* Knight), western spotted cucumber beetle (*Diabrotica undecimpunctata undecimpunctata* Mannerheim), and imported cabbageworm (*Pieris rapae* (L.)). The Syrphidae visited mostly coriander, but this 'preference' was probably influenced by competition from other foragers. Bumblebees and the three pest species visited mostly phacelia, and other species groups were less consistent in their flower choices. The different insect preferences for flowers are discussed in terms of the key

influencing factors which should be considered when assessing the relative attractiveness of insectary plants in the field.

Keywords: Hoverflies, Syrphidae, insectary plants, floral resources, natural enemies

Introduction

Floral resources such as nectar and pollen are important for the growth, development, survival and reproduction of many invertebrate predators and parasitoids (Jervis and Kidd 1996, Landis et al. 2000). Reports of the use of floral pollen and nectar, and extra floral nectar, by a wide range of insect predator and parasitoid families, including the Coccinellidae, Chrysopidae, many parasitoid wasp families, Tachinidae and Syrphidae are widespread (Jervis et al. 1993, Long et al. 1998, al Doghairi and Cranshaw 1999). Plants providing these resources can be added to agroecosystems to conserve and enhance these natural enemies (reviewed in Landis et al. 2000, Pfiffner and Wyss 2004). While candidate plant species under consideration for the augmentation of floral resources should ultimately be screened for a wide range of attributes including their agronomic and economic compatibility with the cropping regime (Gurr et al. 1998), their relative attractiveness to key natural enemy and pest herbivore species in or near the crop field is an important initial consideration.

The relative attractiveness of plant species of available flowers has been demonstrated in some well-studied groups such as the hymenopteran pollinators, and complete specificity in this group is rare (Waser et al. 1996, Goulson 2003). The selective use of floral resources by natural enemies and pests has been reported to a lesser extent, but significant progress needs to be made in this area in order to advance precision in the use of insectary plantings to enhance biological control (Jervis and Kidd 1996, Gurr et al. 2004).

Floral resources are especially important for predatory hoverfly adults, many species of which need to feed on nectar for energy and pollen for gametogenesis

(Schneider 1948, Sturken 1964). Hoverflies use floral resources selectively (Gilbert 1981), although this can vary among species (Haslett 1989a). The differential attractiveness of specific species of flowering plants to hoverflies has been identified in observational studies (Cowgill et al. 1993, Haslett 1989a), as well as in formal experiments (Colley and Luna 2000, Lövei et al. 1993). For those flowers that a community of hoverflies can access, it is not always known whether individuals of a given species or sex are selecting between these resources based on cues and rewards relating individually or in combination, to multiple possible factors (Table 3.1).

Even if there are multiple mechanisms by which a hoverfly individual chooses one flower type or patch over another, differential visitation and feeding patterns observed within the local hoverfly assemblage at specific flower types can still serve as an indicator of preferred floral resources that are more likely to enhance hoverfly predatory activity in a given context. The relative attractiveness of eleven species of insectary plants in garden plots to hoverflies as a group was assessed in previous trials in the Willamette Valley, OR (Colley and Luna 2000), and four of these plant species, alyssum (*Lobularia maritima* (L.) Desv.), coriander (*Coriandrum sativa* L.), buckwheat (*Fagopyrum esculentum* Moench), and phacelia (*Phacelia tanacetifolia* Benth.), were ranked highly on the basis of feeding visit frequencies. Of these, alyssum and coriander are introduced, and all four are cultivated plants. Certain hoverfly species have been found to be the most prevalent aphid natural enemies foraging before harvest within Willamette Valley broccoli fields for the cabbage aphid, *Brevicoryne brassicae* (L.), and the green peach aphid, *Myzus persicae* (Sulzer) (unpublished data). The current work quantified the relative attractiveness of the four insectary plants to these species of

hoverflies and other key beneficial and pest arthropods present in these broccoli fields to screen them before use as insectary plantings in large-scale field experiments.

Materials and Methods

Experimental Design. The experiments were set up at two locations in the Willamette Valley in Oregon in late March 2000. A 2 m x 66 m insectary plant strip was planted at one edge of a newly planted broccoli field in each site. The strip at each site was divided into three randomized blocks, each containing four 2 m x 5.5 m plots of the four plant species. Alyssum and coriander were transplanted in 5 rows in each plot, with a within-row spacing of 40 cm, and 90 cm between rows. Buckwheat and phacelia were sown in nine rows, and thinned to 15 cm within rows, with 45 cm between rows.

Field Sites. The North Site was near Corvallis, OR. The plots were planted/sown 23 March, 2000, 25 days after transplanting (DAT) broccoli in a 15 ha field bordered by corn, strawberry, and grass seed crops on each of three sides, and mature filberts on the fourth side. The South Site was near Eugene, OR, about 90 km south of the North Site. The flowers were planted 24 March, eight DAT broccoli in a 15 ha field bordered by grass seed crops on two sides, young filbert trees on a third side, and a squash field on the fourth side.

Sampling Procedure. Flowering dates, floral densities and arthropod visits were recorded on four dates from 12 July to 2 August at the North Site, and on three dates from 16 - 30 July at the South Site. Relative floral density among treatments on each sampling date was quantified by estimating the number of open flowers in 1 m² quadrats.

The visits made by hoverfly species and other arthropod taxa were quantified by visual observation. Data were also recorded on western tarnished plant bug (*Lygus hesperus* Knight), western spotted cucumber beetle (*Diabrotica undecimpunctata undecimpunctata* Mannerheim), imported cabbageworm (*Pieris rapae* (L.)), as well as the beneficial groups lady beetles (Coccinellidae), vespid wasps (Vespidae), honey bees (*Apis* spp.) and bumble bees (*Bombus* spp.). Reference specimens of all of these taxa were first collected from the plots and then used to confirm sight images for the observer. Observations were made only at times close to mid-day and during sunny conditions to assure accuracy and validity. Since many flower-visiting arthropods are sensitive to the motion and presence of the observer, a stationary technique was used whereby the observer remained motionless and did not cast a shadow on the plots. The number of visits to flowers observed over minute in a 1 m² area of each plot were recorded for each taxon.

Statistical Analysis. The numbers of floral visits by each insect species were pooled across sampling dates and were compared between sites using a two-way analysis of variance (GLM procedure, SAS, 1990). To evaluate effect of flower species on floral visitation, data were pooled across dates for each insect species and transformed using square root ($x + 0.5$). Analysis of variance and an F-protected Least Significant Difference (LSD) test were used to compare mean values (SAS, 1990).

Results

Site Effect on Insect Visitation to Flowers.

More hoverfly species were observed visiting flowers at the North Site, than at the South Site, and there were more frequent flower visits by predatory hoverfly species at the North Site as well ($p = 0.001$) (Table 3.2). *Eupeodes fumipennis* (Thomson), an aphid predator in Oregon broccoli fields, was the most frequent predacious hoverfly visiting flowers at both sites. Two other hoverfly species known to feed on aphids in broccoli, *Sphaerophoria sulphuripes* (Thomson) and *Syrphus opinator* (Osten Sacken), (unpublished data) were found on the flowers only at the North Site. *Toxomerus* spp. (composed of *T. marginatus* (Say) and *T. occidentalis* Curran) were observed visiting flowers at both sites, however *Toxomerus* spp. have not been linked to aphid predation in broccoli. *Melanostoma mellinum* (L.) and *Platycheirus quadratus* (Say) were also present over the flowers at only the North Site in small numbers, but were not observed feeding on them. The non-predatory *Eristalis* spp. were more abundant at the flowers at the South Site ($p = 0.003$) (Table 3.2).

The pest species observed were the same at each site, with greater flower visitation by *D. undecimpunctata undecimpunctata* at the North Site ($p < 0.0001$). The beneficial taxa other than hoverflies were the same at each site, with the South Site having greater numbers of *Apis* spp. ($p = 0.004$), Coccinellidae ($p = 0.001$), and Vespidae ($p = 0.0003$) at the flowers than the North Site.

Relative Frequencies of Flower Visits.

For the hoverflies at the North Site, the predatory species as a group visited coriander to a much greater extent than phacelia or alyssum, with a similar number of visits to buckwheat (Fig. 3.1A). Coriander was also favored over the other three flower

species by the predatory *S. sulphuripes* and the non-predatory *S. pipiens*. *Platycheirus stegnus* visited buckwheat more than alyssum and phacelia, but showed a similar number of visits to coriander. No floral preferences were detected for the predatory hoverflies *E. fumipennis*, *Toxomerus* spp. and *S. opinator*. *Eristalis* spp. visited coriander more frequently than buckwheat or phacelia at this site (Fig. 3.1A). At the South Site, only hoverflies of the taxon *Eristalis* spp. were seen visiting coriander, with nearly four times as many visits to coriander as the other flower species (Fig. 3.2A). Among the other remaining flowers (other than coriander), *E. fumipennis* visited phacelia more frequently than alyssum (Fig. 3.2A).

The pest species *L. hesperus* and *P. rapae* were seen visiting phacelia more often than the other three flowers at the North Site, while *D. undecimpunctata undecimpunctata* preferred phacelia and buckwheat over coriander and alyssum (Fig. 3.1B). This same trend was not evident at the South Site however, with *L. hesperus* and *D. undecimpunctata undecimpunctata* preferring phacelia over only alyssum (Fig. 3.2B).

Among the beneficial insect visitors, bumblebees (*Bombus* spp.) demonstrated a much higher visitation rate at phacelia at both sites (Figs. 3.2A, 3.2B). *Apis* spp. visited alyssum less frequently than the other three plant species at both sites (Figs. 3.2A, 3.2B). For natural enemies other than hoverflies, members of the Coccinellidae visited buckwheat and coriander more than phacelia and alyssum at both sites, while members of the Vespidae primarily visited buckwheat (Figs. 3.2A, 3.2B).

Relative Floral Densities Over Time.

The flowering canopies fully closed by the first sampling date in all flower treatments at both sites except the alyssum, which still had some small gaps of less than 15 cm on the first sampling date. Alyssum, buckwheat and phacelia had approximately 10,000 open flowers per m² at each site over all sampling dates. Coriander, with its compound umbel flower arrangement, had approximately 90,000 open flowers per m² on the first sampling date at each trial, but this number gradually decreased to the same numbers seen for the other three flowers by the final sampling date (data not shown).

Discussion

The clearest differentiation in relative visitation of flowers by insects was not seen for the predatory hoverfly species, but rather *Bombus* spp. and the three main flower-visiting crop pests in the local broccoli system (*D. undecimpunctata undecimpunctata*, *P. rapae* and *L. hesperus*). They visited phacelia more frequently than they did alyssum and coriander at the North Site and were also attracted to buckwheat to a lesser extent. At the South Site, *Bombus* spp. visited phacelia even more frequently, but the relative 'attraction' of the three pest species to phacelia was not as marked as that seen at the North Site. The predatory hoverflies as a group visited mainly coriander at the North Site, but not at the South Site.

One potential explanation for these site differences in pest and hoverfly visitation might be that the relatively high visitation at phacelia by *Bombus* spp. at the South Site caused a displacement of the three pest species. Similarly, the relatively high visitation at coriander by larger, non-predatory hoverflies of the genus *Eristalis* and the equally large

Apis spp. at the South Site versus the North Site may have displaced the predatory hoverfly species. Similar types of inter-specific interference and displacement from foraging competition (Kikuchi 1962, 1963, 1965, Morse 1981) and territoriality (Wellington and Fitzpatrick 1981) among these floral visitors have been demonstrated.

In addition to competition, there are other factors which can contribute to attraction to a particular flower type that should be considered when addressing these inconsistencies between fields. The quality and abundance of floral resources in time and space (ie. nectar and pollen volumes, flower abundance, density and dispersion) can affect the degree of selectivity among floral foragers (Thomson 1981, Waser 1996). Organisms foraging for resources are often observed to be generalists over broad geographical ranges, but may appear to be more specialized when restricted to local communities, so specialization is a flexible attribute when considered at the level of a population (Fox and Morrow 1981). The quality and amount of floral resources has been shown to affect the overall abundance of foraging hoverflies (Ruppert and Molthan 1991, Sutherland et al. 1997; 2001), as well as their competitive interactions (Kikuchi 1963).

If floral resources are not limiting in a given area, however, the degree of selectivity expressed by floral foragers would not be expected to be as greatly affected (Kikuchi 1963, Toft 1983). In this study, the scale of comparison for the relative attractiveness to flowers was among 10 m² plots in a 130 m² strip. Although care was taken to keep the immediate area around the flower blocks free of flowering weeds, there were some flowering weeds present within the foraging range of the observed floral foraging species on the sampling dates, so it is likely that most of these species were not

severely limited for floral resources. Within the experimental flower plots, the actual quantities of pollen and nectar resources were not quantified beyond flower density, since these can vary among individual flowers. The relative mean densities of flowers were higher in the coriander plots on the first two sampling dates at each trial, but there always appeared to be enough available flowers and foraging space in the plots of each plant species, so this floral density difference was not included in the analysis.

Factors relating to the foraging hoverfly individual, such as what they may have learned about relevant cues in the recent past (Goulson and Wright 1998), or changing nutritional requirements over the course of their life (Haslett 1989a, Hickman et al. 2001), will also contribute to differences in visitation with all other factors being equal. Assessing the influence of these factors relating to the individual require specific methods and experimentation, such as tracking the foraging paths of individuals, which can be difficult to perform accurately with hoverflies (Goulson and Wright 1998). This study used the more feasible direct behavioral observation of flower visiting frequencies among flower blocks to estimate the relative attractiveness of the flower types, but observation of visitation frequency is also a function of the time the individual spends at the flower, the spatial pattern of flowers, and the travel time between flowers (Kearns and Inouye 2001). Whether or not certain individuals were switching among flower types, or spending variable amounts of time on and traveling between flowers, it is assumed here that the sample size of observations is large enough to assess the overall relative attractiveness of the four flower types to the foraging species in these communities.

Comparing the results of this study with other evaluations of the relative attractiveness of floral resources in agricultural contexts, consideration must also be given for differences in methods used, foraging arthropod species, plant species, and environmental factors. This is the first report on the relative flower foraging 'preferences' of the particular hoverfly species observed in this study, but results for predatory hoverflies as a group can be compared to those of Colley and Luna (2000) who evaluated the preferences of hoverflies as a group in the same geographic location. The greater relative attractiveness of coriander to this community of hoverflies at the North Site was also seen in their study, but the potential effects of competition from more aggressive foragers described for a similar community at the South Site in this study was not looked at. Other studies of the relative preferences exhibited by individual hoverfly species are less comparable to this study because of differences in hoverfly and/or plant species, environmental context, and the interaction that these factors can have with habitat preferences of each hoverfly species (Branquart and Hemptinne 2000).

The strong preference of *Bombus* spp. in general for phacelia over other flower types has been seen in many contexts (Carreck and Williams 2002), but extreme specialization is also rare for this group, and they demonstrate a flexible preference which enables them to adapt their strategy according to changing spatial and temporal patterns of availability of reward among the available flower species (Goulson 2003). The more frequent visitation to phacelia by the pest herbivore species is to be expected for *P. rapae*, with a longer feeding apparatus well-suited to the deep corolla tube, but this may

be the first report of high visitation to this plant species by *D. undecimpunctata* and *L. hesperus*.

The results of this study help with the selection of insectary plants to use in this cropping context. Hoverflies visited mostly coriander, and the three pest species and bumblebees visited mostly phacelia, while buckwheat and alyssum were visited by both natural enemies and pests. The documentation of flower visiting by pest herbivore species as well as beneficial species is important for this selection process. The observed frequencies of visitation by all species only help to evaluate the relative attractiveness, however, and the relative impact that each flower type has on the fecundity and longevity of these natural enemy and pest species should also be considered. The ultimate decisions about the potential usefulness of insectary plantings should also of course include evaluations of agronomic, economic and phenological factors.

Acknowledgements

We thank Stahlbush Island Farms Inc. for access to the broccoli fields. Dr. Cliff Pereira (Oregon State University) provided statistical assistance. This study was funded by the Western Region Sustainable Agriculture, Research and Education program of the United States Department of Agriculture.

