Imperial College
London

DEPARTMENT OF LIFE SCIENCES

Local and landscape effects of field margins on aerially dispersing beneficial insects and spiders

by

Heather Oaten

A thesis submitted for the degree of Doctor of Philosophy
of Imperial College London

December 2010

RURAL ECONOMY
AND LAND USE

Game & Wildlife
CONSERVATION TRUST

Declaration

I confirm that this thesis and work conducted within is entirely my own apart from the exceptions below:

Chapter 2:

Help with trap setting and D-vac suction sampling was provided by Euan Douglas (undergraduate Exeter University student).

Chapter 3:

Cylindrical sticky traps for fields H1, H2, H3 and H4 were set and collected in by Freya McCall (undergraduate Cardiff University student).

Chapter 4:

Louise Meylan (Masters student at Southampton University) conducted the aphid counts, assisted with trap setting/collecting/insect identification and ran the prepared samples through the Spectrophotometer at the Engineering Department at Southampton University.

Signed: Heather Oaten Date: 13/12/10

Abstract

Field margins were implemented in UK agri-environment schemes with the aim to increase farmland biodiversity. Recently aerially dispersing aphid enemies have been shown to provide the majority of aphid control in winter wheat fields but there is a lack of research conducted on the aerial predator guild. This thesis examines the effect field margins have on aphid predators at the single field scale, the landscape scale and, using results from a marking study, examines the direct use of a pollen and nectar rich field margin by *Episyrphus balteatus*.

At the single field scale, field margins had a positive effect of the numbers of Cantharidae, Empididae, Linyphiidae and *Tachyporus* spp. in fields with sown margins compared to those without during wheat growth and total aphid predator numbers were significantly higher in fields with margin surrounds in early May but not later in the year. At the landscape scale, results from twelve winter wheat fields with varying densities of surrounding field margins showed predatory *Tachyporus* spp. to exhibit a positive correlation at scales above 500m radius and Cantharidae to exhibit a negative correlation at local scales. Implications for field margins exerting both positive and negative influences on the presence of aerially dispersing aphid predators in winter wheat fields are discussed. A marking study using rubidium chloride proved direct utilisation of a pollen and nectar rich field margin by the Syrphid *Episyrphus balteatus*, and the traps used in this study also highlighted the association in distributions between Empididae and cereal aphids.

Overall it was concluded that the presence of field margins does have an effect on the spatial and temporal distributions of some aerially dispersing aphid predators, but the response of each predator group varies depending on numerous interlinking components of their life history and directions for future research are discussed.

Acknowledgements

Thanks to my main supervisors, Dr John Holland, Dr Barbara Smith (both at the Game and Wildlife Conservation Trust) and Dr Simon Leather (Imperial College London) for their continued support and advice, especially during the write up period. Also thanks to Dr Nicholas Aebischer (Game and Wildlife Conservation Trust) for valuable statistical advice.

Thanks to the many farmers, especially Peter Shellcross and Julian Gibbons for the use of their land, allowing access and being so interested in the project and for the sheep herding/ straw stooking experience.

Thanks to the Entomology lab at the GWCT, Steve M, Sue, Tom, Johnny and Steve B. and to the students Euan, Freya, Louise B., Mark and Louise M. and GWCT GIS personnel, Dr Julie Ewald and Neville Kingdon for their advice and extending my sense of humour in times of statistical, GIS and weather frustrations.

Thanks also (I think!) to Dr John Holland for suggesting I pursue a Ph.D. and initiating the project in the first place and to Mum and Dad for not asking if it 'was finished yet'.

Contents

Introduction

Do 6m florally enhanced field margins have an effect on aerially dispersing aphid predators in winter wheat?

General Discussion and Conclusions

List of Tables

List of Figures

Chapter 1

Introduction

1.1. **Aphids**

1.1.1. A yield reducing problem

Aphids are common agricultural pests able to inflict significant crop damage (Tatchell, 1989). There are many species of aphid that affect a wide range of crops in the UK, and these have been shown to cause yield reductions and associated economic loss for the farmer.

Three aphid species in particular cause problems in winter wheat fields in the UK through two different modes of crop damage. *Sitobion avenae* and *Metopolophium dirhodum* colonize cereal fields in May and June and multiply very rapidly in June until numbers are high enough to incur direct wheat feeding damage (Winder *et al.,* 2000). *Sitobion avenae* feeds on the leaves of wheat plants but primarily on the ears during grain development; growth stage 58 to 79 (Zadoks, 1974), causing a reduction in grain weight (Wratten, 1978) and/or quality (Lee *et al.,* 1981). *Metopolophium dirhodum* feeds solely on the leaves but also leads to a reduction in grain size and quality through feeding on the flag leaf of the plant (Wratten, 1978). It does not seem to achieve yield reducing levels as often as *S. avenae* (Wratten et al., 1975; Duffield *et al*., 1997). At higher densities both aphid species result in the wheat plant becoming covered in aphid honey-dew, a sticky waste product produced by aphids. This coating attracts saprophytic fungi which can potentially further decrease wheat yields through blocking light for photosynthesis and accelerating leaf aging (Rabbinge *et al.,* 1981). *S. avenae* is considered to be more damaging than *M. dirhodum* due to the extended length of time it can remain on the wheat plant through ear feeding and the high rate of population increase, which is double on the ear than that on the flag leaf (Vereijken, 1979).

A third species, *Rhopalosiphum padi,* does not cause enough direct feeding damage to contribute to a direct yield loss in the UK, but does act as a vector for Barley yellow dwarf virus (BYDV) (Carter *et al.,* 1980; Vickerman *et al.,* 1987; Leather *et al.,* 1989) due to the aphids' migratory life history. BYDV results in stunted plant growth and a reduction in the ear size of infected wheat plants. In winter wheat the most susceptible time is during the initial growth in autumn when aphids migrating from infected plants settle and feed on the new wheat growth. The earlier the infection, the greater the attributable yield loss (De Wolf, 2002). *Rhopalosiphum padi* infects crops in the autumn so most fields are routinely sprayed. This study focuses on the control of *S. avenae* and *M. dirhodum* due to the potential synchronisation of aphid predators with the population growth of these two species in winter wheat fields during late spring/early summer.

1.1.2. Why are cereal aphids so successful?

Both *S. avenae* and *M. dirhodum* reproduce by parthogenesis as well as through sexual reproduction and so are able to respond to more suitable conditions rapidly through extremely fast population increases and expansion. The ability of aphids to produce alate forms in response to external driving factors such as population density and food quality (Watt & Dixon, 1981) enables them to respond to the rapidly changing environments typical of modern arable systems. The overwintering of the monoeceous *S. avenae* on perennial grasses (Leather, 1993) and even on cereal seedlings themselves (Hand, 1989) ready to invade in the spring also situates it in close proximity or already on the developing crop ready to feed on it.

1.1.3. Cereal aphid control

Aphids became a major problem on cereal crops in the UK in 1968 (Dixon, 1987), attributed to increased nitrogen inputs (Duffield *et al.,* 1997 and references within), widespread use of broad spectrum insecticides and simplification of the landscape limiting the numbers of invertebrate aphid enemies (Jansen, 2000 and Bianchi *et al.,* 2006). The high crop losses associated with the late 1960s/early 1970s aphid outbreaks initiated a programme of research (Dixon, 1987). As a consequence this led to the development of guidelines for carrying out aphid population assessments (incidence counts) that can be implemented quickly by farmers/agronomists themselves to determine the necessity of insecticide spraying. In addition to increased knowledge in aphid biology, the predators and parasitoids of cereal aphids themselves were more understood (Wratten, 1975; Edwards *et al*., 1979). In particular, the indirect effects that insecticide spraying had/has on predator and parasitoid ability to respond to aphid population outbreaks (Duffield & Aebischer, 1994; Longley et al., 1997; Desneux et al., 2007 and references therein). Past research has also highlighted the potentially large negative impact that aphid predators and parasitoids can have on aphid population numbers limiting the need for insecticide spraying (discussed further in section 1.3).