References Cited

- al Doghairi, M. A., and W. S. Cranshaw. 1999. Surveys on visitation of flowering landscape plants by common biological control agents in Colorado. *J. Kansas Entomol. Soc.* 72: 190-196.
- Branquart, E., and J. L. Hemptinne. 2000. Selectivity in the exploitation of floral resources by hoverflies (Diptera : Syrphinae). *Ecography* 23: 732-742.
- Carreck, N. L., and I. H. Williams. 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *J. Insect Cons.* 6: 13-23.
- Colley, M. R., and J. M. Luna. 2000. Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environ. Entomol.* 29: 1054-1059.
- Cowgill, S. E., S. D. Wratten, and N. W. Sotherton. 1993. The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. *Ann. Appl. Biol.* 122: 223-231.
- Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? *Science* 211: 887-893.
- Gilbert, F. S. 1981. Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecol. Entomol.* 10: 385-392.
- Goulson, D. 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspect. Plant Ecol. Evol. Syst.* 2: 185-209.
- Goulson, D. 2003. Choice of flower species, pp. 95-106. *In* D. Goulson (ed.), *Bumblebees: Behaviour and Ecology*. Oxford University Press, Oxford.
- Goulson, D., and N. P. Wright. 1998. Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.). *Behav. Ecol.* 9: 213.
- Gurr, G. M., H. F. van Emden, and S. D. Wratten. 1998. Habitat manipulation and natural enemy efficiency: implications for the control of pests, pp. 155-183. *In* P. Barbosa (ed.), *Conservation Biological Control*. Academic Press, San Diego, CA.
- Gurr, M., S. D. Wratten, and M. A. Altieri. 2004. *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publications, Melbourne.

- Haslett, J. R. 1989a. Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia* 81: 433-442.
- Haslett, J. R. 1989b. Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera: Syrphidae). *Oecologia*, 81: 361-363.
- Herrera, C. M. 1989. Pollinator abundance, morphology, and flower visitation rate: analysis of the "quantity" component in a plant-pollinator system. *Oecologia* 80: 241-248.
- Herrera, C. M. 1995. Microclimate and individual variation in pollinators: flowering plants are more than their flowers. *Ecology* 76: 1516-1524.
- Hickman, J. M., S. D. Wratten, P. C. Jepson, and C. M. Frampton. 2001. Effect of hunger on yellow water trap catches of hoverfly (Diptera: Syrphidae) adults. *Agric. and For. Entomol.* 3: 35-40.
- Jervis, M. A., N. A. C. Kidd, M. G. Fitton, T. Huddleston, and H. A. Dawah. 1993. Flower-visiting by hymenopteran parasitoids. *Journal of Natural History* 27: 67-105.
- Jervis, M. A., and N. A. C. Kidd. 1996. Phytophagy, pp. 375-394. *In* M. Jervis and N. Kidd (eds.), *Insect natural enemies: practical approaches to their study and evaluation*. Chapman and Hall, London, UK.
- Kearns, C. A., and D. W. Inouye. 2001. *Techniques for pollination biologists*. University Press of Colorado, Niwot, CO.
- Kikuchi, T. 1962. Studies on the coaction among insects visiting flowers II. Dominance relationship in the so-called drone fly group. *Sci. Rep. Tohoku Univ. Ser. IV* 28: 47-51.
- Kikuchi, T. 1963. Studies on the coaction among insects visiting flowers IV. Preferring behavior of some Syrphid flies, *Eristalis tenax*, *Eristalis cerealis*, and *Sphaerophoria cylindrica*, in relation to the age of the flower of *Chrysanthemum leucanthemum*. *Sci. Rep. Tohoku Univ. Ser. IV* 29: 9-14.
- Kikuchi, T. 1965. Role of interspecific dominance-subordination relationship on the appearance of flower-visiting insects. *Sci. Rep. Tohoku Univ. Ser. IV* 31: 275-296.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Ann. Rev. Entomol.* 45: 175-201.

- Long, R. F., A. Corbett, C. Lamb, C. Reberg Horton, J. Chandler, and M. Stimmann. 1998. Beneficial insects move from flowering plants to nearby crops. *Calif. Agric.* 52: 23-26.
- Lövei, G. L., D. J. Hodgson, A. MacLeod, and S. D. Wratten. 1993. Attractiveness of some novel crops for flower-visiting hoverflies (Diptera: Syrphidae): comparisons from two continents, pp. 368-370. *In* S. Corey, D. Dall and W. Milne (eds.), *Pest control and sustainable agriculture*. CSIRO, Canberra, Australia.
- Morse, D. H. 1981. Interactions among syrphid flies and bumblebees on flowers. *Ecology* 62: 81-88.
- Pfiffner, L., and E. Wyss. 2004. Use of sown wildflower strips to enhance natural enemies of agricultural pests, pp. 165-186. *In* G. M. Gurr, S. D. Wratten and M. A. Altieri (eds.), *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publishing, Melbourne.
- Rothery, F. A. 1994. Hoverfly foraging on hedgerow flowers. *Bull. OILB SROP* 17: 148-155.
- Ruppert, V., and J. Molthan. 1991. Augmentation of aphid antagonists by field margins rich in flowering plants, pp. 243-247 *In* L. Polgar, R. J. Chambers, A. F. G. Dixon and I. Hodek [eds.], *Behavior and Impact of Aphidophaga*. IOBC, Godollo, Hungary.
- SAS Institute. 1990. *Procedures Guide, Version 6, 3rd ed.* SAS Institute, Cary, NC.
- Schneider, F. 1948. Beitrag zur Kenntnis der Generationsverhältnisse und Diapause räuberischer Schwebfliegen (Syrphidae, Dipt.). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 21: 249-285.
- Sturken, K. 1964. Die Bedeutung der Imaginalernahrung für das Reproduktionsvermögen der Syrphiden. *Z. Angew. Zool.* 51: 385-417.
- Sutherland, J. P., G. M. Poppy, A. Cooper, and J. Power. 1997. Spatial and temporal distribution of aphidophagous hoverflies (Diptera: Syrphidae) in sown wild flower patches in a winter barley crop, pp. 135-142. *In* A. Cooper and J. Power (eds.), *Species dispersal and land use processes*, Ulster, UK.
- Sutherland, J. P., M. S. Sullivan, and G. M. Poppy. 1999. The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. *Entomol. Exp. et Appl.* 93: 157-164.

- Sutherland, J. P., M. S. Sullivan, and G. M. Poppy. 2001. Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agric. and For. Entomol.* 3: 57-64.
- Thomson, J. D. 1981. Spatial and Temporal Components of Resource Assessment by Flower-Feeding Insects. *J. Animal Ecol.* 50: 49-59.
- Toft, C. A. 1983. Community patterns of nectivorous adult parasitoids (Diptera, Bombyliidae) on their resources. *Oecologia* 57: 200-215.
- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043-1060.
- Wellington, W. G., and S. M. Fitzpatrick. 1981. Territoriality in the drone fly, *Eristalis tenax* (Diptera: Syrphidae). *Can. Entomol.* 113: 695-704.

Table 3.1. Factors affecting the selection of different floral resources by hoverflies.

Factors	References
<u>Characteristics of the flowers</u>	
Color	Haslett 1989a, Sutherland et al. 1999
Morphology	Gilbert 1981
Odor	
Flower size	Kickuchi 1963, Sutherland et al.
1999	
Nectar and pollen quality and/or amount	Sutherland et al. 1999
Flower abundance and patch size	Sutherland et al. 1997; 2001
Flower age and/or marks from previous visitors	Kickuchi 1963, Goulson 1999
<u>Exogenous factors</u>	
Climate and microclimate	Herrera 1995
Time of day	Rotheray 1994
Competition with other foragers	Morse 1981, Herrera 1989
<u>Characteristics of the foragers</u>	
Changing nutritional requirements	Haslett 1989b, Hickman et al. 2001
Sex and age	Sunderland 1999
Adjustments in behavior based on forager learning in response to cues	Goulson and Wright 1998
Resource specificity inherent to the species	Branquart and Hemptinne 2000

Table 3.2. Relative mean numbers (with standard errors) of all insect groups and species observed visiting flowers over all treatments and sampling dates at each site (units are mean number of individuals/2 min./m²).

Species or Group	North Site	South Site
<u>Predatory hoverflies</u>		
All predatory hoverflies	1.67 ± 0.66*	0.58 ± 0.33
<i>Eupeodes fumipennis</i>	0.88 ± 0.19	0.42 ± 0.16
<i>Sphaerophoria sulphuripes</i>	0.27 ± 0.09*	0.00 ± 0.00
<i>Toxomerus</i> spp. [†]	0.25 ± 0.09	0.08 ± 0.06
<i>Platycheirus stegnus</i>	0.17 ± 0.06	0.08 ± 0.05
<i>Syrphus opinator</i>	0.10 ± 0.05	0.00 ± 0.00
<u>Non-predatory hoverflies</u>		
<i>Eristalis</i> spp.	0.10 ± 0.05	0.78 ± 0.27*
<i>Syritta pipiens</i>	0.04 ± 0.03	0.03 ± 0.03
<u>Other beneficial insects</u>		
<i>Bombus</i> spp.	1.77 ± 0.41	2.08 ± 0.59
<i>Apis</i> spp.	1.46 ± 0.34	3.06 ± 0.47*
Coccinellidae	0.52 ± 0.13	1.53 ± 0.30*
Vespidae	0.02 ± 0.02	0.78 ± 0.25*
<u>Pest insects</u>		
<i>D. undecimpunctata undecimpunctata</i>	3.54 ± 0.43*	1.19 ± 0.20
<i>Lygus hesperus</i>	0.73 ± 0.19	0.31 ± 0.10
<i>Pieris rapae</i>	0.23 ± 0.07	0.11 ± 0.05

* Means with an asterisk are significantly greater than the other mean in the same row at $\alpha = 0.05$

[†] *Toxomerus* spp. consists of *T. marginatus* (Say) and *T. occidentalis* Curran

Figure 3.1. Mean number of hoverflies (with SE bars) observed visiting the four flower treatments over all sampling dates at A) the North Site, and B) the South Site. Means within a group of four bars followed by the same letter do not differ ($\alpha = 0.05$) according to the Least Significant Difference test.

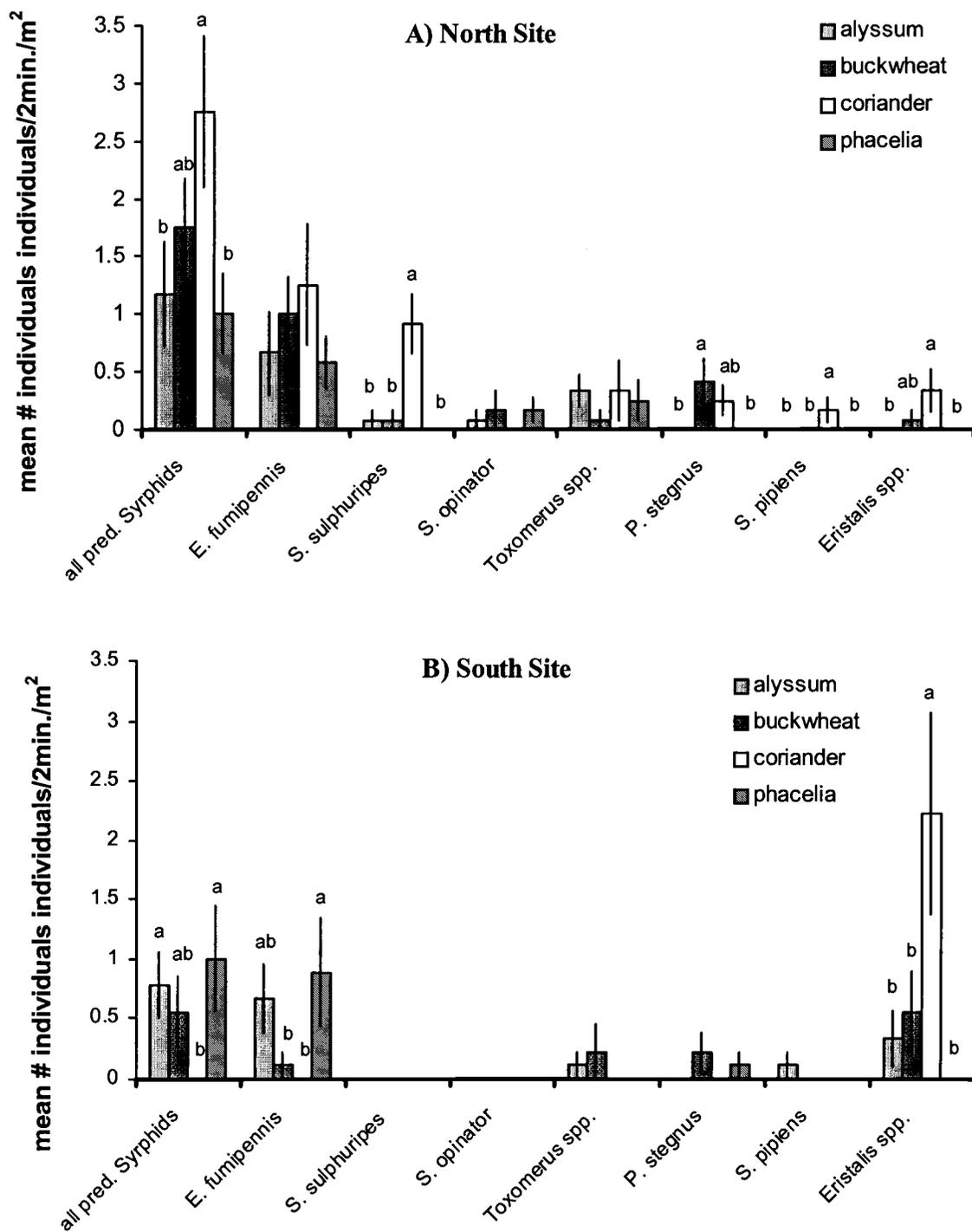
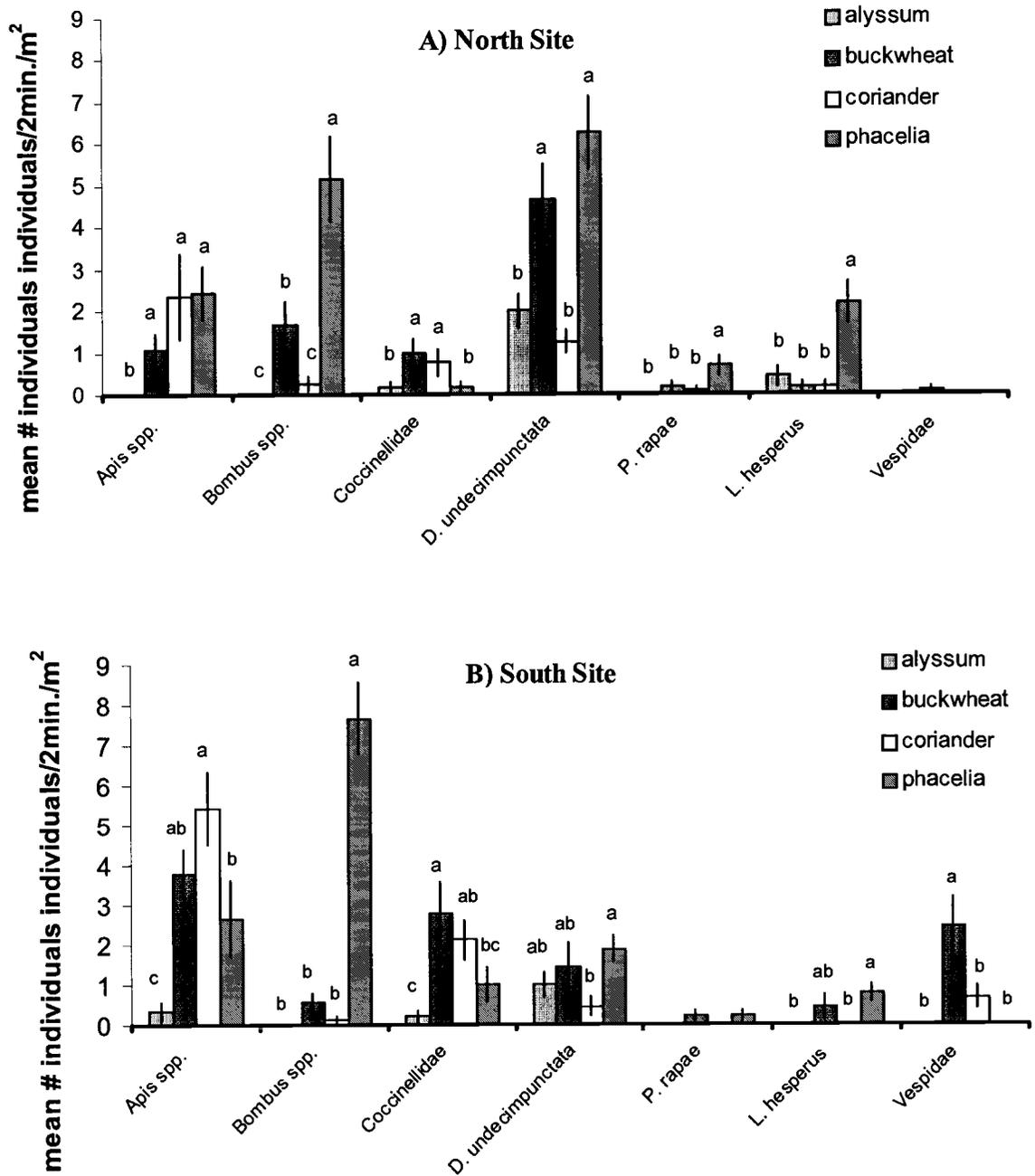


Fig. 3.2. Mean number of beneficial and pest insects (with SE bars) observed visiting the four flower treatments over all sampling dates at A) the North Site, and B) the South Site. Means within a group of four bars followed by the same letter do not differ ($\alpha = 0.05$) according to the Least Significant Difference test.