Pesticides are now a less attractive option for use by farmers due to the following:

- Associated health risks both during application and residue presence in the food chain (Nasreddine & Parent-Massin, 2002)
- Public perception and abhorrence of pesticide usage and pesticide residues in food (Eom, 1994 and references therein)
- Direct costs such as purchasing and application costs (Wratten *et al*., 1990)

Although aphid outbreaks in winter wheat are becoming rarer in the UK (Holland *et al.,* 2008a), they are a useful model system to use to determine the most effective way of implementing habitat manipulation to the benefit of natural enemies. Aphids that inhabit wheat fields and their associated natural enemies are therefore the focus for this study.

1.2. **The role of Conservation biocontrol in arable systems**

During the 1980s, coupled with increasing aphid populations, there was an associated reduction in invertebrate pest predator numbers attributed to:

- Use of broad spectrum insecticides acting on non- target invertebrates both by direct toxicity (Jansen, 2000) and indirectly through loss of prey other than the pest (Duffield & Aebischer, 1994). In some cases, the insecticide actually has a greater negative impact on the aphid enemies than on the aphids themselves (Longley & Jepson, 1997).

- Increase in use of fertilisers and herbicides altering the floral composition of field boundaries reducing their suitability as overwintering sites (Holland & Luff, 2000).
- Loss of mixed farms and changes in crop rotations (Stoate, 1996).
- Increased use of more efficient herbicides creating a distinct crop monoculture (Holland & Luff, 2000).
- Reduction of "natural habitat" – land that is not used for either pasture or crop cultivation, larger fields and removal of hedges, woodlands and other natural areas resulting in simplified agricultural habitats (Bianche, *et al.,* 2006).

Reductions of natural enemy populations and drivers to reduce pesticide usage have resulted in a need to encourage biological control in arable systems.

There are three basic forms of biological control (van Driesche & Bellows, 1996). Firstly, Classical biological control, where natural enemies are imported to an area where they do not naturally occur, secondly, augmentative control (encompassing both inundative and innoculative release), where numbers of naturally occurring enemies are added to either control the pest directly, or reproduce and the resulting offspring control the pest, and finally, Conservation biological control (CBC). CBC attempts to increase and enhance pest natural enemies already present within the ecosystem by providing suitable key ecological resources. The aim is to preserve natural enemies in the area and encourage them in from other areas, potentially increasing natural enemy numbers. Consequently, natural enemies reduce the numbers of their chosen prey, the organism considered a pest (Wratten *et al.,* 2003). CBC mostly concerns reducing the impact of insecticides on natural enemies and, as defined by Ehler (1998), consists of "actions that preserve or protect natural enemies" including beneficial habitat manipulation. In addition to preserving or protecting natural enemies habitat manipulation is also concerned with reducing the ability of the herbivore pest to find the resource (in this case the crop) known as the "resource concentration hypothesis" (Root, 1973).

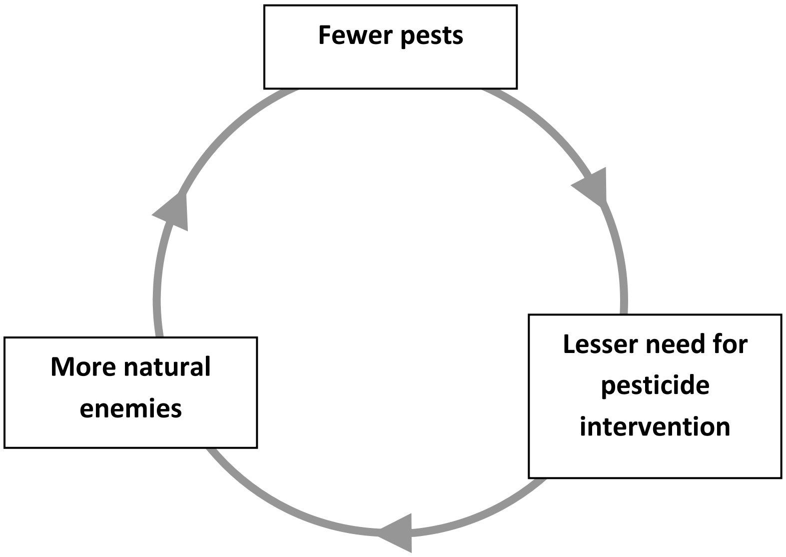


Figure 1.1: The "I.P.M. treadmill" showing the positive feedback loop between pesticide reduction and natural enemies. Taken from Gurr *et al.,* (2000) where it was adapted from Tait (1987).

A reduction in the amount of pesticides used can lead to the I.P.M. treadmill (Fig 1.1). Using aphids as the model pest, a drop in pest numbers lessens the need for insecticide application, which, in turn, leads to more natural aphid enemies. This model, however, relies on insecticides being the sole reason for suppression of natural enemies (Gurr *et al.,* 2000). There may be limiting factors other than pesticide usage that prevent the build up of natural enemy populations, such as the lack of key ecological resources (Gurr *et al.,* 2000). These include:

- Provide undisturbed overwintering habitat (Dennis & Fry, 1992).
- Provisioning of food, either directly in the form of pollen and nectar, or indirectly though providing alternative prey for the pests' natural enemies (Meek *et al.,* 2002).
- A refuge during farming practices such as ploughing and drilling (Lagerlof & Wallin, 1993).

The main problem with the reliance on aphid enemies for sole control of cereal aphids is that there is an element of perceived risk. The advice of pesticide manufacturers is more accessible and pesticides and their associated costs can be directly calculated. Potential wheat yield gains as a result of controlling of aphids by natural enemies are less calculable therefore natural control is perceived to be more risky and farmers are risk-adverse (Rossing *et al*, 1994; Cowen & Gunby, 1996).

1.3. **Enemies of aphids**

Aphids have a wide range of invertebrate enemies including parasitoids, terrestrially moving generalist and polyphagous predators, such as species belonging to the families Carabidae, Staphylinidae and the superfamily Araneae, and aerially dispersing polyphagous and aphidophagous predators, such as those belonging to the families Coccinellidae and order Neuroptera. Invertebrates may consume aphids for part of their life history, for example, Syrphids in the subfamily Syrphinae (Vockeroth & Thompson 1987), of which only the larvae are voraciously aphidophagous. In other species, e.g. *Adalia bipunctata*in the Coccinellid family, both adults and larvae predate on aphids throughout their lives (Ellingsen, 1969).

The majority of research carried out so far has been on terrestrially moving aphid predators (Holland, 2002) as well as Syrphidae and parasitoids both on movements in the field (Holland *et al.,* 2004) and feeding studies in controlled environments (e.g. Sopp & Wratten, 1986; Chiverton, 1988; Bilde & Toft 1997; Kollet-Palenga & Basedow, 2000). Terrestrial moving invertebrates are easier to study as they generally move in a 2D environment (the ground surface, although few, such as *Demetrias* spp., are able to climb) so can be easily caught in pitfall traps and can be marked for capture-mark-release studies (Griffiths *et al.,* 2001). They have also been shown to predate aphids in high quantities in controlled environments (Bilde & Toft, 1997) and tend to be polyphagous. Polyphagous predators are considered useful for conservation biocontrol as they are able to survive by consuming alternative prey during times when the pest to be targeted is low in number (Bryan & Wratten 1984). Maintenance of an adequate predator population is essential. It enables a fast predator response to an increasing aphid population to be achieved. If a time lag occurs the predator population may struggle to catch up with the prey population. Predator numbers increase by immigration into prey patches as they have only a single generation per year, whereas most pest populations can increase throughout the season through multiple cycles of reproduction. Additionally, the predator may not reduce the pest population as the alternative prey may be consumed in preference to pest prey (Madsen *et al.,* 2004). Overall, the expected effect would be for generalist polyphagous predators to have a greater effect at the beginning of the season, when aphid numbers are relatively low (Bommarco & Fagan 2002), but specialist aphidophagous predators to have a greater effect when they enter cereal fields later in the season.

1.4. **Predation effect depends on enemy guild**

Schmidt *et al.,* (2003) investigated the effect on aphid populations by different groups of aphid enemies grouped according to their method of locomotion. This was carried out by setting up a series of exclosures within the field, releasing into the exclosures a known number of aphids, and excluding the following predator assemblages by physical barriers:

1. Ground-dwelling predators
2. Flying predators and parasitoids
3. Both ground-dwelling and flying aphid predators and parasitoids.

The aphid populations within each exclosure were counted at set periods after release. On average, all of the exclosures experienced an increase in aphid population numbers compared to the control, but at very different levels. In the exclosures excluding only ground-dwelling predators, aphid numbers were 18% higher, on average, than the control, for the exclusion of flying aphid predators aphid numbers were 70% higher; and for the exclusion of all aphid predators, aphid numbers were 172% higher. This study highlights a number of issues. Firstly, flying aphid enemies seem to have a much greater impact on aphid populations, and secondly, the combination of both flying and ground dwelling predators are complementary to each other and enhance aphid mortality. The effect of flying aphid enemies on aphid populations was mainly attributed to parasitoids, as few flying aphid predators were found, and a large proportion of parasitized aphids were counted. Such high parasitism rates are not reported in other studies (Schmidt *et al.,* 2003) so this may have been a very favourable year for parasitoids but variation between years can be expected. A similar study has since been implemented in the UK with the additional aim of determining the effect of field margin presence on predation rates and relative guild response (Holland *et al.,* 2008a). There was a very different community of flying aphid predators present that aphid control was attributed to. For example, very low numbers of parasitized aphids (≤12%) were found, but flying aphid predators were still found to provide the majority of aphid control. For comparison, flying predators alone reduced the inoculated aphid populations by 93% whereas epigeal predators solely reduced aphid numbers by 40% and 18% dependent on the presence of standard field margins or wide field margins respectively. Tscharntke *et al.,* (2005) points to different groups pervading each year to provide satisfactory cereal aphid control, but the predator/parasitoid community structure does not remain constant from year to year. Despite this it is still the flying aphid predators that have provided the greatest aphid control from year to year (Schmidt *et al.,* 2003; Thies *et al.,* 2005).

Overall, these studies indicate that flying aphid predators may have been underestimated in their ability to control aphid populations. Aerially dispersing aphid predators may be more effective at controlling aphid populations for several reasons:

- Many are aphidophagous and rely solely on aphids for prey (Colyer & Hammond 1968).
- They are able to have a larger range, so may be more likely to come in contact with an aphid population.
- They have a higher searching ability by using long range olfactory and/or visual

cues (Kevan & Baker 1983; Noldus 1989; Bugg 1992) and so are more able to locate pest patches, most pests being heterogeneously distributed (Winder *et al.,* 2001; Ferguson *et al.,* 2003)

- They are not reliant on aphids falling from the crop, as terrestrial predators are (Winder 1990), due to their flying ability.
- Within a heterogenous landscape with regular crop rotations, they are able to move between fields and are less likely to be hindered by barriers e.g. linear features (Fernandez Garcia *et al.,* 2000).
- Non-crop habitat can only support a limited number of polyphagous ground active predators (Holland, 2006) but flying predators from other areas can be focussed into arable areas and are not reliant on solely increasing numbers through reproduction.

Aphids are not distributed randomly throughout the field but form aggregations (Holland *et al.,* 1999). The ability of aphid predators to identify and influence aphid numbers may depend on their ability to disperse quickly throughout the crop and suppress local aphid population increases (Coombes & Sotherton 1986; MacLeod *et al.,* 2004). Terrestrially moving predators have been proved to consume aphids (Sunderland *et al.,* 1987) and have been shown to be effective at reducing the aphid population (Collins *et al.,* 2002), but they have a disadvantage that by dispersing more slowly they possibly are not able to locate aphid aggregations as effectively as aerially dispersing predators. Aerially dispersing aphid predators may enter fields before terrestrial predators and penetrate the centre of fields earlier on in the season (Bugg, 1992) as demonstrated in the comparative study on the movements of the terrestrial predator *Bembidion lampros,* and the aerial predators *Tachyporus hypnorum* and *T. chrysomelinus*, by Petersen (1999). In this study, the two *Tachyporus* spp. which fly readily were fully dispersed by mid-May and end-May respectively before the terrestrially moving *B. lampros*, although this was not conclusively attributable to their dispersal ability. Bommarco & Fagan (2002) also observed that the solely terrestrially moving *Poecilus cupreus* had slow population dispersal due to asynchronous rest periods, but movement was essential in order to locate prey aggregations. The detectability of prey by terrestrially moving *P. cupreus* may also be hindered by the heterogeneous spatial distributions of aphids (Bommarco *et al.,* 2007).

1.5. **Field margins**

The term "field margin" is used in this context to mean a perennial habitat strip between the boundary edges (such as hedges, fences etc.) and the crop edge (the outer edges of the cropped area in a field), (Greaves & Marshall 1987). Typically, on arable farms, the areas given over to field margin habitats have lower yields owing to larger levels of shading in the presence of hedges and shelter belts, higher levels of drought (Kuemmel, 2003 and references within) and increased weed abundance (Boatman and Sotherton, 1988). The movement of the crop headland inward away from the "natural" field edge does not result in an overall shift in the reduced yield area inward but, instead, removes the lower yielding strip from production and gives it over to another use (Sparks *et al*, 1998). Concerns among farmers that field margins encourage weeds to invade the crop are generally unfounded. The majority of plant species present in arable field margins do not then invade the adjacent crop as they are maladapted for survival in the rapidly changing crop environment (Marshall, 1989; Marshall & Arnold, 1995). Field margins are therefore potentially useful as a method of increasing biodiversity on arable farms without significantly affecting crop yield or introducing weeds into the crop.

Field margins can vary in their attributes and botanical composition depending on several factors:

- Method of creation, either through natural regeneration or being sown directly (Critchley *et al.,* 2006).
- The seed mix used; a variety of field margin seed mixes are recommended though UK agri-environment schemes (see below).
- Width of margin, commonly between 2m and 6m.

- Adjacent habitat, e.g. woodland, hedgerows (Asteraki *et al.,* 1995; Marshall & Arnold, 1995).
- Shading of field margins by trees or buildings (De Cauwer *et al.,* 2006).

Each of these factors affects the attractiveness of the field margin habitat to different aerially dispersing aphid enemies and can affect the resultant predator assemblage (Meek *et al.,* 2002; Haenke *et al.,* 2009).

1.5.1. Agri-environment schemes

The increase in the demand for food produced in an environmentally sound manner, and concern about the environmental impact of agriculture has led to the implementation of agri-environment scheme options which endeavour to encourage biodiversity (Kleijn and Sunderland, 2003). Agri-environment schemes aim to compensate farmers financially for land that is managed for the benefit of the environment or biodiversity, and remove the dependence of payments from agricultural output. There are three main objectives of agri-environment schemes in Europe (Kleijn and Sunderland, 2003):

i) Reduction of nutrient and pesticide emissions.
ii) Protection of biodiversity.
iii) Restoration of landscapes.
iv) Protection of resources.