MANUSCRIPT 4

**SPATIAL AND TEMPORAL DISTRIBUTION OF PREDATORY HOVERFLIES (DIPTERA:
SYRPHIDAE) AND APHIDS (HOMOPTERA: APHIDIDAE) IN A FLOWER-ENHANCED
BROCCOLI FIELD**

AUTHORS:

M.D. Ambrosino, J.M. Luna, P.C. Jepson, S.D. Wratten, and C.B. Pereira

JOURNAL:

Submitted to:

Biological Control

Entomological Society of America

10001 Derekwood Lane, Suite 100

Lanham MD, 20706-4876

SPATIAL AND TEMPORAL DISTRIBUTION OF PREDATORY HOVERFLIES (DIPTERA: SYRPHIDAE) AND APHIDS (HOMOPTERA: APHIDIDAE) IN A FLOWER-ENHANCED BROCCOLI FIELD

Abstract

The effect of in-field insectary plantings on the timing and spatial distribution of hoverflies (Diptera: Syrphidae), their eggs and aphid prey was measured over the course of a season at different distances from the plantings in a broccoli field. Seven species of predatory hoverflies were observed, trapped, or reared from eggs oviposited in the broccoli field. Three of these species, *Eupeodes fumipennis* (Thomson), *Sphaerophoria sulphuripes* (Thomson), and *Syrphus opinator* Osten Sacken also fed on and oviposited next to *B. brassicae* in captivity. Linear modeling and generalized linear modeling both found strong evidence of increasing hoverfly eggs with increasing aphids as well as evidence of decreasing eggs with increasing distance from flowers. Although areas near the insectary plantings had greater densities of hoverfly eggs, the early arrival of gravid individuals of these hoverfly species suggests that they may not have been limited for resources at that time in terms of oviposition capacity. The time separation of several weeks between the arrival of gravid females and the appearance of eggs on the broccoli near harvest was most likely due to a requirement for a sufficient density of aphids to be present before oviposition occurs.

Keywords

conservation biological control; floral resources; hoverflies; Syrphidae; *Brevicoryne brassicae*; broccoli; insectary planting

Introduction

Predatory hoverflies have attracted interest as candidates for biological control programs because of their demonstrated ability to reduce aphid populations in various production systems (Chambers 1988). Eggs are laid near aphid colonies, and a single larva can consume hundreds of aphids in its lifetime. Hoverfly adults require pollen as a protein source for egg development (Schneider 1948), and nectar as a source of energy. Various non-crop plants can provide these resources, but many farming practices, including cultivation and herbicide use, reduce or remove these from farming landscapes (Landis et al. 2000). Adding or conserving 'insectary' floral resources of the appropriate type has potential to enhance (or re-establish) local natural enemy populations between seasons and their activity within a season when they are resource limited (Gurr et al. 1998; Pfiffner and Wyss 2004).

Floral resources may enhance hoverfly activity through a number of behavioral and physiological mechanisms. These include long-range attraction, short-range attraction and arrestment, increased survivorship, improved prey-finding ability (e.g. reduced 'commute' time between floral and aphid resources), as well as increased survivorship, longevity and fecundity of individuals. If these processes are synchronized with crop and pest phenology, the manipulation of habitat with floral resource subsidies could represent an effective conservation biological control tactic (Gurr et al. 2004).

The potential effect of flowers on the local effectiveness of predacious hoverflies has long been recognized (Fluke 1929). Experiments investigating the use of this strategy have looked at the effect of both naturally occurring and added flowers on the

attraction, retention, oviposition and aphid-limiting activities of hoverflies. The attraction of predacious hoverfly adults to whole fields by insectary flowers has been demonstrated (Harwood et al. 1992; Hickman and Wratten 1996), as has an increase in the abundance and richness of adults in areas within fields, close to the added or conserved floral resources (Klinger 1987; Ruppert and Molthan 1991; Cowgill et al. 1993; White et al. 1995; Lovei et al. 1992, 1993, 1998). Studies that marked hoverflies with paint (MacLeod 1999), rubidium (Long et al. 1998) and ingested *Phacelia* pollen (Holland et al. 1994; Lovei et al. 1993, 1998) have all shown retention of marked flies in fields at various distances from insectary plantings.

The spatial relationship between hoverfly oviposition and the availability of floral resources has been investigated for over four decades. Van Emden (1965) found greater oviposition closer to floral borders, although others (Chandler 1968a; Pollard 1971; Chambers 1987) could not detect this effect. More recently, Hickman and Wratten (1996) demonstrated increased hoverfly oviposition at distances up to 100 m from flower strips in wheat fields. This effect has also been demonstrated in other flower-enhanced wheat fields (Hausammann 1996). These later two studies also demonstrated a greater reduction of aphid numbers in crop fields containing the floral resources, and a reduction in aphids in flower-enhanced sugar beet fields was attributed to hoverfly activity (Sengonca and Frings 1988).

Although floral resources can attract hoverflies to crop fields and enhance their activity in some cases, results have been variable and it is important to also consider the spatial scale over which these effects can occur, the variation in response among species,

and the role of aphid prey in attracting and arresting hoverflies. Little information of this type exists for North American predatory hoverflies.

The cabbage aphid, *Brevicoryne brassicae* (L.), is a major contaminant pest of broccoli in the Willamette Valley of Oregon. Predatory hoverflies are consistently seen as one of the main taxa attacking and having an impact on cabbage aphids in cole crops (Metcalf 1913; Petherbridge and Mellor 1936; George 1957, van Emden 1965). The predacious hoverfly species that most commonly visit insectary plantings next to broccoli fields in Oregon have been identified (Ambrosino et al. 2006), but the relative contribution of each of these species within broccoli fields needs to be determined to assist local management decisions. The main objectives of this research were therefore to: 1) identify the main species of hoverflies which oviposit next to and prey on *B. brassicae* colonies in a commercial broccoli field, and 2) quantify the effect that added flowering plants have on hoverfly attraction, oviposition and aphid abundance.

Materials and Methods

Experimental Design. The experimental site was a section of a 15 ha broccoli field located four miles east of Corvallis, Oregon. Residue of the previous grass seed crop was killed with herbicide in March 2001, and broccoli was transplanted on 0.9 m wide beds on 28 May along with a soil incorporation of azadiractin and oxyflourfen. The border of the section of the field that contained the experiment was dominated by various woody species and blackberry shrubs (Fig. 4.1).

The experiment was set up in a 160 x 400 m section of the field. An 18 m (= 20 row) strip of broccoli (running the whole 400 m) was left untreated with the aphicides that were applied to the rest of the field (Fig. 4.1). The aphicides used were imidicloprid 43 days after transplanting, and pyrethrin with piperonyl butoxide 67 days after transplanting. Two insecticide applications were made for lepidopteran pests in the field, consisting of tebufenozide at 43 days, and spinosad at 67 days after transplanting.

Within this 18 x 400 m strip, two 18 x 18 m plots of alyssum seedlings (*Lobularia maritima* (L.) var. 'New Carpet of Snow') were transplanted with a spacing of 45 x 90 cm between plants. Alyssum was identified as highly attractive to the local hoverfly complex (Colley and Luna 2000), and not attractive to pest insect common in local broccoli fields (Ambrosino et al. 2006). Flowers were transplanted 24 days after broccoli planting. One of the alyssum blocks was set 90 m from one end of the strip, and the other 90 m from the other end, with a distance of 190 m between the two flower blocks, forming four 'field sections' within the strip (Fig. 4.1).

Pan Trap Sampling. To determine species of adult hoverflies present and their reproductive condition, transects of yellow pan traps (18 cm diameter Solo[®] plastic bowls painted with Rustoleum[®] 'Safety Yellow') were placed at distances of 0, 1, 5, 10, 20, 40 and 80 m from the flower plots along transects radiating perpendicularly in all four cardinal directions. These only extended 40 m in each of the eastward transects because of field configuration (Fig. 4.1). Each of the 54 pan traps in the eight transects was filled with a dilute solution of water, dish soap and propylene glycol. Pan trap contents were collected at 5-7 day intervals over the season and returned to the laboratory for insect identification and hoverfly dissection. Pan trap height was kept at least 15 cm below the

broccoli canopy height as the broccoli grew during the season. To determine the reproductive condition of trapped female hoverflies, specimens were dissected and the total number of eggs and chorionated eggs were counted. Pollen content in the guts of these flies was quantified using a scale of zero to five (zero being empty, five being full).

Crop Plant Sampling. The unsprayed area was divided into four sections for arthropod sampling, with two sections on either side of each flower block (Fig. 4.1).

Arthropod abundance at distances of 5, 15, 25, 35, 45, 55, 65 and 75 m from the flowers in each of the unsprayed field sections was estimated by randomly selecting one plant from each of rows 3, 6, 9, 12, 15, and 18 at each of these distances, forming a grid of 192 plants in total. The six largest leaves in the middle of the canopy of each plant were examined for hoverfly eggs and larvae, cabbage aphid (*B. brassicae*), green peach aphid (*Myzus persicae* (Sulzer)), potato aphid (*Macrosiphum euphorbiae* (Thomas)), and other aphid natural enemies such as cecidomyiid larvae and eggs (Diptera: Cecidomyiidae), parasitized aphid mummies, spiders, lady beetles (Coleoptera: Coccinellidae), and lacewings (Neuroptera). Sampling took place on 11 occasions, at intervals of four to six days, starting 19 days after broccoli transplanting (five days before the alyssum was planted) until broccoli harvest.

All hoverfly eggs found on the sampled crop plants were collected and transported to the laboratory to be photographed and placed in Petri dishes with moist cotton wool and aphid prey until eclosion to identify the species depositing eggs in the field.

Flower Block Sampling. The alyssum flower blocks in the field were sampled for hoverfly presence to verify if the pan traps were collecting all species of hoverflies

that were visiting the flower blocks. Visual observations were undertaken for 15 minutes in each flower block on a weekly basis. The average number of flowers in 1 m² quadrats was also estimated in each round of flower observation.

Hoverfly oviposition and development tests. To determine if hoverfly species that appeared in the pan traps could find and prey on *B. brassicae*, oviposition and development tests were conducted in the laboratory for all trapped or observed hoverfly species. Adult hoverflies were placed in 1 m³ screen cages contained potted broccoli plants infested with *B. brassicae*. The extent to which these hoverfly species could oviposit next to and then complete development on these aphid species was then recorded.

Sampling at Harvest. At harvest, mature broccoli heads were randomly selected within the same four field section grids described for the crop plant sampling, giving a total of 192 heads. Each head was cut apart in sections smaller than 1 cm³ and visually examined for the presence of arthropods. Inspection was standardized to five minutes per head.

Data Analysis. Hoverfly oviposition counts (192 observations from 4 field sections each in an 8 X 6 grid) were modeled as a function of both aphid density and distance from flower source using both standard linear modeling (SAS mixed procedure) and generalized linear modeling (SAS genmod procedure). For the standard linear modeling (multiple linear regression) the oviposition counts were square root transformed to improve the normality and homogeneity of residuals. For the generalized linear modeling, Poisson-type regression with a log link was used. Due to visual evidence from exploratory plots and the simplicity of the back-transformed model (simple multiplicative

power function), $\log(\text{distance})$ was used as one predictor and (since there were some zero aphid densities) $\log(\text{aphid density} + 1)$ was used as the second predictor. To incorporate overdispersion, the negative binomial distribution was used for the conditional response. Similar results (not shown) were obtained using the quasiliikelihood approach to incorporate overdispersion. All initial models included field section as a design factor (allowing both additive effects and interactions) and up to quadratic polynomials in the aphid and distance predictors. To achieve parsimonious models, non-significant effects ($p > 0.05$) were dropped.

Spatial autocorrelation can lead to bias in the p-values from the above models. Therefore, the assumption of independence for the modeling was assessed using the residuals from the above parsimonious linear model. Moran's I (under the three neighborhood definitions of 'rook, queen and bishop') did not detect significant spatial autocorrelation (SAS macros provided by Schabenberger and Pierce (2002)). Semi-variogram analysis did not suggest any spatial structure (SAS variogram procedure). Adding spatial covariance structure did not significantly improve the fit over that under the independence assumption (SAS mixed procedure).

All analyses were done using version 8.2 of SAS (2000).

Results

Seven species of predatory hoverflies were observed, trapped, or reared from eggs oviposited in the broccoli field (Table 4.1). Three out of seven of these species, *Eupeodes fumipennis* (Thomson), *Sphaerophoria sulphuripes* (Thomson), and *Syrphus*

opinator Osten Sacken fed on and oviposited next to *B. brassicae* in captivity (Table 4.1). These three species have also been reported to feed on *B. brassicae* in the literature (Table 4.1). The only evidence of other natural enemies observed on the broccoli plants before harvest were spiders, cecidomyiid larvae and eggs, and parasitized *B. brassicae*, but these were in very low numbers and very late in the growing season. Predatory lady beetles and lacewings were also found in the traps, but in low numbers (data not shown). The aphid species *M. persicae* and *M. euphorbiae* comprised less than 5% of the aphids on the leaves sampled.

The arrival of adult hoverflies and their distribution in the field over time.

Temporal distribution of pan-trapped hoverflies. Adults of *E. fumipennis*, *S. sulphuripes*, and *Platycheirus stegnus* (Say) first appeared in the pan traps in the first three to four weeks of the 11-week broccoli season (Fig. 4.2). This arrival coincided with the planting of the flowering alyssum plants. Very few hoverflies were seen, and only one hoverfly was trapped in the field before this date. *Syrphus opinator* was the only species that did not appear in the pan traps but was seen foraging on the broccoli or the alyssum flowers.

Toxomerus marginatus (Say), *Toxomerus occidentalis* Curran, and a single individual of a *Paragus* sp. were also collected in the pan traps. *Toxomerus marginatus* was the most common hoverfly species, ranging from 38 to 96% of the hoverflies trapped on a given sampling date. Although *T. marginatus* was the most commonly trapped predatory hoverfly species, this species did not oviposit at or feed on *B. brassicae* in laboratory tests (Table 4.1), and no eggs of *Toxomerus* sp. were collected from within the

experimental broccoli field. Therefore were not included in the analysis of the pollen and egg numbers of trapped hoverflies.

Eggs and pollen in trapped hoverflies. Pollen and chorionated eggs were prevalent in the trapped female flies, even on the earliest sampling dates (Table 4.2). The relative percentage of female *S. sulphuripes* with chorionated eggs was always greater than 86% among sampling dates. The relative percentage of female *E. fumipennis* with chorionated eggs was always greater than 50%. The relative percentage of *P. stegnus* with chorionated eggs was 100% on most dates, but 0% on two dates where only a few female flies were trapped. The relative percentage of all hoverflies with at least some pollen in their guts was always close to 100% among sampling dates. Most of the flies contained many different types of pollen. There were no noticeable trends of different amounts of eggs or pollen at different sampling distances from the flower blocks for each species (data not shown).

The arrival of hoverfly eggs and their spatial distribution.

Temporal distribution of hoverfly eggs on broccoli. Hoverfly eggs first appeared on broccoli crop plants three weeks before harvest, and began to increase rapidly just before the start of harvest (Fig. 4.3). Species determinations were made after rearing field-collected eggs in the lab. Both *S. sulphuripes* and *E. fumipennis* have a 'ridged' egg chorion morphotype which could not be separated from each other in the field, and had to be retained as a single group for subsequent analyses. Eggs of *S. opinator* ('knobby' chorion) and *P. stegnus* (long eggs with a smooth chorion) were readily distinguishable (Ambrosino 2006). A few other egg chorion morphotypes were also observed on broccoli crop plants in very small numbers, but could not be reared successfully.