In the UK there is considerable investment in agri-environment schemes towards the promotion of wildlife conservation and biodiversity through habitat manipulation. Environmental management is carried out by the landowner using a set of guidelines, and payment is made providing the agreements are met (DEFRA website, Environmental Stewardship Handbook, 2005). Some of these manipulations may additionally benefit the farmer/landowner by encouraging an increase in the number of pest predators. This may result in increased predation of the pest and decreases the need for pesticide applications, lessening the negative effect of these inputs on non-target invertebrates (Thomas *et al.,* 2001).

Field margins are one of the most widely adopted management options within UK agri-environment schemes with 29,675 hectares of cereal field margins present in the UK in 2005 (UK-BAP reporting 2005). This has led to a network of field margin habitat throughout the UK.

Field margins were originally implemented in the UK Environmentally Sensitive Area (ESA) agri-environment scheme in the late 1980's and early 1990's as part of the Countryside Stewardship Scheme (CSS) with the general aim to 'conserve and restore landscapes in the wider countryside' (Morris *et al.,* 2000). Since then field margins have been incorporated into the more recent and goal focussed agri-environment schemes, primarily Environmental Stewardship (ES) set up in 2005. ES is comprised of the Entry-level scheme (ELS), Organic Entry Level Stewardship (OELS) and Higher Level Stewardship (HLS). ELS and OELS aim to 'encourage large numbers of farmers and land managers across England to deliver simple yet effective environment management' including 'Improving conditions for farmland wildlife' (DEFRA 1st Edition ELS Handbook, 2005). In addition HLS aims to:

- Conserve wildlife (biodiversity)
- Maintain and enhance landscape quality and character
- Protect the historic environment and natural resources
- Promote public access and understanding of the countryside
- Protect natural resources

Of the three strands of ES, ELS and OELS are open to all farmers and landowners (in the case of OELS this is dependant on organic certification). They provide a broad range of options, of which field margin introduction and management forms a component. HLS aims to provide more overall detailed management of specific areas and subsequently provides higher payments for more labour intensive and costly field margin implementations. Table 1.1 shows the field margin options open to farmland under ELS and HLS. OELS options are omitted from the table as they are outside the realms of this study but the majority are the same or similar to ELS options.

Table 1.1 Field margin and associated options from the ELS and HLS schemes (DEFRA 1st Edition ELS Handbook, 2005 & DEFRA 1st Edition HLS Handbook 2005) with percentage uptake by agreement holders as determined by Boatman *et al.,* (2007).

ES Code	**Type of habitat & management**	**% uptake by agreement holders**
Entry Level Scheme options		
EE1	2 m buffer strips on cultivated land	5.7
EE2	4 m buffer strips on cultivated land	11.3
EE3	6 m buffer strips on cultivated land	17.3
EE4	2 m buffer strips on intensive grassland	2.2
EE5	4 m buffer strips on intensive grassland	2.5
EE6	6 m buffer strips on intensive grassland	3.9
EF2	Wild bird seed mixture	9.9
EF4	Pollen and nectar flower mixture	5.7
EF5	Pollen and nectar flower mixture on set-aside land	0.5
EF7	Beetle banks	1.3
EF11	6m uncropped, cultivated margins on arable land	1.3
Additional options available under the Higher Level Scheme		
HE10	Floristically enhanced grass margin	
HF12	Enhanced wild bird seed mix plots (rotational or non-rotational)	
HF16	Cultivated fallow plots or margins for arable flora as an enhanced setaside option (rotational or non-rotational)	
HF20	Cultivated fallow plots or margins for arable flora (rotational or non-rotational)	

Despite of the range of options open to create a variety of field margin habitats on farmland, this has not been reflected in field margin habitat types actually implemented. ELS relies on farmers' decisions and choice. Some of the option, e.g. pollen and nectar mixtures have associated increased establishment and management costs compared to buffer strips and grass cultivated margins. These additional costs are not subsidised enough to economically recompense the farmer/landowner and hence are less likely to be realised. Boatman *et al.,* (2007) observed a high skewed distribution in the uptake of ELS options that involved less additional work or were already likely to be present through farmers' current management. Subsequently, field margins with floral components which are likely to be of the greatest benefit to aphid predators with the capacity for high aphid consumptions are likely to occur less frequently in arable farming systems.

Despite prior ES objective setting by DEFRA, the success, or otherwise, of UK agri-environment schemes have only been assessed in a few cases (Ovenden *et al.,* 1998; Kleijn & Sutherland, 2003; Kleijn *et al.,* 2006; Whittingham, 2007) and even so the management of habitat manipulations requires ongoing input (Carvell *et al.,* 2007). Field margins were initially re-introduced as a non-crop habitat with the aim to increase floral biodiversity on farmland (DEFRA website, Environmental Stewardship Handbook, 2005) and act as a buffer for insecticide applications as well as other drivers (Marshall, 2002) but it was also realised that they could act as an alternative arable pest control measure (Thies & Tscharntke, 1999; Marshall & Moonen, 2002; Landis *et al.,* 2003).

1.5.2. Field margin effects at the single field scale

Many studies have looked at the various positive aspects of field margins, reviewed in detail by Marshall & Moonen (2002), concluding that they are effective as enhancers of biodiversity (Meek *et al.,* 2002; Critchley *et al.,* 2006; Marshall *et al.,* 2006) useful overwintering habitat for polyphagous predators (Dennis & Fry, 1992) and resource providers for predators and parasitoids (Meek *et al.,* 2002). They are also useful within the agricultural system as possible corridors for the dispersal of species through the landscape (Dover, 1994), but may also restrict the dispersal of pest predators by attracting them away from the field in which pests are to be controlled (Holland *et al.,* 2006) and acting as barriers to movement (Thomas et al,. 2001; Mauremooto et al., 2005)

It is also not known whether field margins act as sources, or sinks, for aphid predators. Beetle banks have been shown to retain a third of the beetle population in spring (Thomas et al., 1991) and the presence of a field margin, by providing food resources such as pollen, and harbouring invertebrate prey, including aphids, may draw aphid enemies away from the site where biocontrol is required. This concern voiced by Sunderland (2001) who noted that the hoverfly, whose larvae are aphidophagous, *Episyrphus balteatus*, demonstrated a very positive association with wildflower habitat set up to encourage conservation biocontrol, and was rarely seen in the crop. Hoverfly dispersal may also be constrained by field boundaries, such as hedges (Wratten *et al.,* 2003), but there is little information about spatial and temporal movements within this aphidophagous group and other very little or no data on aerial movements of aphid predators within and between cereal fields,

Both field margins and beetle banks have been demonstrated to supply terrestrially moving aphid predators (studies tend to focus on Carabidae and Staphylinidae) to the adjacent cereal field (Dennis and Fry, 1992; Collins *et al.,* 2002), but the single field scale represents a constrained sampling unit especially when considering aphid predators that can potentially cover large distances through flight (Chapman *et al.,* 2004). Despite flying aphid enemies providing the greatest levels of aphid population suppressions during peak wheat ripening, there is a lack of information on this guild of aphid predators, mainly attributed to the scale over which they may operate (Thomas *et al.,* 2001; Tscharntke & Brandl, 2003) and there is a lack of biological knowledge of their life history and habitat requirements that warrant further investigation, especially predatory Empididae and Dolichopodidae families of Diptera (Schmidt et al, 2003).

Table 1.2 shows the range of aerially dispersing aphid groups, their mobility and actual or potential utilisation of field margins. The information in the table is skewed towards well studied taxa despite those taxa potentially not providing the majority of aphid control. Studies of invertebrates on agricultural land tend to focus on those that are more easily collected, such as by pitfall trapping for Carabidae and Staphylinidae, those that utilise pollen and nectar as part of their life cycle and those that can be reared for release in glasshouse systems, especially visually attractive invertebrates such as the Syrphidae.

Table 1.2 Aerially dispersing aphid predator groups, their mobility, efficacy as predators and ability or potential to utilise field margins where known.

Group	**Species that consume cereal aphids (from Sunderland *et al.,* 1987 unless stated otherwise)**	**Predaceous life stage**	**Aerial mobility**	**Utilises field margins?**	**Further information e.g. effectiveness, feeding rates, populations etc. where known.**
Linyphiidae (Arachnidae)	*Lepthyphantes tenuis* *Erigone atra* *Erigone dentipalpus* *Bathyphantes gracilis*	All Polyphagous	Very mobile (Halley *et al.,* 1996); Can disperse 30km in 6 hours (Thomas *et al.,* 2003).	Field margins act as a source habitat for *L. tenuis* (Bell *et al.,* 2002).	Direction and distance relies on wind. Influenced by percentage non-crop habitat at landscape scales of 3km radius (Schmidt *et al.*, 2005a). Locate webs where aphid prey density high (Harwood *et al.,* 2001 & 2003).
Anthocoridae (Hemiptera)	*Anthocoris* spp. *Anthocoris nemorum* is the most common species in arable fields.	All Polyphagous	Directional flight observed but range and distance unknown.	Unknown but overwinters on perennial vegetation (Sigsgaard *et al.,* 2010) also feed on pollen as adults (Sigsgaard *et al.,* 2007).	Not present in large numbers in arable fields.
Nabidae (Heteroptera)	Typically *Nabis ferus* (Löbner & Hartwig, 1994)	All Polyphagous	Directional flight observed but range and distance unknown.	Possibly used for alternative prey.	Typically present in very low numbers in arable fields during aphid population peaks (Löbner & Hartwig, 1994; Roth, 2003).

Chrysopidae (Neuroptera)	Primarily *Chrysoperla carnea.*	Adults & larvae, larvae have a high capacity for aphid predation	Very mobile. Capable of long distance migration (Chapman *et al.,* 2006).	Possibly for pollen and nectar sources and alternative prey.	Attracted to large patches of flowering plants (Villenave *et al.,* 2006). Shown to use alternative habitat and subsequently move into adjacent crops (Long *et al.,* 1998).
Macropterous Carabidae (Coleoptera)	*Loricera pilicornis,* *Notiophilus biguttatus,* *Amara* spp., *Poecilus cupreus* *Agonum* spp. *Dromius* spp. *Bembidion lampros* *Harpalus rufipes* & *Asaphidion flavipes* (Greenslade & Southwood, 1962)	All Polyphagous	Mobility dependent on species, *N. biguttatus* undergoes long distance migration by flight (Chapman *et al.,* 2005). *L. pilicornis, Amara familiaris*, and *Bembidion* spp., trapped in an aerial net (Chapman *et al.,* 2004).	Used for overwintering and a source of alternate prey.	Although Carabidae are often cited as very useful for the control of emergent aphid populations, very few arable related Carabidae species fly. Other species possess wings but little evidence for flight exists (van Huizen, 1990).
Staphylinidae (Coleoptera)	*Tachyporus* spp. (primarily *T. hypnorum* and *T. chrysomelinus*) *Stenus* spp. *Philonthus* spp.	All Polyphagous	Mobility dependent on species. *Tachyporus* spp. known to be common fliers.	Used for overwintering and a source of alternate prey.	*Tachyporus* spp. can exist in high densities in wheat fields and T. hypnorum in particular has been recorded consuming up to 33 *M. dirhodum* per day (Vickerman *et al.,* 1987)

Cantharidae (Coleoptera)	*Cantharis lateralis* (Landis & van der Werf, 1997) *Cantharis nigricans* (Vickerman & Sunderland, 1975) *Cantharis rufa* *Rhagonycha fulva*	All but larvae considered more predaceous than adults (Landis & van der Werf, 1997)	Common fliers but range & distance not known.	Adults are known to use field margins as a source of pollen and nectar (Meek *et al.,* 2002).	
Coccinellidae (Coleoptera)	*Adalia 2-punctata* *Coccinella septempunctata* *Propylea 14-punctata* *Adalia 10-punctata* are the most common in UK cereal fields	All	Strong fliers and can travel long distances (Hodek *et al.,* 1993)	Have been found to be abundant in weedy strips adjacent to fields in Italy (Burgio *et al.,* 2006).	Larvae consume approximately 188 aphids prior to pupation. An adult egg-laying pair can consume a mean of 34 aphids per day, in laboratory studies (Ellingsen, 1969).
Dolichopodidae (Diptera)	Many species (Ulrich, 2005)	Adults Polyphagous.	Strong fliers but range and distance unknown.	Potentially for alternative prey and nectar in species that have modified mouthparts (Brooks, 2005).	See Ulrich (2005) for a more comprehensive review.
Empididae (Diptera)	Many species (Cumming, 2006)	Adults	Strong fliers but range and distance unknown.	Potentially for alternative prey and nectar (Cumming, 2006) and pollen (Downes & Smith, 1969)	

Syrphidae (Diptera)	Primarily *Episyrphus balteatus* in cereal fields. *Eupeodes corolla,* *Sphaerophoria scripta* Melanostoma spp. Plus occasionally other species found less commonly in agricultural areas.	Larvae	Adults are strong fliers.	Predominantly field margins with a floral component (Cowgill *et al.,* 1993a, 1993b; Hickman *et al*., 2001).	Syrphidae are potentially very useful in controlling aphid population outbreaks (Chambers *et al.,* 1983) but adults may be retained in suitable habitat and not enter fields where aphid control is required (Sutherland *et al.,* 2001).

1.6. **Scales of pest management**

From the summary table 1.1 it can be seen that most of the groups of aerially dispersing aphid predators are able to cover distances greater than the single field scale. Integrated pest management (IPM) schemes rely on the ability to predict the movements of pests and their associated predators (Aylor & Irwin, 1999) in an open habitat. The problems associated with studying an open habitat have been somewhat overcome by studies looking at larger scales, rather than concentrating on single field or farm. A common problem with predicting the effectiveness of pest predators is the inability to know how far a natural enemy may move to control the pest and, as aerially dispersing aphid predators are known to cover large areas, it is necessary to look at larger scales than single fields to establish the effectiveness of habitat manipulations (Aylor & Irwin 1999). Single field studies are unable to gauge whether habitat manipulations are increasing numbers of predators locally or redistributing them by attracting them in from surrounding areas. Looking at the impact of habitat manipulations at larger landscape scales can investigate this but studies carried out over such large areas are a relatively new concept within agricultural entomology.

1.6.1. Field margins at the landscape scale

The question of scale is an issue when addressing general ecosystem stability in rapidly changing environments (Loreau *et al.,* 2001), such as within arable agriculture. Non-crop habitats, even if ephemeral, have greater importance placed on them to provide stable levels of biodiversity and invertebrate pest management for whole areas taken over by arable farming. Invertebrates are unique in their ability to respond to habitats at both very local, single field scales (e.g. Marshall, 2006) but also to exhibit variations in their biodiversity right up the scales to countrywide levels (e.g. Brooks *et al.,* 2008). The implementation of field margins nationwide therefore is likely to affect invertebrate populations at both local and landscape scales.

Recently there has been a focus on the effect of non-crop habitat on ecosystem services at the landscape scale, which demonstrated that increasing percentages of uncropped land can potentially enhance ecosystem services such as pollination (Steffan-Dewenter *et al.,* 2002), pest control (Thies & Tscharntke, 1999) and biodiversity (Bergman *et al.,* 2004). Greater percentages of non-crop habitat can provide a high level of biodiversity theoretically resulting in a greater diversity of functional groups responding to pest outbreaks (Loreau *et al.,* 2003). Such diversity may serve to reduce the risk of pest outbreaks because the predators have a wider temporal period of activity and mechanisms by which they can locate and reduce pests.