The 'ridged' group of eggs representing *S. sulphuripes* and *E. fumipennis* were the first to appear and were the most abundant on the broccoli plants on all dates, while the eggs of all other taxa were present only within a week of the start of harvest (Fig. 4.3). Eggs of *S. sulphuripes* and *E. fumipennis* on crop plants were generally observed four to five weeks after gravid individuals of these species had first been trapped in the field (Table 4.1, Figures 4.2 & 4.3). Eggs of *S. opinator* were also found in small numbers four to five weeks after this species was first observed foraging in the field and *P. stegnus* eggs were found in small numbers seven to eight weeks after this species was first trapped. Hoverfly larvae were not commonly observed on broccoli crop plants with this non-destructive sampling method, and were not included in the analysis. Predacious hoverfly larvae often remain hidden on and around herbaceous plants away from aphid colonies during the day (Rotheray 1993).

Aphid seasonal abundance. The relative proportion of crop plants containing aphids increased gradually over the season until harvest, when almost 100% of the plants sampled had aphids (Fig. 4.4). Most of the aphids counted throughout the season were *B. brassicae*, with an occasional individual or colony of *M. persicae* or even less frequently *M. euphorbiae* (data not shown). The mean number of aphids and hoverfly eggs increased rapidly on the last sampling date, right at the onset of harvest (Fig. 4.3). When the timing of appearance of hoverfly eggs in the whole field is viewed with the aphid population trajectory, it can be seen that the bulk of oviposition did not occur until most of the plants were colonized by aphids (Fig. 4.4).

Spatial distribution of eggs. When the data from all four crop plant field sections were pooled to see the overall trend, greater numbers of total hoverfly eggs per sampled

broccoli plant were found at sampling distances closer to the flower plots only on the final sampling date (Fig. 4.5). This was however, the only sampling date when substantial numbers of hoverfly eggs were found. On this final date, 82% of the eggs collected over the whole field were from the egg morphotype group representing *S. sulphuripes* and *E. fumipennis*, 11% were from *P. stegnus*, 4% were from *S. opinator*, and the remaining 3% were from three different egg morphotypes representing other unidentified hoverfly species.

The analysis of the oviposition response to aphids at different distances from the flower blocks focused on the group of eggs representing *S. sulphuripes* and *E. fumipennis*. Eggs of *P. stegnus* were not included in the analysis because their larvae were not successfully reared on cabbage aphids and their eggs appeared in clusters of 2-10 eggs often not near cabbage aphid colonies. This pattern for *P. stegnus* eggs is common on herbaceous plants (Davidson 1922), and ovipositing females of this species were probably seeking *M persicae* (Vockeroth 1990). The eggs of *S. opinator* and the three remaining egg morphotypes were also not included in the analysis because they appeared in very low numbers.

Without accounting for aphid density differences, the number of ridged eggs generally decreased with distance from the flower source in each of the four field sections (Fig. 4.6). However, it is important to also account for any effects of aphid densities on the number of ridged eggs, when assessing evidence of trends with distance to the flower source. Multiple linear regression modeling (with the square root of the egg count as the response) detected a strong positive linear trend between hoverfly eggs and aphids ($p < 0.0001$). (Due to less evidence of a trend in one of the field sections, there as some

evidence that this positive trend varied with field section ($p = 0.041$ for field section by aphid interaction)). Adjusting for the trend with aphid density (i.e., with aphid density in the model), there was still evidence of a negative trend between ridged eggs and distance ($p = 0.028$). Over the range of data observed, there was no evidence of quadratic curvature in these models, nor interaction between aphids and distance ($p > 0.14$ all terms). There was no evidence of bias in the p -values due to spatial autocorrelation (see methods).

Since the hoverfly egg data consisted of counts (which cannot be negative), and the variance increased with the mean, the spatial oviposition response was also modeled using Poisson-type generalized linear regression models with a log link and a negative binomial distribution to allow for over-dispersion. The resulting parsimonious model included both effects of aphid density and distance from flowers. The model confirmed the linear regression results in that egg counts increased significantly with increasing aphids [positive parameter estimate (0.4) with $p < 0.0001$] and that the egg counts decreased significantly with increasing distance from the flowers [negative parameter estimate (-0.23) with $p = 0.004$], even with aphids in the model. For this modeling, there was little evidence of field section effects or lack of fit due to quadratic curvature or aphid-distance interaction ($p > 0.05$ all tests).

The resulting parsimonious generalized linear model can be back-transformed to illustrate the average effects observed in this data set. Using the model parameter estimates, the expected mean number of eggs of this morphotype on a group of six leaves related to aphid density and distance to flowers as follows:

$$\text{eggs} = (1.85) * (\text{aphids} + 1)^{0.4} * (\text{distance})^{-0.23}$$

Spatial distribution of aphids on crop plants at harvest. At harvest, there was no correlation between aphid abundance on the crop plants or broccoli heads and distance from floral plantings (data not shown). Even though the relative percentage of sampled crop plants infested with aphids was close to 100% at the end of the season (Fig. 4.4), the relative percentage of sampled heads that were infested was only 7%. Each of the infested heads contained fewer than 10 aphids.

Discussion

Although though female hoverflies with fully developed eggs were arriving to all parts of the broccoli field as much as eight weeks before harvest, the appearance of hoverfly eggs on the broccoli crop did not occur until the few weeks before harvest. All of the predatory syrphid species sampled in this trial demonstrated this apparent delay in oviposition. The most likely reason for this delay is that oviposition by these hoverfly species is stimulated by a "threshold" density of *B. brassicae* (van Emden 1965; Oatman & Platner 1969). Similar delays in the appearance of hoverfly eggs in the field until *B. brassicae* densities are sufficiently large have been seen for other hoverfly species in brassica crops (Wnuk and Wojciechowicz 1993), as well as for other hoverfly species and aphid species in other systems (Neuenschwander et al. 1975; Carroll and Hoyt 1984).

The timing of hoverfly oviposition at aphid colonies in crop fields can also vary among species in different years due to the effect of different climatic conditions on hoverfly overwintering (Krause and Poehling 1996), or migration into the crop (Tenhumberg and Poehling 1995). A diapause or some form of quiescence at this time could have also caused such a delay. Some univoltine hoverfly species with long life

cycles can demonstrate a facultative 'partial diapause' in an adult stage that feeds and has a prolonged period of ovarian development (Schneider 1948), but this tends to occur under conditions less optimal than those seen under the summer field conditions in this study.

Although the predatory hoverflies that attack the cabbage aphid were not trapped within the broccoli field until the flowering alyssum seedlings were planted, some individuals of these species were observed foraging in areas around the field before the flowers were planted. Additionally, the first female hoverflies of these species that were trapped had fully developed eggs and guts full of pollen of several morphotypes. This indicates that although the added flower plots may have attracted these species of hoverflies into the field, the woody and riparian areas bordering the field could have provided sufficient floral resources, alternate hosts and shelter for the predacious hoverfly community early in the broccoli season. Plants known to attract hoverflies such as hogweed (*Heracleum lanatum* Michx) and Queen Anne's lace (*Daucus carota* L.) were flowering in the field borders early in the crop season. Even when the field border vegetation has a lower floral density than that of the field, however, the abundance of predatory hoverflies can be greater in the border vegetation (e.g. Sutherland et al. 2001). The hoverfly species which oviposited on the broccoli plants in this study can all prey on multiple aphid species, and the importance of similar woody and riparian habitats as sources of alternate hosts of syrphids and other aphid predators has been recognized elsewhere (Carroll and Hoyt 1984; Fluke 1929; Bribosia 2002). Alternate hosts are often not present in sufficient numbers early enough in the crop season however to enhance syrphid populations in time for the crop season (Salveter 1998). The dense vegetation

surrounding this field could have also provided the type of shelter that has been shown to attract predatory hoverflies (Lewis 1965), especially at times of the year when physical conditions are more extreme (Sarthou et al. 2005).

With the strong dispersal ability of hoverflies, it is also possible that the individuals present in the field were supported by these same resources beyond the immediate vicinity of the broccoli field. The need for landscape-scale studies of the effects of floral resources on predatory hoverflies has been noted elsewhere (Bugg 1993). Increased arrival at wheat fields by predatory hoverflies in more diverse landscapes has been observed (Krause and Poehling 1995), and certain predatory hoverfly species have been reported to make use of sources of pollen up to one kilometer away from a crop field and return to the field within the same day (Schneider 1958). The landscape surrounding this field had many areas with habitat similar to the field border, and it has been noted that these resources in and next to a given field in complex landscapes can make less of a difference for the enhancement of highly dispersive natural enemies than they do in fields located in simple landscapes (Thies and Tschardtke 1999; Tschardtke et al. 2005).

The floral resources were placed in the middle of the field in this study in order to see any effects on the spatial redistribution of hoverfly adults, hoverfly eggs and/or aphids that might occur within the field aside from the effects that the field margins or landscape might have. The spatial distribution of the adults of hoverfly species of interest could not be determined since so few individuals of these species were captured in the pan and sticky traps. Very few larvae were observed on the broccoli plants, even when destructive and nondestructive whole-plant sampling techniques were used (M. D.

Ambrosino, unpublished data). Hoverfly eggs were the most readily quantifiable indicator of hoverfly presence at aphid colonies, but it must be noted that the mortality of predacious hoverfly eggs in the field can be as high as 40% (van Emden 1965), and infertile eggs are sometimes oviposited when aphid prey numbers are low (Schneider 1948). This study showed strong evidence of decreasing hoverfly eggs with increasing distance, and increasing eggs with increasing aphids. This effect of insectary plantings on local oviposition has been demonstrated for hoverflies in other systems (Sengonca and Frings 1988; Haussammann 1996; Hickman and Wratten 1996), but such spatial effects on natural enemy enhancement can be diminished when resources in the border of the field or in the overall landscape are abundant (Thies and Tschardtke 1999).

The relative proportion of broccoli plants with *B. brassicae* gradually increased throughout the season, but there were very few aphids in the broccoli heads at harvest, and no trend of decreasing aphids on the plants or in the heads at distances closer to the flower plots. Eggs of the hoverfly species *S. sulphuripes* and *E. fumipennis* arrived to *B. brassicae* colonies the most quickly and in the greatest numbers, but this response was most likely not rapid enough to decrease infestations before harvest, as no decrease in *B. brassicae* densities were noted at this time. Although the insectary plantings initially attracted the target species of hoverflies into the field and influenced oviposition in the vicinity of the plantings at the end of the season, they did not seem to influence the timing of oviposition response as much as aphid density. This same effect has been seen in other attempts at enhancing hoverfly oviposition with insectary plantings (van Emden 1965; Sengonca and Frings 1988; Hausammann 1996). Attempts to enhance the activities of predacious hoverflies with other types of non-prey resource manipulations

such as food sprays have also shown a pattern of increased attraction and/or arrestment of adults, but no substantial oviposition has been observed in these studies as well until aphid numbers reached sufficient densities (Hagen 1970; Ben Saad and Bishop 1976; Hagley and Simpson 1981). With the importance of an early response by hoverflies for the effective limitation of aphid pest species (Hagen and van den Bosch 1968), and the apparent short time frame over which this enhancement must occur in many vegetable crop systems, future efforts to enhance the timing of the aphid-limiting activity of predacious hoverflies in this system might focus on applying food sprays containing known ovipositional cues, such as aphid kairomones, directly to the crop plants.

Acknowledgements

We thank Stahlbush Island Farms Inc. for access to the broccoli and for allowing us to alter their operations in certain parts of the field. We also thank Amanda Griffith and Lourdes Irwin for assistance with sampling and specimen sorting, and Renate McKenzie for help translating some of the references. This study was funded by the Western Region Sustainable Agriculture, Research and Education program of the United States Department of Agriculture.

References Cited

- Ambrosino, M. D., Luna, J. M., Jepson, P. C., and Wratten S. D., 2006. The relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects and herbivores. *Env. Entomol.*, In Press.
- Ambrosino, M.D., 2006. Enhancing the predatory potential of hoverflies on aphids in Oregon broccoli fields with floral resources. Ph.D. Thesis. Oregon State University. Corvallis, OR.
- Ben Saad, A. A., and Bishop G. W., 1976. Effect of artificial honeydews on insect communities in potato fields. *Entomophaga* 5, 49-57.
- Bugg, R. L., 1993. Habitat manipulation to enhance the effectiveness of aphidophagous hover flies (Diptera: Syrphidae). *Sustainable Agriculture* 5, 12-15.
- Bribosia, E., 2002. The black elder (*Sambucus nigra*): alternate plant for aphidophagous syrphids. *Fruit Belge* 70, 151-153.
- Carroll, D. P., and Hoyt, S. C., 1984. Natural enemies and their effects on apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), colonies on young apple trees in central Washington. *Environ. Entomol.* 13, 469-481.
- Chambers, R. J., 1987. Oviposition by aphidophagous hoverflies (Diptera: Syrphidae) in relation to aphid density and distribution in winter wheat. *Ann. Appl. Biol.* 110, 115-121.
- Chambers, R. J., 1988. Syrphidae. In: Minks, A. K., Harrewijn, P. (Eds.), *Aphids: their biology, natural enemies, and control*. Vol. C. Elsevier Publications, Amsterdam, The Netherlands, pp. 259-270.
- Chandler, A. E. F., 1968. Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). *Ann. Appl. Biol.* 61, 402-414.
- Colley, M. R., and Luna, J. M., 2000. Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environ. Entomol.* 29, 1054-1059.
- Cowgill, S., Wratten, S. D., and Sotherton, N., 1993. The effect of weeds on the numbers of hoverfly (Diptera: Syrphidae) adults and the distribution and composition of their eggs in winter wheat. *Ann. App. Biol.* 123, 499-515.
- Davidson, W. M., 1922. Notes on certain species of *Melanostoma* (Diptera: Syrphidae). *Trans. Am. Ent. Soc.* 48, 35-47.

- Fluke, C. L., 1929. The known predacious and parasitic enemies of the pea aphid in North America. *Bull. Wis. Agric. Exp. Sta.* 93, 1-47.
- George, K. S., 1957. Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). *Bull. Entomol. Res.* 48, 619-629.
- Gurr, G. M., van Emden, H. F., and Wratten, S. D., 1998. Habitat manipulation and natural enemy efficiency: implications for the control of pests. In: Barbosa, P. (Ed.), *Conservation Biological Control*. Academic Press, San Diego, CA, pp. 155-183.
- Gurr, M., Wratten, S. D., and Altieri, M. A., 2004. *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publications, Melbourne.
- Hagen, K. S., 1970. The use of food sprays to increase effectiveness of entomophagous insects. In: *Proceedings 2nd Tall Timbers Conference on Ecological Animal Control by Habitat Management*. Tall Timbers Research Station, Tallahassee, Florida, pp. 59-81.
- Hagen, K. S., and van den Bosch, R., 1968. Impact of pathogens, parasites and predators on aphids. *Annual Review of Entomology* 13, 325-284.
- Hagley, E. A. C., and Simpson C. M., 1981. Effect of food sprays on numbers of predators in an apple orchard. *Canadian Entomologist* 113, 75-77.
- Harwood, R. W. J., Wratten, S. D., and Nowakowski, M., 1992. The effect of managed field margins on hoverfly (Diptera: Syrphidae) distribution and within-field abundance. In: *Proceedings of the Brighton Crop Protection Conference - Pests and Diseases*. November 1992, Brighton, England, pp. 1033-1037.
- Hausammann, A. 1996. The effects of weed strip-management on pests and beneficial arthropods in winter wheat fields. *J. Plant Dis. Prot.* 103: 70-81.
- Hickman, J. M., and Wratten, S. D., 1996. Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *J. Econ. Entomol.* 89, 832-840.
- Holland, J. M., Thomas, S. R., and Courts, S., 1994. *Phacelia tanacetifolia* flower strips as a component of integrated farming. In: Boatman, N. (Ed.), *Field margins: integrating agriculture and conservation*. 18-20 April 1994. BCPC, Coventry, UK, pp. 215-220.

- Klinger, K., 1987. Effects of margin strips along a winter wheat field on the predatory arthropod fauna and cereal aphid infestation. *J. Appl. Entomol.* 104, 47-58.
- Krause, U., and Poehling, H. M., 1995. Population dynamics of hoverflies (Diptera: Syrphidae) in Northern Germany in relation to different habitat structure. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie* 10, 509-512.
- Krause, U., and Poehling, H., 1996. Overwintering, oviposition and population dynamics of hoverflies (Diptera: Syrphidae) in northern Germany in relation to small and large-scale landscape structure. In: Booij, C. J. H., and den Nijs, L. J. M. F. (Eds.), *Arthropod natural enemies in arable land II. Survival, reproduction and enhancement.* Acta Jutlandica Vol. 71(2). Aarhus University Press, Denmark, pp. 157-169.
- Landis, D. A., Wratten, S. D., and Gurr, G. M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175-201.
- Lewis, T., 1965. The effects of an artificial windbreak on the aerial distribution of flying insects. *Ann Appl Biol.* 55, 503-512.
- Long, R. F., Corbett, A., Lamb, C., Reberg Horton, C., Chandler, J., and Stimmann, M., 1998. Beneficial insects move from flowering plants to nearby crops. *Calif. Agric.* 52, 23-26.
- Lovei, G. L., McDougall, D., Bramley, G., Hodgson, D. J., Wratten, S. D., and Popay, A. J., 1992. Floral resources for natural enemies: the effect of *Phacelia tanacetifolia* (Hydrophyllaceae) on within-field distribution of hoverflies (Diptera: Syrphidae). In: *Proceedings of the Forty Fifth New Zealand Plant Protection Conference.* 11-13 August 1992, Wellington, New Zealand, pp. 60-61.
- Lovei, G. L., Hickman, J. M., McDougall, D., and Wratten, S. D., 1993. Field penetration of beneficial insects from habitat islands: hoverfly dispersal from flowering crop strips. In: *Proceedings of the Forty Sixth New Zealand Plant Protection Conference.* 10-12 August 1993, Christchurch, New Zealand, pp. 325-328.
- Lovei, G. L., Macleod, A., and Hickman, J. M., 1998. Dispersal and effects of barriers on the movement of the New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. *J. App. Entomol.* 122, 115-120.
- MacLeod, A., 1992. Alternative crops as floral resources for beneficial hoverflies (Diptera: Syrphidae). In: *Proceedings of the Brighton Crop Protection Conference - Pests and Diseases.* November 1992, Brighton, England, pp. 997-1002.

- MacLeod, A., 1999. Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. *Agric. Ecosys. Environ.* 73, 237-244.
- Metcalf, C. L., 1913. The Syrphidae of Ohio. *Ohio Biological Survey Bull.* 1, 123pp.
- Neuenschwander, P., Hagen, K.S., and Smith, R.F., 1975. Predation on aphids in California's alfalfa fields. *Hilgardia* 43, 53-78.
- Oatman, E. R., and Platner, G. R., 1969. An ecological study of insect populations on cabbage in southern California. *Hilgardia* 40, 1-40.
- Petherbridge, F. R., and Mellor, J. E. M., 1936. Observations on the life history and control of the cabbage aphid, *Brevicoryne brassicae* L. *Ann. of Appl. Biol.* 23, 329-241.
- Pfiffner, L., and Wyss, E., 2004. Use of sown wildflower strips to enhance natural enemies of agricultural pests. In: Gurr, G. M., Wratten, S. D., and Altieri, M. A. (Eds.), *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publishing, Melbourne, pp. 165-186.
- Pollard, E., 1971. Hedges. VI. Habitat diversity and crop pests. A study of *Brevicoryne brassicae* and its syrphid predators. *J. Appl. Ecol.* 8, 751-780.
- Rojo, S., Marcos-Garcia, A., Nieto, J., and Mier, M., 2003. A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. *CIBIO Ediciones*, Alicante, Spain, pp. 319.
- Rotheray, G. E., 1993. Colour guide to hoverfly larvae (Diptera, Syrphidae) *Dipterists Digest* No. 9. Whiteley, Sheffield, UK, 159 pp.
- Ruppert, V., and Molthan, J., 1991. Augmentation of aphid antagonists by field margins rich in flowering plants. In: Polgar, R. J. C. L., Dixon, A.F.G., and Hodek, I. (Eds.), *Behavior and Impact of Aphidophaga*. IOBC, Godollo, Hungary, pp. 243-247.
- SAS Institute, 2000. SAS version 8. SAS Institute, Cary, NC.
- Salveter, R., 1998. The influence of sown herb strips and spontaneous weeds on the larval stages of aphidophagous hoverflies (Dipt., Syrphidae). *Journal of Applied Entomology* 122, 103-114.
- Sarthou, J. P., Ouin, A., Arrignon, F., Barreau, G., and Bouyjou, B., 2005. Landscape parameters explain the distribution and abundance of *Episyrphus balteatus* (Diptera : Syrphidae). *European Journal of Entomology* 102, 539-545.

- Schneider, F., 1948. Beitrag zur Kenntnis der Generationsverhältnisse und Diapause rauberischer Schwebfliegen (Syrphidae, Dipt.) [Contribution to knowledge of the number of generations and the diapause of predatory hoverflies (Syrphidae, Dipt.)]. Mitteilungen Schweizerische Entomologische Gesellschaft 21, 249-285.
- Sengonca, C., and Frings, B., 1988. The effect of *Phacelia tanacetifolia* on populations of pests and beneficial insects in sugarbeet fields. *Pedobiologia* 32, 311-316.
- Sutherland, J. P., Sullivan, M. S., and Poppy, G. M., 2001. Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agric. For. Entomol.* 3, 57-64.
- Tenhumberg, B., and Poehling, H. M., 1995. Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. *Agriculture, Ecosystems and Environment* 52, 39-43.
- Thies, C., and Tschardtke, T., 1999. Landscape Structure and Biological Control in Agroecosystems. *Science* 285, 893-895.
- Tschardtke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters* 8, 857-874.
- van Emden, H. F., 1965. The effect of uncultivated land on the distribution of cabbage aphid (*Brevicoryne brassicae*) on an adjacent crop. *J. Appl. Ecol.* 2, 171-196.
- Vockeroth, J. R., 1990. Revision of the Nearctic species of *Platycheirus* (Diptera, Syrphidae). *Can. Entomol.* 122, 659-766.
- Vockeroth, J. R., 1992. The Insects and Arachnids of Canada, Part 18: The flower flies of the subfamily Syrphinae of Canada, Alaska, and Greenland: Diptera, Syrphidae. Canadian Communication Group, Ottawa, Canada.
- White, A. J., Wratten, S. D., Berry, N. A., and Weigmann, U., 1995. Habitat manipulation to enhance biological control of Brassica pests by hover flies (Diptera: Syrphidae). *J. Econ. Entomol.* 88, 1171-1176.
- Wnuk, A., and Wojciechowicz, E., 1993. Syrphid predators (Diptera, Syrphidae) occurring in colonies of the cabbage aphid, *Brevicoryne brassicae* (L.), on cabbage and cauliflower. *Polskie Pismo Entomologiczne* 62, 215-229.

Table 4.1. Predatory hoverfly species present in the broccoli field.

Syrphid species	first gravid adults in field	first eggs on broccoli	local cabbage aphid test*	host records in literature [†]
<i>Eupeodes fumipennis</i>	28 June	19 July	feeding, ovip	17, CA, GPA
<i>Sphaerophoria sulphuripes</i>	22 June	19 July	feeding, ovip	6, CA
<i>Syrphus opinator</i>	22 June	24 July	feeding, ovip	20, CA, GPA
<i>Platycheirus stegnus</i>	14 June	9 August	no feeding	5, GPA
<i>Paragus</i> sp.	22 June	no eggs	inconclusive	unknown
<i>Toxomerus marginatus</i>	22 June	no eggs	no response	8
<i>Toxomerus occidentalis</i>	2 July	no eggs	no response	unknown

* 'feeding' means that larvae of the species can survive to adults when fed only cabbage aphids (*B. brevicoryne*) in tests performed by the authors; 'ovip' means that adults of the species will oviposit on plants with cabbage aphid colonies on potted broccoli seedlings in a confined 1m³ area in tests performed by the authors; 'inconclusive' means that very little oviposition and larval feeding occurred in a small sample size of individuals; 'no response' means that no oviposition or feeding occurred

[†] the number in this column includes the number of aphid prey species on record for each hoverfly species (Vockeroth 1992, Rojo et al. 2003); and whether or not cabbage aphid, 'CA' (*B. brevicoryne*) and/or green peach aphid, 'GPA' (*M. persicae*) are included in these lists.

Table 4.2. Mean pollen scores and number of chorionated eggs (with standard errors) for hoverflies captured in yellow pan traps.

Syrphid species	Sampling Date								
	14 June	22 June	26 June	28 June	2 July	9 July	23 July	2 August	14 August
Mean Pollen Score*									
<i>E. fuminpennis</i>	— [§]	—	—	4.0 [†]	—	3.3 (1.1)	3.8 (0.3)	4.0 (0.4)	4.0 [†]
<i>S. sulphuripes</i>	—	4.0 [†]	3.3 (0.4)	2.8 (0.8)	3.9 (0.2)	3.1 (0.2)	3.1 (0.3)	3.3 (0.4)	—
<i>P. stegnus</i>	5.0 [†]	—	4.5 (0.5)	2.9 (1.5)	2.0 [†]	4.3 (0.3)	3.6 (0.4)	—	5.0 [†]
Mean # Eggs									
<i>E. fuminpennis</i>	—	—	—	25.0 [†]	—	—	2.0 (2.0)	25.3 (25.3)	62.0 [†]
<i>S. sulphuripes</i>	—	—	13.0 (5.1)	7.3 (4.2)	20.3 (4.9)	9.6 (2.8)	17.1 (5.9)	21.3 (12.4)	—
<i>P. stegnus</i>	35.0 [†]	—	15.0 [†]	9.0 [†]	6.0 [†]	0.0 (0.0)	0.0 (0.0)	—	36.0 [†]

* pollen score for a given individual ranges from 0 (no noticeable pollen in gut) to 5 (gut full of pollen)

§ no flies of that species trapped on that date

† n = 1

Fig. 4.1. Aerial view of the field with the locations of flower plots and sampling transects.

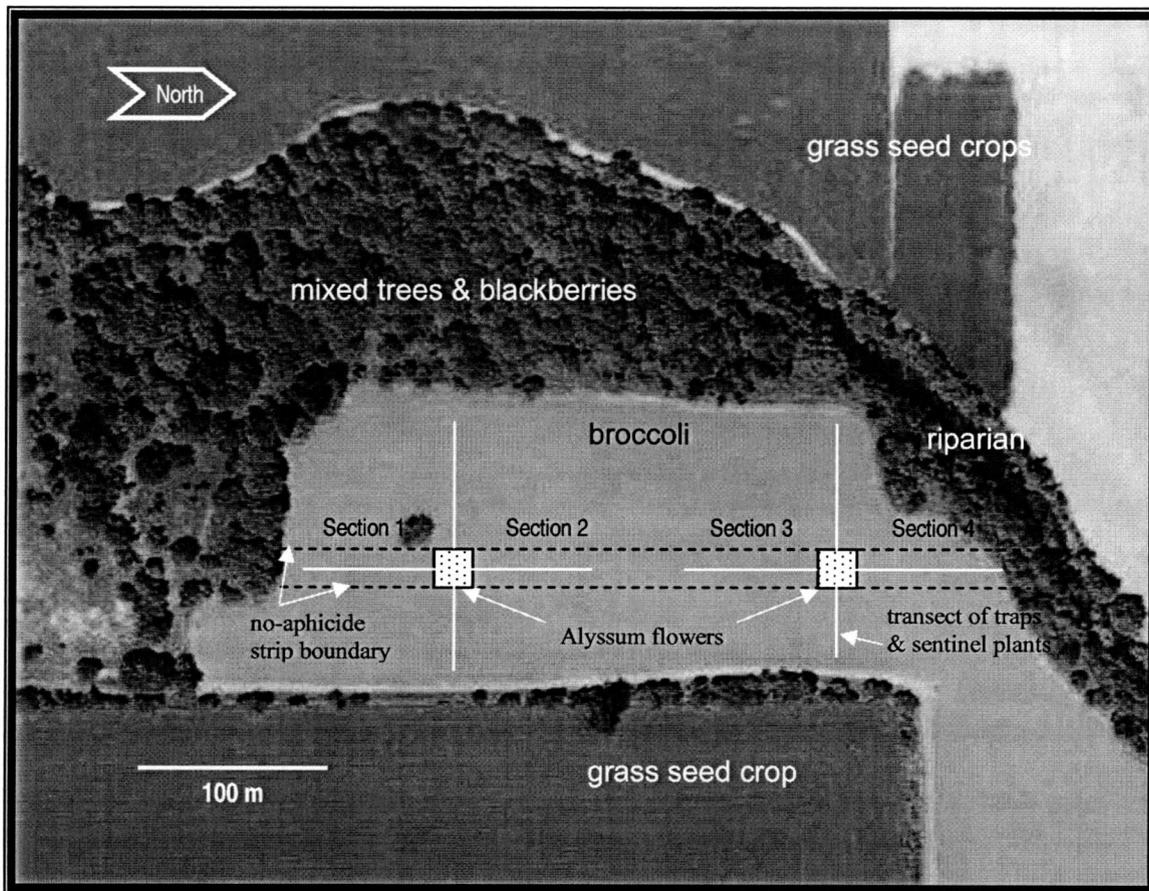


Fig. 4.2. The abundance of selected hoverfly species captured in the pan traps.

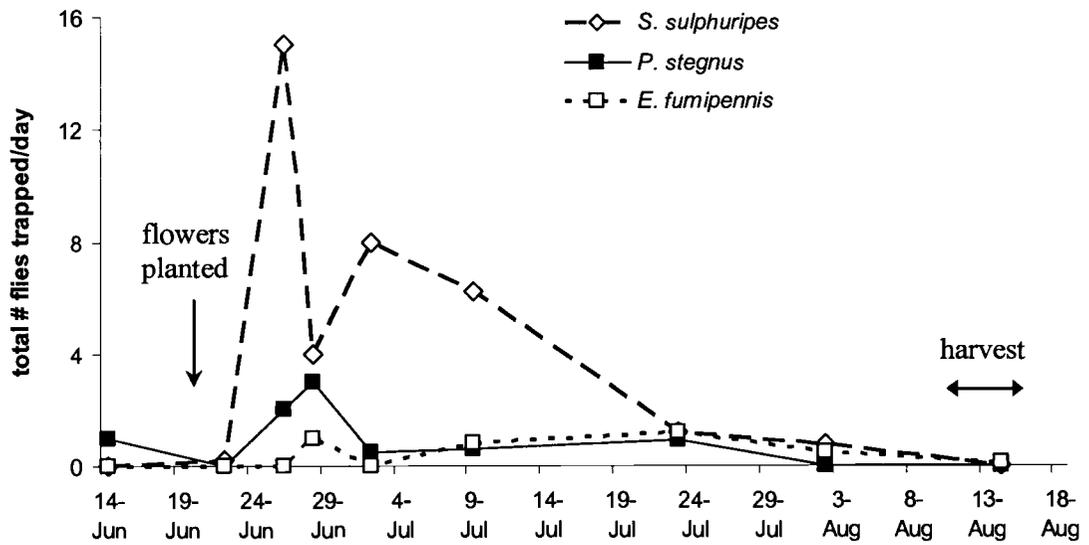
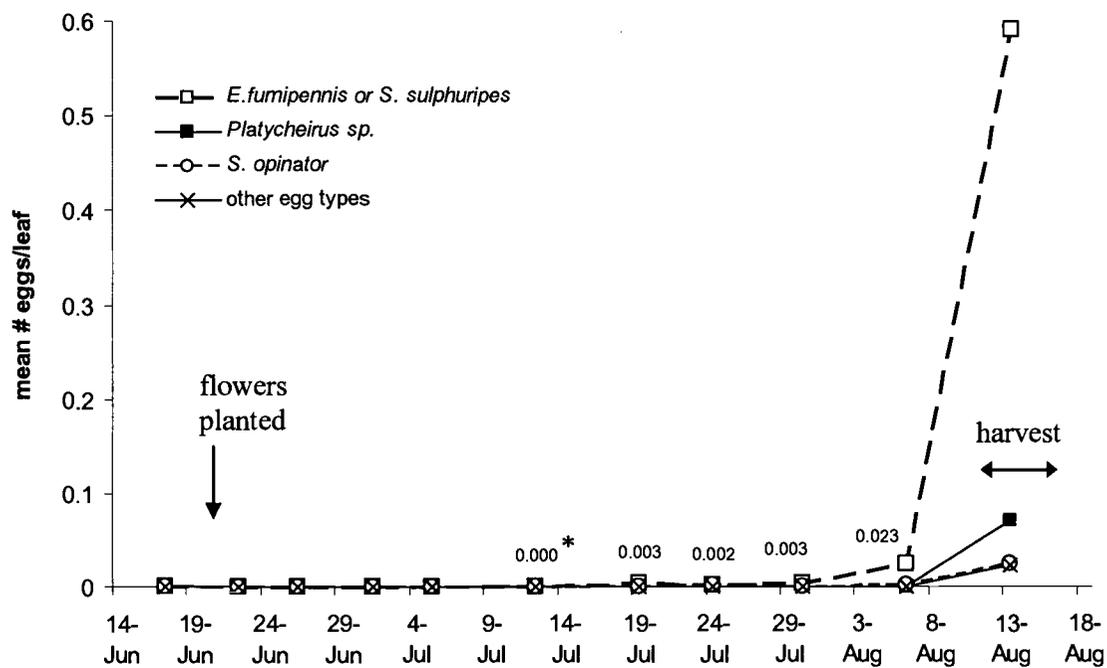


Fig. 4.3. The abundance of hoverfly eggs of each type on the broccoli crop plants.