It is, however, not simply a case of increasing landscape complexity. Removal of large areas of land in order to promote conservation biocontrol within crops is not realistic, especially since higher levels of non-crop habitat can also be beneficial to the pest itself. Thies *et al.,* (2005) examined cereal aphid and parasitoid interactions over varying landscape scales measuring percentage cover of arable land as an indicator of landscape complexity. Although aphid mortality increased where landscape complexity was greater, there were also higher levels of associated aphid colonisation resulting in aphid population levels remaining static leading to a 'no net effect'. Additionally, the authors found parasitoid infection rates were affected by landscapes at a local scale of 0.5 to 2km diameter compared to aphid numbers which responded to landscape complexity at larger scales, up to 6km in diameter. This mismatch illustrates the limitations of landscape complexity in influencing pest control but does expand understanding of the spatial scales over which the pest and parasitoid are functioning.

1.6.2. Field margins benefits due to location

Field margins increase the area of non-crop habitats to a small extent but not to levels that have a noticeable impact on landscape complexity owing to the small areas that they cover. They have, however, several benefits over other non-crop habitats when they are considered in the context of aphid pest control:

- They typically provide habitat suitable for predators of aphids whether through providing overwintering habitat or resources such as pollen and nectar. For example, tussocky grass mixes have been shown to create a microclimate suitable for the overwintering of carabid predators (Lee & Landis, 2002) and wildflower field margins have been shown to increased numbers of hoverflies in adjacent fields (Harwood *et al.,* 1994).

- They can form a network of non-crop habitat throughout an intensive arable landscape (Donald & Evans, 2006).
- They act as corridors to movements of predatory invertebrates (e.g. Hoverflies: Jauker *et al.,* 2009)
- They enable rapid recolonisation of cropped areas by predatory post disturbance (Gurr *et al.,* 2000).

The main reason field margins are potentially so important is their proximity to the crop in which aphid control is required. This reduces the distance aphid predators need to travel in order to locate prey and hence provide control. When considering habitat creations on arable farmland it has been demonstrated that the benefit to biodiversity may depend on the setting rather than the size of the habitat itself. For example, whilst investigating the effect that flower mixtures have on bumble bees, Heard *et al.,* (2007), found numbers of bumblebees were proportional to the size of the area sampled, but where the proportions of agricultural land were greatest, the flower mix areas were of higher relative attractiveness to bumblebees. It may not, therefore be the size of the area of the resource that is important but the location of the resource itself.

1.7. **Summary**

Aerially dispersing aphid predators have been demonstrated in more than one study to be the most effective guild at controlling aphids in arable crops but most of the invertebrates within this guild remain the least studied aphid predators.

Despite the widespread implementation of field margins into UK arable farming through agri-environment schemes there is not a clear picture on their overall performance on providing aerially dispersing aphid predators or cereal aphid control at either the single field scale or at larger landscape scales. Field margin type, location and density are likely to affect numbers and species of aerially dispersing aphid predators found in winter wheat fields during peak aphid abundance and warrant further investigation.

1.8. **Aims and Hypothesis**

The overall aim is to determine whether field margins have an effect on the spatial and temporal distributions of aerially dispersing aphid predators. Within this three main Hypotheses are proposed below.

Hypotheses:

Chapter 2: At the single field scale, the presence of a field margin affects the numbers of aerially dispersing aphid predators in adjacent winter wheat fields.

Chapter 3: Higher proportional areas of uncropped land (primarily composed of field margin habitat) surrounding winter wheat fields increase the number of aerially dispersing aphid predators within them and thereby levels of aphid control.

Chapter 4: Aerially dispersing aphid predators utilise field margin resources directly and subsequently move into adjacent winter wheat fields.

Chapter 2

Does the presence of a 6m florally enhanced field margin surround significantly enhance the numbers of aerially dispersing aphid predators trapped within winter wheat fields?

2.1. **Introduction**

In the UK a common way of boosting natural enemy numbers in agricultural crops has been by providing perennial habitat strips, typically between the field boundary and the crop (Critchley *et al.* 2006) termed field margins. Field margins are a management option within UK agri-environment schemes (DEFRA, 2005).

Previously field margin habitat manipulations have been shown to be effective at providing a source of ground active natural enemies (Dennis & Fry 1992; Pfiffner & Luka 2000), which then have the potential to reduce pest numbers, typically aphids, within the crop by consuming aphids early in the season and reducing the likelihood of the aphid population increasing to the threshold that precedes an outbreak (Dennis & Fry 1992; Schmidt *et al.* 2004). For example, Östman *et al*. (2003), showed the aphid *Rhopalosiphum padi* (L.) population could be reduced by the presence of ground dwelling natural enemies to the extent of increasing barley yields by 23% during a year of high aphid abundance.

Recently it has been found that aerially dispersing aphid predators, as a guild, provide the greatest levels of aphid control in winter wheat (Schmidt *et al*., 2003; Tscharntke *et al*., 2005; Holland *et al*., 2008a, 2008b) compared with terrestrial predators but there is little knowledge on their movement and utilisation of field margins. Aerially dispersing aphid predator groups can be divided into two groups. Species that are aphidophagous for part or all of their life cycle include lacewings (Neuroptera: Chrysopidae), ladybirds (Coccinellidae: Coleoptera), soldier beetles (Cantharidae: Coleoptera) and hoverflies (Syrphidae: Diptera). Polyphagous predators such *Tachyporus* spp. (Staphylinidae: Coleoptera), money spiders (Linyphiidae: Arachnidae) and predatory flies (some species belonging to the families Empididae & Dolichopodidae: Diptera) are likely consume aphids as part of their diet where present. Within both of these groups are those families/species that consume pollen and/or nectar. Previous studies looking at field margins as a source of aphid predators have focussed on either field margins as overwintering habitat or the use of pollen and nectar in field margins.

Both the effect of the presence of a field margin and the varying life histories and therefore resource utilisation by aerially dispersing aphid predators is likely to affect the timing of dispersal and distance from field edge that they travel. This will be investigated in this study.

2.1.1. Dispersal of overwintering aphid predators after emergence from field margins

Although this study focuses on field margins, much research has been carried out on the movements of aphid predators that utilise beetle banks as an overwintering site. Beetle banks are very similar to grassy field margins in their vegetative composition and are used to divide up large fields and provide a higher non-crop habitat boundary to field area ratio in order to enhance cereal crop pest control. They have been shown to support high numbers of overwintering aphid predators (Thomas *et al*., 1991) which can then move into the adjacent crop and provide a reduction in aphid populations (Collins *et al*., 2002). Penetration, however, of the crop by predators that overwinter in beetle banks is relatively slow and short in distance. Collins *et al*., (2002) found even through the division of large fields by beetle banks, the focus of aphid predation was still mainly at 58m and less from the beetle bank. This dispersal distance concurs with a wide scale study of arable invertebrate distributions by Holland *et al*., (1999) who found that many of the terrestrial predator species occurred predominantly within 60m of the field edge.

Most of the studies focussing on trapping boundary-overwintering aphid predators use pitfall traps as a method of capture. This is likely to result in a higher ratio of invertebrate individuals being trapped that use solely terrestrial locomotion as opposed to flight being caught. For those species that both overwinter in non-crop habitat and fly, such as *Tachyporus* spp. an incomplete picture is likely to be presented through using solely pitfall traps. For these reasons, and the necessity of trapping flying species, alternative trapping strategies were used.

2.1.2. Movements of aphid predators that utilise field margin floral resources

Field margins can provide floral resources, either through the planting of flowering species, or through natural regeneration. Florally enhanced margins can attract greater numbers of both pollen and nectar consuming insects compared to grassy or natural regenerated margins although these studies have focused either on hoverflies (Harwood *et al*., 1994; MacLeod, 1999; Haenke *et al*., 2009) and/or bees (Meek *et al*., 2002; Carvell *et al*., 2007). Hoverfly numbers tend to be greater within or in close proximity to floral resources (Cowgill *et al*., 1993a; Sutherland *et al*, 2001). Through using *Phacelia tanacetifolia* pollen as a marker, individuals have, however, been found up to 200m from the pollen source within winter wheat fields (Wratten *et al*., 2003b).