* All numbers shown in plot are values for the egg group '*E. fumipennis* or *S. sulphuripes*', all values for other egg groups were zero on these dates, except for *S. opinator*, which had 0.002 eggs/leaf on 24 July and 6 August.

Fig. 4.4. The proportion of crop plants with cabbage aphids and hoverfly eggs.

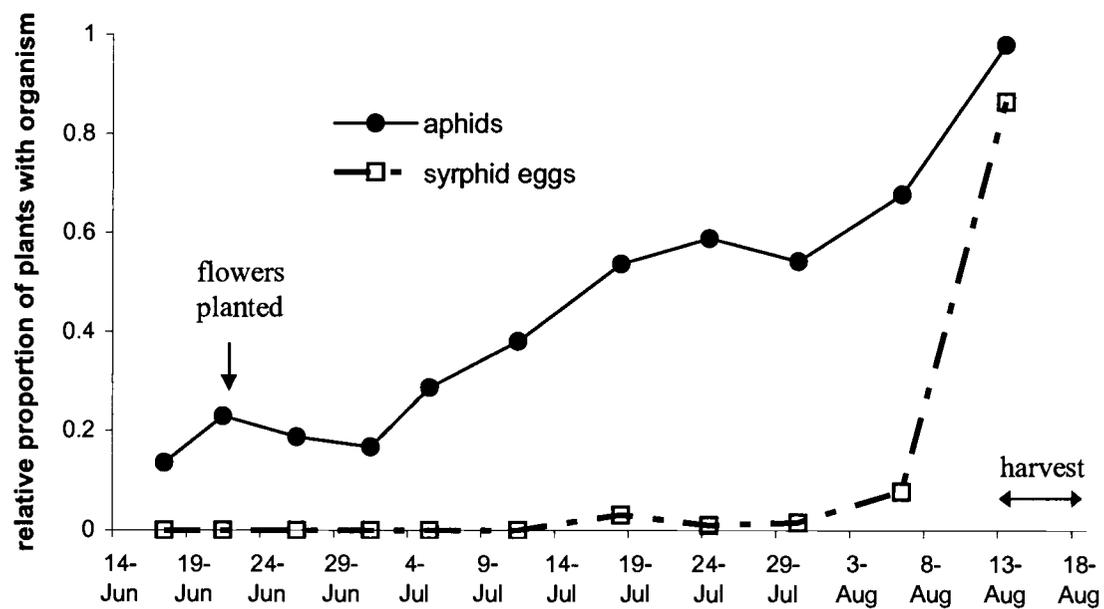
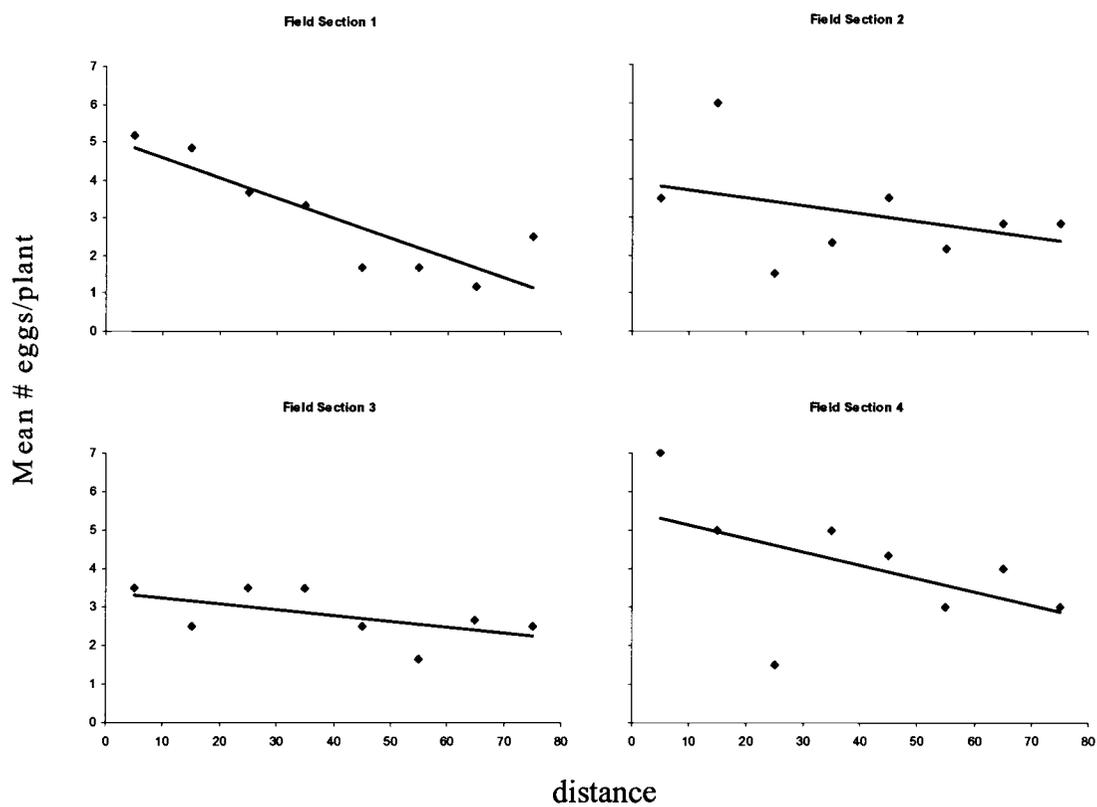


Fig. 4.6. Mean number of hoverfly eggs in the group representing *S. sulphuripes* and *E. fumipennis* at each distance class in each field section on the last date that crop plants were sampled.



OVERALL CONCLUSIONS

This project had the main goals of first identifying the main species of hoverflies which oviposit next to and prey on *B. brassicae* colonies in commercial broccoli fields, then assessing the aphid-limiting abilities of predacious hoverflies and then investigating if this background level of activity could be enhanced with pre-screened floral resources. Preliminary work in this project and other projects have observed that they were the most consistent natural enemy group that attacks the contamination pest *B. brassicae* in commercial broccoli fields in the Willamette Valley of Oregon. It was not known however, if they are limited for their required floral resources in this environment. After the identities, phenologies and predacious activity levels of the main species attacking *B. brassicae* in broccoli fields were determined, candidate floral resources were screened in the broccoli field environment. An attempt was then made to add a large enough volume of these resources so that any effect on their behaviors could be detected at the scale of a commercial broccoli field.

The five studies conducted in three different broccoli fields over the course of two broccoli field seasons showed that the suite of predatory hoverfly species present foraging around broccoli plants, as well as on floral resources in and around the fields were the same in each study. A formal wide-scale survey of the most common predatory hoverfly species present in broccoli fields was not attempted in this project, but the species in this suite (*E. fumipennis*, *S. sulphuripes*, *S. opinator*, *P. stegnus*, *T. marginatus*, *T. occidentalis*, and a *Paragus* sp.), were also the same species observed by the author in many other broccoli fields examined throughout the Willamette Valley in those years, as

well as in other years. The species *E. fumipennis*, *S. sulphuripes* and *S. opinator* were the most common species of this suite present as eggs and larvae in broccoli fields, and they are also common on other brassica crops in Oregon, as well as in the brassica-growing areas along the Central Coast of California (Bill Chaney and Ramy Colfer, pers. comm.). These three species were then the target for enhancement with insectary plantings.

Although *P. stegnus* eggs were also commonly observed near colonies of *B. brassicae* on broccoli plants in these studies, its ability to prey on *B. brassicae* could not be confirmed since it was not successfully cultured on *B. brassicae* in captivity as were the other species that appeared near *B. brassicae* colonies. There are four prey species on record for *P. stegnus* (Davidson 1922). It is possible that the *P. stegnus* which oviposit on broccoli are going after *M. persicae*, or they may only be facultative predators on aphids, and be able to survive on plant matter (Davidson 1922). This behavior of facultative predation has been reported for other members of this Genus (Vockeroth 1992). The eggs of this species are often laid in tight batches of approximately five to nine eggs further away from aphid colonies (Davidson 1922). This oviposition behavior has been termed "phytozetic", as opposed to the more typical "aphidozetic" behavior seen for predatory hoverflies of laying eggs singly and close to aphid colonies (Chandler 1968b). This phytozetic oviposition pattern was also seen for *P. stegnus* in the insectary planting field study, which, along with the fact that the eggs of this species showed the greatest delay in appearance on broccoli plants after gravid females were trapped, may be an indication that their oviposition may not have been driven by aphid numbers on the

broccoli plants as much as was the case for *E. fumipennis*, *S. sulphuripes*, and *S. opinator*.

A few individuals of a *Paragus* sp. were also caught in the insectary planting field experiment, but the larvae of this species developed very slowly on *B. brassicae* in culture, and were therefore not important predators of *B. brassicae*. The final species common in the broccoli fields, the two *Toxomerus* spp., were highly abundant on the insectary plantings and in the pan traps, but none of their eggs were observed on the broccoli plants. These species are known to be aphid predators (Rojo 2003), and it is likely that they were going after aphids hosted by the abundant weeds in and around this broccoli field.

Another key aspect of the predatory activities of these hoverfly species that was investigated in this project was their ability to develop on and kill *B. brassicae*. The three most common species on *B. brassicae* colonies, *E. fumipennis*, *S. sulphuripes*, and *S. opinator*, were tested for these abilities and the species *S. pyrastris* was included because it is the most common species of hoverfly found attacking *B. brassicae* on individual plants or very small plots of broccoli in gardens. It was the species out of the four that had the highest voracity for *B. brassicae* and developed the most quickly. This is not surprising considering how much larger it is than the other species, but it is not known why it does not exploit the abundant *B. brassicae* and *M. persicae* resources found in most commercial broccoli fields. *S. pyrastris* has one of the widest host ranges of any predatory hoverfly species (Rojo 2003), and it may be foraging for other aphid hosts that are more preferred, or those that simply more accessible in terms of foraging efficiency.

Another possibility is that it is generally not active, or possibly in a diapause phase of some sort, during the main part of the broccoli growing season in this area. A third possibility is that this species does not forage in wide open spaces as large as commercial broccoli fields. Considering the high aphid-limiting potential of this species once it reaches a broccoli plant, future studies of its life history for enhancing its potential to oviposit on broccoli in large fields would be justified.

For the group of species that did commonly oviposit on broccoli in large fields, the first step in trying to enhance their potential was to screen candidate species of insectary plants. The flowers were screened adjacent to large broccoli fields so that the community of hoverflies and other floral foragers would better represent the situation in which they might be used as insectary plants for enhancing aphid control in this crop. The results of the screening showed that crop pest arthropod species were also using certain species of the floral resources, and that other beneficial arthropods were influencing the floral preference responses of the target group of predatory hoverflies through competition. This shows the importance of considering the community context under which insectary plantings might be implemented.

The attempt to enhance the aphid-limiting activity of these target species of hoverflies in a commercial broccoli field resulted in the attraction of these species into the field, as well as increased oviposition closer to these resources at the end of the season, but the timing of hoverfly oviposition did not appear to be enhanced. These species did not appear to be limited for floral resources, since the first female individuals arriving to the field had fully developed eggs and guts with pollen, and floral resources

were present in and around the field throughout the course of the study. The insectary plantings had a high density of flowers, and were placed in the middle of the fields early in the season so that any potential effects could be seen relative to these background levels of floral resources. However, they were still not enough of an influence to alter how they respond to naturally occurring aphid densities.

This project provided specific information that is needed for determining the aphid-limiting potential of predatory hoverflies in this system, as well as for assessing the costs and benefits of insectary plantings for their enhancement. These results also show that conservation biological control planning and interventions must take into account the phenologies, host/prey response relationships, and landscape-scale patterns of resource use and dispersal of the target natural enemies before they can be realistically implemented. This is especially true for organisms with “life history omnivory” (Polis and Strong 1996) such as predatory hoverflies, whereby the adults and immatures exploit different resources, and therefore the relationships between adult feeding sites and host/prey foraging sites become complex.

BIBLIOGRAPHY

- Agarwala, B. K., A. K. Bhaumik, and F. S. Gilbert. 1989. Relative development and voracity of six species of aphidophagous syrphids in cruciferous crops. *Proceedings of the Indian Academy of Sciences, Animal Sciences* 98: 267-274.
- al Doghairi, M. A., and W. S. Cranshaw. 1999. Surveys on visitation of flowering landscape plants by common biological control agents in Colorado. *J. Kansas Entomol. Soc.* 72: 190-196.
- Allison, P. D. 1999. *Logistic Regression Using the SAS System*. SAS Institute, Cary, North Carolina, USA.
- Ambrosino, M. D., Luna, J. M., Jepson, P. C., and Wratten S. D., 2006. The relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects and herbivores. *Env. Entomol.*, In Press.
- Ambrosino, M. D. 2006. Enhancing the predatory potential of hoverflies on aphids in Oregon broccoli fields with floral resources. Ph.D. Thesis. Oregon State University.
- Ankersmit, G. W., H. Dijkman, N. J. Keuning, H. Mertens, A. Sins, and H. M. Tacoma. 1986. *Episyrphus balteatus* as a predator of the aphid *Sitobion avenae* on winter wheat. *Entomol. Exp. Appl.* 42: 271-277.
- Banks, C. J. 1952. The natural enemies of aphids. *Rep. Rothamstead Exp. Sta.*: 116-117.
- Bansch, R. 1966. On prey-seeking behaviour of aphidophagous insects., pp. 123-128. *In* I. Hodek [ed.], *Proc. Prague Symposium Ecology of Aphidophagous Insects*. Academia, Prague.
- Bargen, H., K. Saudhof, and H. M. Poehling. 1998. Prey finding by larvae and adult females of *Episyrphus balteatus*. *Entomol. Exp. Appl.* 87: 245-254.
- Barlow, C. A. 1979. Energy utilization by larvae of the flower fly, *Syrphus corollae* (Fabr.) (Dipt., Syrphidae). *Can. Entomol.* 111: 897-904.
- Barlow, C. A., and J. A. Whittingham. 1984. Feeding economy of larvae of a flower fly, *Metasyrphus corollae*: partial consumption of prey. *Entomophaga* 31: 39-47.
- Belliure, B., and J. P. Michaud. 2001. Biology and behavior of *Pseudodorus clavatus* (Diptera: Syrphidae), an important predator of citrus aphids. *Ann. Entomol. Soc. America* 94: 91-96.

- Ben Saad, A. A., and Bishop G. W., 1976. Effect of artificial honeydews on insect communities in potato fields. *Entomophaga* 5: 49-57.
- Branquart, E., J. L. Hemptinne, C. Bauffe, and L. Benfekih. 1997. Cannibalism in *Episyrphus balteatus* (Dipt.: Syrphidae). *Entomophaga* 42: 145-152.
- Branquart, E., and J. L. Hemptinne. 2000. Selectivity in the exploitation of floral resources by hoverflies (Diptera : Syrphinae). *Ecography* 23: 732-742.
- Bribosia, E., 2002. The black elder (*Sambucus nigra*): alternate plant for aphidophagous syrphids. *Fruit Belge* 70: 151-153.
- Bugg, R. L., 1993. Habitat manipulation to enhance the effectiveness of aphidophagous hover flies (Diptera: Syrphidae). *Sustainable Agriculture* 5: 12-15.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*. Springer Verlag, New York. 488 pp.
- Budenberg, W. J., and W. Powell. 1992. The role of honeydew as an ovipositional stimulant for two species of syrphids. *Entomol. Exp. Appl.* 64: 57-61.
- Carreck, N. L., and I. H. Williams. 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *J. Insect Cons.* 6: 13-23.
- Carroll, D. P., and Hoyt, S. C., 1984. Natural enemies and their effects on apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), colonies on young apple trees in central Washington. *Environ. Entomol.* 13: 469-481.
- Chambers, R. J. 1986. Preliminary experiments on the potential of hoverflies (Diptera: Syrphidae) for the control of aphids under glass. *Entomophaga* 31: 197-204.
- Chambers, R. J. 1987. Oviposition by aphidophagous hoverflies (Diptera: Syrphidae) in relation to aphid density and distribution in winter wheat. *Ann. Appl. Biol.* 110: 115-121.
- Chambers, R. J. 1988. Syrphidae, pp. 259-270. *In* A. K. Minks, and Harrewijn, P. [eds.], *Aphids: their biology, natural enemies, and control*. Elsevier, Amsterdam, The Netherlands.
- Chambers, R. J. 1991. Oviposition by aphidophagous hoverflies (Diptera: Syrphidae) in relation to aphid density and distribution in winter wheat. pp. 115-121. *In* L.E.A. Polgar [ed.], *Behaviour and impact of aphidophaga: proceedings of the 4th*

meeting of the IOBC "Ecology of Aphidophaga". SPB Academic Publishing, The Hague, The Netherlands.

- Chambers, R. J., Sunderland, K. D., Wyatt, I. J., and Vickerman, G. P. 1983. The effects of predator exclusion and caging on cereal aphids in winter wheat. *J. Appl. Ecol.* 20: 209-224.
- Chambers, R. J., and Adams, T. H. L. 1986. Quantification of the impact of hoverflies (Diptera: Syrphidae) on cereal aphids in winter wheat: an analysis of field populations. *J. Appl. Ecol.* 23: 895-904.
- Chambers, R. J., Sunderland, K. D., Stacey, D. L., and Wyatt, I. J. 1986. Control of cereal aphids in winter wheat by natural enemies: aphid-specific predators, parasitoids and pathogenic fungi. *Ann. Appl. Biol.* 108: 219-231.
- Chandler, A. E. F. 1967. Oviposition responses by aphidophagous Syrphidae (Diptera). *Nature* 213: 736.
- Chandler, A. E. F. 1968a. Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). *Ann. Appl. Biol.* 61: 402-414.
- Chandler, A. E. F. 1968b. Some host-plant factors affecting oviposition by aphidophagous Syrphidae (Diptera). *Ann. Appl. Biol.* 61: 415-423.
- Chandler, A. E. F. 1968c. The relationship between aphid infestations and oviposition by aphidophagous Syrphidae (Diptera). *Ann. Appl. Biol.* 61: 425-34.
- Chandler, A. E. F. 1968d. Height preferences for oviposition of aphidophagous Syrphidae (Diptera). *Entomophaga* 13: 187-195.
- Chandler, A. E. F. 1968e. A preliminary key to the eggs of some of the commoner aphidophagous Syrphidae (Diptera) occurring in Britain. *Trans. R. Ent. Soc. Lond.* 120: 199-217.
- Colley, M. R., and J. M. Luna. 2000. Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environ. Ent.* 29: 1054-1059.
- Cowgill, S., S. D. Wratten, and N. Sotherton. 1993a. The effect of weeds on the numbers of hoverfly (Diptera: Syrphidae) adults and the distribution and composition of their eggs in winter wheat. *Ann. Appl. Biol.* 123: 499-515.

- Cowgill, S., S. D. Wratten, and N. Sotherton. 1993b. The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. *Ann. Appl. Biol.* 122: 223-231.
- Davidson, W. M., 1922. Notes on certain species of *Melanostoma* (Diptera: Syrphidae). *Trans. Am. Ent. Soc.* 48, 35-47.
- Debaraj, Y., and T. K. Singh. 1998. Studies on some aspects of prey-predator interaction with reference to cabbage aphid, *Brevicoryne brassicae* (Linnaeus) and its predatory insects. *J. Adv. Zool.* 19: 50-54.
- Dixon, T. J. 1959. Studies on oviposition behaviour of Syrphidae (Diptera). *Trans. R. Ent. Soc. Lond.* III: 57-80.
- Dixon, T. J. 1959. Studies on oviposition behaviour of Syrphidae (Diptera). *Trans. R. Ent. Soc. Lond.* III: 57-80.
- Dixon, A. F. G. 2000. *Insect predator-prey dynamics: ladybird beetles and biological control.* Cambridge University Press, Cambridge. 257 pp.
- Dziock, F. 2005. Evolution of prey specialization in aphidophagous syrphids of the genera *Melanostoma* and *Platycheirus* (Diptera : Syrphidae) - 1. Body size, development and prey traits. *Eur. J. Entomol.* 102: 413-421.
- Entwistle, J. C., and A. F. G. Dixon. 1989. The effect of augmenting grain aphid (*Sitobion avenae*) numbers in a field of winter wheat in spring on the aphid's abundance in summer and its relevance to the forecasting of outbreaks. *Ann. Appl. Biol.* 114: 397-408.
- Fluke, C. L., 1929. The known predacious and parasitic enemies of the pea aphid in North America. *Bull. Wis. Agric. Exp. Sta.* 93, 1-47.
- Frazer, B. D. 1972. A simple and efficient method of rearing aphidophagous hoverflies (Diptera: Syrphidae). *J. Ent. Soc. Brit. Columbia* 69: 23-24.
- Fréchette, B., A. F. G. Dixon, C. Alauzet, N. Boughenou, and J. L. Hemptinne. 2006. Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey? *Entomol. Exp. Appl.* 118: 121-127.
- Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? *Science* 211: 887-893.

- George, K. S. 1957. Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). *Bulletin of Entomological Research* 48: 619-629.
- Gilbert, F. S. 1981. Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecol. Entomol.* 10: 385-392.
- Goulson, D. 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspect. Plant Ecol. Evol. Syst.* 2: 185-209.
- Goulson, D. 2003. Choice of flower species, pp. 95-106. *In* D. Goulson (ed.), *Bumblebees: Behaviour and Ecology*. Oxford University Press, Oxford.
- Goulson, D., and N. P. Wright. 1998. Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.). *Behav. Ecol.* 9: 213.
- Gurr, G. M., H. F. van Emden, and S. D. Wratten. 1998. Habitat manipulation and natural enemy efficiency: implications for the control of pests, pp. 155-183. *In* P. Barbosa (ed.), *Conservation Biological Control*. Academic Press, San Diego, CA.
- Gurr, G. M. and Wratten S. D. (Eds.) 2000. *Biological control: measures of success*. Kluwer, Dordrecht, The Netherlands.
- Gurr, M., S. D. Wratten, and M. A. Altieri. 2004. *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publications, Melbourne.
- Hagen, K. S., 1970. The use of food sprays to increase effectiveness of entomophagous insects. *In*: *Proceedings 2nd Tall Timbers Conference on Ecological Animal Control by Habitat Management*. Tall Timbers Research Station, Tallahassee, Florida, pp. 59-81.
- Hagen, K. S., and van den Bosch, R., 1968. Impact of pathogens, parasites and predators on aphids. *Ann. Rev. Entomol.* 13, 325-284.
- Hagen, K. S., N. J. Mills, G. Gordh, and J. A. McMurtry. 1999. Chapter 16 Terrestrial arthropod predators of insect and mite pests, pp. 451-452. *In* T. S. Bellows and T. W. Fisher [eds.], *Handbook of Biological Control*. Academic Press, San Francisco.
- Haslett, J. R. 1989a. Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia* 81: 433-442.

- Haslett, J. R. 1989b. Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera: Syrphidae). *Oecologia*, 81: 361-363.
- Herrera, C. M. 1989. Pollinator abundance, morphology, and flower visitation rate: analysis of the "quantity" component in a plant-pollinator system. *Oecologia* 80: 241-248.
- Herrera, C. M. 1995. Microclimate and individual variation in pollinators: flowering plants are more than their flowers. *Ecology* 76: 1516-1524.
- Hickman, J. M., S. D. Wratten, P. C. Jepson, and C. M. Frampton. 2001. Effect of hunger on yellow water trap catches of hoverfly (Diptera: Syrphidae) adults. *Agric. For. Entomol.* 3: 35-40.
- Hagley, E. A. C., and Simpson C. M., 1981. Effect of food sprays on numbers of predators in an apple orchard. *Can. Entomol.* 113: 75-77.
- Hagvar, E. B. 1974. Effectiveness of larvae of *Syrphus ribesii* and *S. Corollae* [Diptera: Syrphidae] as predators on *Myzus persicae* [Homoptera: Aphididae]. *Entomophaga* 19: 123-134.
- Harwood, R. W. J., Wratten, S. D., and Nowakowski, M., 1992. The effect of managed field margins on hoverfly (Diptera: Syrphidae) distribution and within-field abundance. In: *Proceedings of the Brighton Crop Protection Conference - Pests and Diseases*. November 1992, Brighton, England, pp. 1033-1037.
- Haslett, J. R. 1989. Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia*: 433-442.
- Hasken, K. H., and H. M. Poehling. 1995. Effects of different intensities of fertilisers and pesticides on aphids and aphid predators in winter wheat. *Agric. Ecosys. Environ.* 52: 45-50.
- Hausammann, A. 1996. The effects of weed strip-management on pests and beneficial arthropods in winter wheat fields. *J. Plant Dis. Prot.* 103: 70-81.
- Hickman, J. M., and Wratten, S. D., 1996. Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *J. Econ. Entomol.* 89, 832-840.

- Hickman, J., S. D. Wratten, P. C. Jepson, and C. M. Frampton. 2001. Effect of hunger on yellow water trap catches of hoverfly (Diptera: Syrphidae) adults. *Agric. For. Entomol.* 3: 35-40.
- Hindayana, D., R. Meyhofer, D. Scholz, and H. M. Poehling. 2001. Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biol. Cont.* 20: 236-246.
- Holland, J. M., Thomas, S. R., and Courts, S., 1994. *Phacelia tanacetifolia* flower strips as a component of integrated farming. In: Boatman, N. (Ed.), *Field margins: integrating agriculture and conservation*. 18-20 April 1994. BCPC, Coventry, UK, pp. 215-220.
- Horn, D. J. 1981. Effect of weedy backgrounds on colonization of collards by green peach aphid, *Myzus persicae*, and its major predators. *Environ. Entomol.* 10: 285-296.
- Hagvar, E. B. 1972. The effect of intra- and interspecific larval competition for food (*Myzus persicae*) on the development at 20 C of *Syrphus ribesii* and *Syrphus corollae* [Diptera: Syrphidae]. *Entomophaga* 17: 71-77.
- Hughes, R. D. 1963. Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). *J. Anim. Ecol.* 32: 393-424.
- Hughes, R. D. 1988. Biological control in the open field., pp. 175-198, Chapter 11.2.1. In A. K. Minks, and P. Harrewijn [eds.], *Aphids: their biology, natural enemies, and control*. Elsevier, Amsterdam, The Netherlands.
- Hussein, S., and F. Gilbert. 2000. Aphid suitability and its relationship to oviposition preference in predatory hoverflies. *J. Anim. Ecol.* 69: 771-784.
- Jervis, M. A., N. A. C. Kidd, M. G. Fitton, T. Huddleston, and H. A. Dawah. 1993. Flower-visiting by hymenopteran parasitoids. *Journal of Natural History* 27: 67-105.
- Jervis, M., and N. Kidd. 1996. *Insect natural enemies: practical approaches to their study and evaluation*. Chapman & Hall, London. 491 p.
- Jervis, M. A., and N. A. C. Kidd. 1996. Phytophagy, pp. 375-394. In M. Jervis and N. Kidd (eds.), *Insect natural enemies: practical approaches to their study and evaluation*. Chapman and Hall, London, UK.
- Kearns, C. A., and D. W. Inouye. 2001. *Techniques for pollination biologists*. University Press of Colorado, Niwot, CO.

- Kikuchi, T. 1962. Studies on the coaction among insects visiting flowers II. Dominance relationship in the so-called drone fly group. *Sci. Rep. Tohoku Univ. Ser. IV* 28: 47-51.
- Kikuchi, T. 1963. Studies on the coaction among insects visiting flowers IV. Preferring behavior of some Syrphid flies, *Eristalis tenax*, *Eristalis cerealis*, and *Sphaerophoria cylindrica*, in relation to the age of the flower of *Chrysanthemum leucanthemum*. *Sci. Rep. Tohoku Univ. Ser. IV* 29: 9-14.
- Kikuchi, T. 1965. Role of interspecific dominance-subordination relationship on the appearance of flower-visiting insects. *Sci. Rep. Tohoku Univ. Ser. IV* 31: 275-296.
- Kan, E. 1988a. Assessment of aphid colonies by hoverflies. I Maple aphids and *E. balteatus* (Diptera: Syrphidae). *J. Ethol.* 6: 39-48.
- Kan, E. 1988b. Assessment of aphid colonies by hoverflies. II Pea aphids and 3 syrphid species: *Betasyrphus serarius*, *Metasyrphus frequens* and *Syrphus vitripennis* (Diptera: Syrphidae). *J. Ethol.* 6: 135-142.
- Kan, E. 1989. Assessment of aphid colonies by hoverflies. III Pea aphids and *Episyrphus balteatus* (Diptera: Syrphidae). *J. Ethol.* 7: 1-6.
- Kindlmann, P., and Z. Ruzicka. 1992. Possible consequences of a specific interaction between predators and parasites of aphids. *Ecol. Mod.* 61: 253-265.
- Klinger, K., 1987. Effects of margin strips along a winter wheat field on the predatory arthropod fauna and cereal aphid infestation. *J. Appl. Entomol.* 104, 47-58.
- Krause, U., and H. M. Poehling. 1995. Population dynamics of hoverflies (Diptera: Syrphidae) in Northern Germany in relation to different habitat structure. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie* 10: 509-512.
- Krause, U., and Poehling, H., 1996. Overwintering, oviposition and population dynamics of hoverflies (Diptera: Syrphidae) in northern Germany in relation to small and large-scale landscape structure. In: Booij, C. J. H., and den Nijs, L. J. M. F. (Eds.), *Arthropod natural enemies in arable land II. Survival, reproduction and enhancement.* *Acta Jutlandica* Vol. 71(2). Aarhus University Press, Denmark, pp. 157-169.
- Kidd, N., and M. Jervis. 1996. Population dynamics, pp. 293-374. In M. Jervis and N. Kidd [eds.], *Insect Natural Enemies*. Chapman and Hall, London.

- Lal, R., and E. Haque. 1955. Effect of nutrition under controlled conditions of temperature and humidity on longevity and fecundity of *Sphaerophoria scutellaris* (Fabr.) (Syrphidae, Diptera) - efficacy of its maggots as aphid predators. *Indian J. Entomol.* 17: 317-325.
- Landis, D. A., Wratten, S. D. and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Ann. Rev. Ent.* 45: 175-201.
- Laska, P. 1984. A method of comparing the role of aphid parasitoids and predators exemplified by the cabbage aphid, *Brevicoryne brassicae*. *Acta Entomol Bohemoslov. Praha : Ceskoslovenska akademie ved* 81: 81-89.
- Legendre, P. and M. J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.
- Lewis, T., 1965. The effects of an artificial windbreak on the aerial distribution of flying insects. *Ann Appl Biol.* 55, 503-512.
- Long, R. F., A. Corbett, C. Lamb, C. Reberg Horton, J. Chandler, and M. Stimmann. 1998. Beneficial insects move from flowering plants to nearby crops. *Calif. Agric.* 52: 23-26.
- Lovei, G. L., McDougall, D., Bramley, G., Hodgson, D. J., Wratten, S. D., and Popay, A. J., 1992. Floral resources for natural enemies: the effect of *Phacelia tanacetifolia* (Hydrophyllaceae) on within-field distribution of hoverflies (Diptera: Syrphidae). In: *Proceedings of the Forty Fifth New Zealand Plant Protection Conference*. 11-13 August 1992, Wellington, New Zealand, pp. 60-61.
- Lovei, G. L., D. J. Hodgson, A. MacLeod, and S. D. Wratten. 1993. Attractiveness of some novel crops for flower visiting hoverflies (Diptera: Syrphidae): comparisons from two continents. pp. 368-370 In: Corey, S., Dall, D. and W. Milne [eds.] *Pest Control and Sustainable Agriculture*. Canberra, CSIRO.
- Lovei, G. L., Hickman, J. M., McDougall, D., and Wratten, S. D., 1993. Field penetration of beneficial insects from habitat islands: hoverfly dispersal from flowering crop strips. In: *Proceedings of the Forty Sixth New Zealand Plant Protection Conference*. 10-12 August 1993, Christchurch, New Zealand, pp. 325-328.
- Lovei, G. L., J. M. Hickman, D. McDougall, and S. D. Wratten. 1994. Field penetration of beneficial insects from habitat islands: hoverfly dispersal from flowering strip crops. *Proc. 46th N. Z. Plant Prot. Conf.*, pp. 325-328.