For other species of aerially dispersing aphid predators, information on how field margins affect their numbers, densities and subsequent populations and movements into the adjacent crop is sparse at best. Coccinellidae have been shown to be present in field margins (Burgio *et al*., 2006) and Cantharidae occur preferentially in field margins as opposed to crop (De Cauwer *et al*., 2006) utilising pollen and nectar produced within field margins (Meek *et al*., 2002). For other pollen and/or nectar consuming species, the effect of field margins on their numbers and activity is not known.

2.1.3. Hypothesis, objectives and aims.

Hypothesis:

At the single field scale the presence of a 6m florally enhanced field margin surround significantly enhances the numbers of aerially dispersing aphid predators trapped within winter wheat fields.

Objectives:

1. Investigate which aerially dispersing aphid predators occur in winter wheat fields.
2. Investigate the distance into winter wheat fields that aerially dispersing aphid predators are able to penetrate.
3. Determine when during the season aerially dispersing aphid predators are most abundant.

Aim: Determine if 6m field margins can provide a significant source of aerially dispersing aphid predators in winter wheat fields during the time of the aphid population increase and peak.

2.2. **Methodology**

2.2.1. Invertebrates sampled above the crop

Eight winter wheat fields were selected, four with 6m wide florally enhanced margins surrounding the entire field, four without sown margins (margins <1m wide). All fields were located in Tisbury, Wiltshire (51°03′20.05″N, 2°04′31.61″W) and were similarly managed with no insecticide being used on the crop either prior to, or during the study. The 6m margins had been established for two years using seed from a local hay meadow.

In each field four transects were set up originating from the cropped area edge and running into the centre of the field. Two transects ran along a north-south line, originating from opposite sides of the field and two transects ran along an east- west line, again originating from opposite sides of the field, to give a "cross" transect design in each field (see Fig 2.1). This was to enable the effect of prevailing wind carrying insects to be taken into account, if necessary.

Along each transect three trapping stations were situated at 20, 40 and 80m from the cropped edge, i.e. a total of ninety-six trapping stations. Each trapping station consisted of a 3m high pole sunk into the ground to a depth of approx. 0.5m. Two T-bars were bolted to the main pole and between these T-bars a double-sided sticky trap was strung. The sticky traps were A4 size sheets of 2mm clear acrylic with A4 acetate coated in Tanglefoot (The Tanglefoot Corporation, Grand Rapids, USA). Each trap could be raised so as to maintain a 1.0m height above the canopy as the crop grew. The effect of the air on the ground creates a braking effect but equally vegetation (in this case the crop) can act as the ground and provide a similar braking effect (Taylor, 1974). By maintaining the height of the trap at 1m above crop height the air movements above the vegetation should have remained relatively consistent according to wind speed. Additionally a 1m gap between the trap and the vegetation helped to ensure only flying insects were caught rather than those that may hop from the crop or be lifted from the crop by the wind and blown onto the trap.

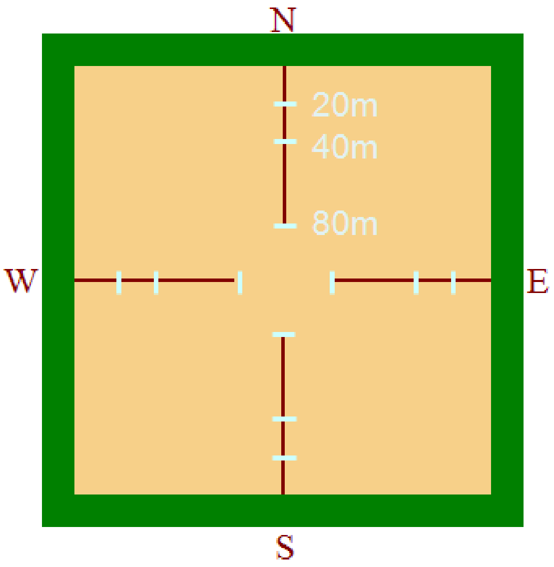


Figure 2.1 The arrangement of trapping stations (short dark lines) along four transects in a hypothetical field with a margin (dark band around the edge). The trapping stations closest the margin are situated 20m from the margin, the next trapping station on the transect is at 40m and the final trapping station is located at 80m. Not drawn to scale.

All sticky traps were run for five days every two weeks from beginning of April until before harvest except when herbicide spraying was in progress. Logistics only allowed four fields of traps to be changed a day therefore collections were staggered. Four fields were randomly selected and trapping started, continuing on the following day for the remaining fields, apart from the last date where all traps were started and finished on the same day. The first date of trapping has been omitted from the results as high winds led to many traps being destroyed. Fields were labelled 1 to 10 with fields 3 and 4 omitted. This was due to the fields being used in another study so field numbers remained the same so as not to cause confusion.

Table 2.1 Mean sampling dates for sticky traps and D-vac suction samples.

	Date 2	Date 3	Date 4	Date 5	Date 6
Sticky traps	7th May	22nd May	5th June	19th June	2nd July
D-vac suction samples	12th May	25th May	10th June	25th June	No sampling

Table 2.2 Mean sticky trapping dates with corresponding actual trapping dates.

Mean date	Field Numbers	Actual dates sampled
7th May	Fields 1, 2, 5, 9	4-9th May 2005
	Fields 6, 7, 8, 10	5-10th May 2005
22nd May	Fields 1, 2, 5, 6	19-24th May 2005
	Fields 7, 8, 9, 10	20-25th May 2005
5th June	Fields 5, 8, 9, 10	2-7th June 2005
	Fields 1, 2, 6, 7	3-8th June 2005
19th June	Fields 1, 5, 6, 10	16-21st June 2005
	Fields 2, 7, 8, 9	17-22nd June 2005
2nd July	All fields	29th June-4th July 2005

2.2.2. Invertebrates sampled within the crop

Invertebrates were sampled from within the crop using a D-vac suction sampler. Whilst the sticky traps were active, or as soon as possible after, two D-vac samples were taken at each trapping station. Each sample consisted of ten times ten second sucks. As the nozzle of the D-vac is $0.1m^2$, each sample taken extracted crop dwelling invertebrates from a $1m^2$ area.

Invertebrates in the groups Cantharidae, Carabidae, Coccinellidae, Dolichopodidae, Empididae, Linyphiidae, Nabidae, Neuroptera and Staphylinidae were caught and identified. *Tachyporus* spp. in the family Staphylinidae were identified to genus.

2.2.3. Vegetation Survey

The same eight fields as above were used for this survey. In each field the field margin (where present) and boundary flora was assessed both in terms of species cover-abundance and structure as well as categorising the adjacent habitat.

2.2.3.1. Environmental variables

Around each field, eight areas were assessed and the following environmental variables measured:

- Aspect (N, E, S or W)
- Margin (presence or absence)
- Sterile Strip (presence or absence)
- Bank (presence or absence)
- Trees (presence or absence)
- Hedge (presence or absence)
- Hedge height

2.2.3.2. Vegetation Assessment

The higher plant species present in the margin and boundary were subdivided into ground flora (0-1m, this included field margins), mid height vegetation (1-4m, typically hedges/scrub) and tall vegetation (including trees) (>4m). Each species present was given a score (0-9) based on a modified Braun-Blanquet cover-abundance score (Westhoff and Maarel, 1973)(Table 2.3).

A section of the field boundary (approx 15m) was selected as typical for that boundary and this area used for the vegetation assessment. Two assessments were done for each transect – one on each side of the transect so each field had a total of eight areas surveyed.