- Lovei, G. L., Macleod, A., and Hickman, J. M., 1998. Dispersal and effects of barriers on the movement of the New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. *J. App. Entomol.* 122, 115-120.
- MacLeod, A., 1992. Alternative crops as floral resources for beneficial hoverflies (Diptera: Syrphidae). In: *Proceedings of the Brighton Crop Protection Conference - Pests and Diseases*. November 1992, Brighton, England, pp. 997-1002.
- MacLeod, A., 1999. Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. *Agric. Ecosys. Environ.* 73, 237-244.
- Makhmoor, H. D., and A. K. Verma. 1987. Bionomics of major aphidophagous syrphids occurring in mid-hill regions of Himachal Pradesh. *J. Biol. Cont.* 1: 23-31.
- McGrath, D.M. 2000. Conservation of arthropod natural enemies in broccoli with relay strip-cropping. Ph.D. Thesis, Oregon State University, Corvallis, OR.
- McIver, J. D. 1984. A three-trophic-level perspective on factors influencing herbivore abundance on collard. Oregon State University, Corvallis, OR.
- Medvey, M. 1988. On the rearing of *Episyrphus balteatus* (Deg.) (Diptera: Syrphidae) in the laboratory. pp. 61-63. In E. Niemczyk and A. F. G. Dixon [eds.], *Ecology and effectiveness of aphidophaga*. SPB Academic Publishing, The Hague.
- Metcalf, C. L., 1913. The Syrphidae of Ohio. *Ohio Biological Survey Bull.* 1, 123pp.
- Meyling, N. V., A. Enkegaard, and H. Brødsgaard. 2003. Two *Anthocoris* bugs as predators of glasshouse aphids – voracity and prey preference. *Entomol. Exp. Appl.* 108: 59-70.
- Michaud, J. P. and B. Belliure. 2001. Impact of syrphid predation on production of migrants in colonies of the brown citrus aphid, *Toxoptera citricida* (Homoptera: Aphididae). *Biol. Cont.* 21: 91-95.
- Morse, D. H. 1981. Interactions among syrphid flies and bumblebees on flowers. *Ecology* 62: 81-88.
- Murdoch, W. W., and C. J. Briggs. 1996. Theory for biological control: recent developments. *Ecology* 77: 2001-2013.
- Nawrocka, B. 1988. Effectiveness of aphidophagous syrphids in controlling the cabbage aphid, *Brevicoryne brassicae* L., pp. 289-294. In E. A. F. G. D. Niemczyk [ed.],

Ecology and effectiveness of aphidophaga. SPB Academic Publishing, The Hague.

- Neuenschwander, P., K. S. Hagen, and R. F. Smith. 1975. Predation on aphids in California's alfalfa fields. *Hilgardia* 43: 53-78.
- Nunnenmacher, L., H. E. Goldbach, S. Finch, and E. Brunel. 1996. Aphids on lettuce: the effects of excluding aphid predators. IOBC/WPRS working group meeting: Integrated control in field vegetable crops. 19: 38-47.
- Oatman, E. R., and Platner, G. R., 1969. An ecological study of insect populations on cabbage in southern California. *Hilgardia* 40, 1-40.
- Petherbridge, F. R., and Mellor, J. E. M., 1936. Observations on the life history and control of the cabbage aphid, *Brevicoryne brassicae* L. *Ann. of Appl. Biol.* 23, 329-241.
- Pfiffner, L., and Wyss, E., 2004. Use of sown wildflower strips to enhance natural enemies of agricultural pests. In: Gurr, G. M., Wratten, S. D., and Altieri, M. A. (Eds.), *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publishing, Melbourne, pp. 165-186.
- Poehling, H. M., B. Tenhumberg, and U. Groeger. 1991. Different pattern of cereal aphid population dynamics in northern (Hannover-Gottingen) and southern areas of West Germany. *Bulletin SROP* 14: 1-12.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *Am. Nat.* 147: 813-846.
- Pollard, E. 1969. The effects of removal of arthropod predators on an infestation of *Brevicoryne brassicae* (Hemiptera, Aphididae) on brussels sprouts. *Entomol. Exp. Appl.* 12: 118-124.
- Pollard, E. 1971. Hedges. VI. Habitat diversity and crop pests. A study of *Brevicoryne brassicae* and its syrphid predators. *J. Appl. Ecol.* 8: 751-780.
- Raworth, D. A. 1984. Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (Homoptera: Aphididae) at Vancouver, British Columbia, V. A simulation model. *Can. Ent.* 116: 895-911.
- Rajo, S., K. R. Hopper, and M. A. Marcos Garcia. 1996. Fitness of the hover flies *Episyrphus balteatus* and *Eupeodes corollae* faced with limited larval prey. *Entomologia Experimentalis et Applicata* 81: 53-59.

- Rojo, S., A. Marcos-Garcia, J. Nieto, and M. Mier. 2003. A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain.
- Rotheray, G. E., 1993. Colour guide to hoverfly larvae (Diptera, Syrphidae) Dipterists Digest No. 9. Whiteley, Sheffield, UK, 159 pp.
- Rotheray, G. P. M. 1984. Searching behaviour in relation to starvation of *Syrphus ribesii*. Entomol. Exp. et Appl. 13: 194-207.
- Rothery, F. A. 1994. Hoverfly foraging on hedgerow flowers. Bull. OILB SROP 17: 148-155.
- Rotheray, G. 1989. Aphid Predators. Richmond Publishing, Slough. pp. 66-70.
- Rotheray, G. E., and P. Martinat. 1984. Searching behaviour in relation to starvation of *Syrphus ribesii*. Entomol. Exp. Appl. 13: 194-207.
- Ruppert, V., and Molthan, J., 1991. Augmentation of aphid antagonists by field margins rich in flowering plants. In: Polgar, R. J. C. L., Dixon, A.F.G., and Hodek, I. (Eds.), Behavior and Impact of Aphidophaga. IOBC, Godollo, Hungary, pp. 243-247.
- Sadeghi, H., and F. Gilbert. 1999. Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. Oecologia 118: 405-411.
- Sadeghi, H., and F. Gilbert. 2000a. The effect of egg load and host deprivation on oviposition behaviour in aphidophagous hoverflies. Ecol. Entomol. 25: 101-108.
- Sadeghi, H., and F. Gilbert. 2000b. Oviposition preferences of aphidophagous hoverflies. Ecol. Entomol. 25: 91-100.
- Sadeghi, H. and F. Gilbert. 2000c. Aphid suitability and its relationship to oviposition preference in predatory hoverflies. J. Anim. Ecol. 69: 771-784.
- Sadeghi, H. 2002. The relationship between oviposition preference and larval performance in an Aphidophagous hover fly, *Syrphus ribesii* L. (Diptera: Syrphidae). Journal of Agricultural Science and Technology 4: 1-10.
- Salveter, R. 1998. The influence of sown herb strips and spontaneous weeds on the larval stages of aphidophagous hoverflies (Diptera, Syrphidae). J. Appl. Entomol. 122: 103-114.
- SAS Institute. 1990. Procedures Guide, Version 6, 3rd ed. SAS Institute, Cary, NC.

- SAS Institute, 2000. SAS version 8. SAS Institute, Cary, NC.
- Sarthou, J. P., Ouin, A., Arrignon, F., Barreau, G., and Bouyjou, B., 2005. Landscape parameters explain the distribution and abundance of *Episyrphus balteatus* (Diptera : Syrphidae). *Eur. J. Entomol.* 102: 539-545.
- Sengonca, C., and Frings, B., 1988. The effect of *Phacelia tanacetifolia* on populations of pests and beneficial insects in sugarbeet fields. *Pedobiologia* 32: 311-316.
- Schneider, F. 1948. Beitrag zur Kenntnis der Generationsverhältnisse und Diapause rauberischer Schwebfliegen (Syrphidae, Diptera). *Mitteilungen Schweizerische Entomologische Gesellschaft* 21: 249-285.
- Scholz, D., and H. M. Poehling. 2000. Oviposition site selection of *Episyrphus balteatus*. *Entomol. Exp. Appl.* 94: 149-158.
- Scott, S. M., and C. A. Barlow. 1984. Effect of prey availability during development on the reproductive output of *Metasyrphus corollae* (Diptera: Syrphidae). *Environ. Entomol.* 13: 669-674.
- Scott, S. M., and C. A. Barlow. 1990. Effect of hunger on the allocation of time among pea plants by the larvae of an aphidophagous hover fly, *Eupeodes corollae* (Dipt.: Syrphidae). *Entomophaga* 35: 163-172.
- Sengonca, C., and B. Frings. 1988. The effect of *Phacelia tanacetifolia* on populations of pests and beneficial insects in sugarbeet fields. *Pedobiologia* 32: 311-316
- Soleyman Nezhadiyan, E., and R. Laughlin. 1998. Voracity of larvae, rate of development in eggs, larvae and pupae, and flight seasons of adults of the hoverflies *Melangyna viridiceps* Macquart and *Symosyrphus grandicornis* Macquart (Diptera: Syrphidae). *Aust. J. Entomol.* 37: 243-248.
- Sood, A. K., K. C. Sharma, K. L. Kakar, C. Usha, and U. Chauhan. 1994. Use of intrinsic rate of increase in the evaluation of biocontrol potential of a syrphid predator *Eupeodes frequens* Matsumura (Diptera : Syrphidae) of the chrysanthemum aphid *Macrosiphoniella sanborni* (Gillette) (Homoptera : Aphididae). *Annal. Entomol.* 12: 39-42.
- Sturken, K. 1964. Die Bedeutung der Imaginalernahrung für das Reproduktionsvermögen der Syrphiden. *Z. Angew. Zool.* 51: 385-417.
- Sutherland, J. P., G. M. Poppy, A. Cooper, and J. Power. 1997. Spatial and temporal distribution of aphidophagous hoverflies (Diptera: Syrphidae) in sown wild

- flower patches in a winter barley crop, pp. 135-142. *In* A. Cooper and J. Power (eds.), *Species dispersal and land use processes*, Ulster, UK.
- Sutherland, J. P., M. S. Sullivan, and G. M. Poppy. 1999. The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. *Entomol. Exp. Appl.* 93: 157-164.
- Sutherland, J. P., M. S. Sullivan, and G. M. Poppy. 2001. Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agric. For. Entomol.* 3: 57-64.
- Sundby, R. A. 1966. A comparative study of the efficiency of three predatory insects *Coccinella septempunctata* L. [Coleoptera, Coccinellidae], *Chrysopa carnea* St. [Neuroptera, Chrysopidae] and *Syrphus ribesii* L. [Diptera, Syrphidae] at two different temperatures. *Entomophaga* 2: 395-404.
- Tamaki, G. 1973. Spring populations of the green peach aphid on peach trees and the role of natural enemies in their control. *Environ. Entomol.* 2: 186-191.
- Tamaki, G. 1974. Life system analysis of the autumn population of *Myzus persicae* on peach trees. *Environ. Entomol.* 3: 221-226.
- Tamaki, G., J. U. McGuire, and J. E. Turner. 1974. Predator power and efficacy: A model to evaluate their impact. *Environ. Entomol.* 3: 625-630.
- Tenhumberg, B. 1995. Estimating predatory efficiency of *Episyrphus balteatus* (Diptera: Syrphidae) in cereal fields. *Environ. Entomol.* 24: 687-691.
- Tenhumberg, B., and H. M. Poehling. 1991. Studies on the efficiency of syrphid larvae, as predators of aphids on winter wheat., pp. 281-288. *In* L. e. a. Polgar [ed.], *Behaviour and impact of aphidophaga*. SPB Academic Publishing, The Hague, The Netherlands.
- Tenhumberg, B., and H. M. Poehling. 1994. Quantification of the predation efficacy of *Episyrphus balteatus* (Diptera: Syrphidae) with the help of traditional models. *Bulletin OILB SROP* 17: 112-126.
- Tenhumberg, B., and H. M. Poehling. 1995. Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. *Agric. Econ. Environ.* 52: 39-43.
- Thies, C., and Tschardtke, T., 1999. Landscape Structure and Biological Control in Agroecosystems. *Science* 285, 893-895.

- Thomson, J. D. 1981. Spatial and Temporal Components of Resource Assessment by Flower-Feeding Insects. *J. Anim. Ecol.* 50: 49-59.
- Tinkeu, L. N., G. Delabye, D. Stilmant, and T. Hance. 1998. Phenology of parasitism and its influence on the predatory efficiency of larvae of *Episyrphus balteatus* (Diptera: Syrphidae). *Integrated control in cereal crops IOBC Bulletin* 21: 133-139.
- Toft, C. A. 1983. Community patterns of nectivorous adult parasitoids (Diptera, Bombyliidae) on their resources. *Oecologia* 57: 200-215.
- Tornier, I., and W. Drescher. 1991. Development of a method for mass production of the pollinator and aphid predator *Episyrphus balteatus* Deg. (Diptera, Syrphidae). *Acta Hortic. Wageningen: Int. Soc. Hort. Sci.* 28: 464-468.
- Trumble, J. T. 1982. Within-plant distribution and sampling of aphids (Homoptera: Aphididae) on broccoli in Southern California. *J. Econ. Entomol.* 75: 587-592.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters* 8, 857-874.
- van Alphen, J. J. M., and M. A. Jervis. 1996. Foraging Behaviour, pp. 1-62. *In* M. Jervis and N. Kidd [eds.], *Insect Natural Enemies*. Chapman and Hall, London.
- van Driesche, R. G., and T. S. Bellows, Jr. 1996. *Biological Control*. Chapman and Hall, New York.
- van Emden, H. F. 1963. Observations on the effect of flowers on the activity of parasitic Hymenoptera. *Entomol. Mon. Mag.* 98: 265-270.
- van Emden, H. F. 1963. A field technique for comparing the intensity of mortality factors acting on the cabbage aphid, *Brevicoryne brassicae* (L.) (Hem.: Aphididae), in different areas of a crop. *Entomol. Exptl.* 6: 53-62.
- van Emden, H. F., 1965. The effect of uncultivated land on the distribution of cabbage aphid (*Brevicoryne brassicae*) on an adjacent crop. *J. Appl. Ecol.* 2, 171-196.
- Vockeroth, J. R., 1990. Revision of the Nearctic species of *Platycheirus* (Diptera, Syrphidae). *Can. Entomol.* 122, 659-766.
- Vockeroth, J. R., 1992. *The Insects and Arachnids of Canada, Part 18: The flower flies of the subfamily Syrphinae of Canada, Alaska, and Greenland: Diptera, Syrphidae*. Canadian Communication Group, Ottawa, Canada.

- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043-1060.
- Wellington, W. G., and S. M. Fitzpatrick. 1981. Territoriality in the drone fly, *Eristalis tenax* (Diptera: Syrphidae). *Can. Entomol.* 113: 695-704.
- White, A. J., S. D. Wratten, N. A. Berry, and U. Weigmann. 1995. Habitat manipulation to enhance biological control of Brassica pests by hover flies (Diptera: Syrphidae). *J. Econ. Entomol.* 88: 1171-1176.
- Wilson, H. B., R. H. J. Verkerk, and F. J. Wright, 2001. The effects of stochastic dynamics in an excitable aphid-natural enemy system. *Ecology* (in press).
- Winder, L., D. J. Hirst, N. Carter, S. D. Wratten, and P. I. Sopp. 1994. Estimating predation of the grain aphid *Sitobion avenae* by polyphagous predators. *J. Appl. Ecol.* 31: 1-12.
- Wnuk, A., and E. Wojciechowicz. 1993. Syrphid predators (Diptera, Syrphidae) occurring in colonies of the cabbage aphid, *Brevicoryne brassicae* (L.), on cabbage and cauliflower. *Polskie Pismo Entomologiczne* 62: 215-229.
- Wratten, S. D., H. F. van Emden, and M. B. Thomas, 1998. Within field and border refugia for the enhancement of natural enemies., pp. 375-403. *In* C. Pickett and R.L. Bugg [eds.], *Enhancing biological control: habitat management to promote natural enemies of agricultural pests*. Univ. Calif. Press, Berkeley.