Table 2.3 Plant abundance score (Table taken from Powell *et al.*, 2004)

Score	Description, % ground cover by eye	% cover used for formal analyses
1	Rare, 1 or 2 plants	0.25
2	Sparse, 3-10 plants	0.5
3	Frequent, <4%cover	1
4	Abundant, 5% cover	2
5	5-12.5%	5
6	12.5-25%	12.5
7	25-50%	25
8	51-75%	50
9	76-100%	75

2.2.4. Statistical analyses

2.2.4.1. Invertebrate trapping analyses

On the 23rd May, during trapping date 3 for this study, approximately 1 to 2m of the field margin was cut and approx 1-2m of the crop cut in fields 1 and 2 to widen the margin for the following year and to implement a wide sterile strip. This was accounted for statistically in the analysis.

Both sticky traps and D-vac suction samples were analysed separately due to the different way in which they operate. Sticky traps are similar to pitfall traps in that they measure activity-density, whereas D-vac samples capture invertebrates from an area and do not rely on the invertebrates being active. D-vacs, however, sample a small area and pinpoint in time depending on the time of day the sampling took place etc.

The effect of the presence of a field margin on aphid predators was tested on $\log_e$ transformed predator data using a nested ANOVA with first order polynomial contrasts (Genstat Release 11.1) to determine if there were linear responses to distance of the trap/sample from the cropped edge. The presence of a field margin and distance from the cropped edge (as linear polynomial contrasts) were treatment factors whereas field, compass point location and distance from the cropped edge (as a factor) were used as nested blocking factors. Where field margins had been cut, “cut” was nested within margin within treatment factors from date 3 onwards.

In addition to determining the effect of field margin presence on aerially dispersing aphid predators, the design of this experiment also allowed analysis of numbers of different aerially dispersing aphid predators penetrating winter wheat fields, and additionally whether the presence of a field margin affected the distance from the crop edge at which aerially dispersing aphid predators were caught or trapped.

Analyses were carried out for each predator group per trapping date due to statistically significant violations of Box's tests for symmetry of the covariance matrix during repeated measures analyses. Additionally the difference in statistical models between dates pre and post margin cutting prevented direct statistical comparisons between dates in repeated measures analyses between dates 2 and all other trapping dates for both sticky and D-vac data.

2.2.4.2. Principal components analyses

The eight fields were compared for differences in vegetation composition of the surrounding margins and/or boundaries depending on whether the field had a margin surround or not. Differences in the plant species assemblages between fields were compared using Canonical Correspondence Analysis (CCA) CANOCO 4.5 on square root transformed percentage data for each species (with rare species down-weighted). Environmental variables were nominalised where necessary and entered as ‘dummy’ variables. Environmental factors on the location of the margins were also included in the analysis to determine the effect they had, if any, on the plant species assemblage observed. Environmental factors included as nominal variables were the ordination location of the margin/boundary; North, East, South, West, whether trees were present along the field boundary (potentially shading the vegetation), the presence of a hedge, and whether adjacent land was arable or grass/pasture.

2.3. **Results**

2.3.1. Trapping techniques

Both sticky traps and D-vac samples caught a wide range of aerially dispersing aphid predators (Table 2.4). Nabidae and Large Staphylinidae are not included in the separate analyses as Nabidae were not caught on sticky traps and Large Staphylinidae were not caught in D-vac samples, however they both were included in the total predator numbers and percentage calculations in table 2.4.

Table 2.4 Sum and percentages for main aphid predator groups trapped for each date.

Date		Cantharidae	Carabidae	Coccinelidae	Dolichopodidae	Empididae	Neuroptera	Linyphiidae	Syrphidae	*Tachyporus* spp.
SUM										
7th May	Sticky	1	0	4	0	74	1	25	56	33
12th May	D-vac	7	109	8	1	18	0	139	34	246
22nd May	Sticky	2	0	3	2	78	3	30	29	3
25th May	D-vac	17	87	26	6	28	4	152	10	417
5th June	Sticky	15	3	6	155	179	36	200	14	39
10th June	D-vac	302	65	39	318	141	3	318	10	215
19th June	Sticky	197	40	94	364	282	155	757	2	263
25th June	D-vac	76	60	62	418	1186	1	354	8	50
2nd July	Sticky	17	5	12	612	236	124	675	4	46
N/a	D-vac	N/a								
PERCENTAGE										
7th May	Sticky	0.5	0.0	1.9	0.0	34.6	0.5	11.7	26.2	15.4
12th May	D-vac	1.2	19.3	1.4	0.2	3.2	0.0	24.6	6.0	43.5
22nd May	Sticky	1.3	0.0	1.9	1.3	49.4	1.9	19.0	18.4	1.9
25th May	D-vac	2.2	11.5	3.4	0.8	3.7	0.5	20.0	1.3	54.9
5th June	Sticky	2.3	0.5	0.9	23.3	27.0	5.4	30.1	2.1	5.9
10th June	D-vac	21.3	4.6	2.7	22.4	9.9	0.2	22.4	0.7	15.2
19th June	Sticky	8.6	1.7	4.1	15.9	12.3	6.8	33.0	0.1	11.5
25th June	D-vac	3.4	2.7	2.8	18.7	53.1	0.0	15.9	0.4	2.3
2nd July	Sticky	0.9	0.3	0.7	34.1	13.1	6.9	37.6	0.2	2.6
N/a	D-vac	N/a								

2.3.2. The effect of field margins

Tables 2.5 to 2.9 provide summaries of the analyses carried out for each of the aphid predator groups studied indicating where the treatment effects were significant at different levels. Since the treatment distance was analysed as both a factor and a linear polynomial effect within the same analyses both have been included. Table 2.5 shows significance levels for mean trapping dates 7th and 12th May for both D-vacs and Sticky traps respectively without the margins having yet been subject to cutting. Tables 2.6 to 2.9 show significance levels for mean trapping dates 22nd May to 2nd July for sticky traps and dates 25th May to 25th June for D-vac samples. Sticky trap and D-vac significance levels are shown side by side in order for comparisons between the significance levels of the two types of trapping techniques to be made.

Each aphid predator group is discussed in this section individually to determine group by group responses to field margins, the cutting of field margins and the penetration of individuals into fields.

Table 2.5 Sticky trap and D-vac sample analyses results outline for mean trapping dates 7th May and 12th May respectively. * significant at P ≤0.05, ** significant at P ≤0.01, * significant at P ≤0.001**

Date 2	Cantharidae		Carabidae		Coccinellidae		Dolichopodidae		Empididae		Neuroptera		Linyphiidae		Syrphidae		*Tachyporus* spp.		Total Predators	
	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac
Margin	ns	ns	Too few individuals for analysis	ns	ns	ns	ns	ns	ns	***	ns	Too few individuals for analysis	ns	*	ns	ns	ns	ns	*	ns
Distance	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns		*	ns	ns	ns	ns	ns	ns	ns
Linear polynomial model	ns	ns		ns	ns	ns	ns	ns	ns	**	ns		**	ns	ns	ns	ns	ns	ns	ns
Deviations from Linear model	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns
Distance*Margin	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns
Linear*Margin model	ns	ns		ns	ns	ns	ns	ns	ns	**	ns		ns	ns	ns	ns	ns	ns	ns	ns
Deviations from Linear*Margin model	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns

Table 2.6 Sticky trap and D-vac sample analyses results outline for mean trapping dates 22nd May and 25th May respectively. * significant at P ≤0.05, ** significant at P ≤0.01, * significant at P ≤0.001. Those in bold are represented graphically.**

Date 3	Cantharidae		Carabidae		Coccinellidae		Dolichopodidae		Empididae		Neuroptera		Linyphiidae		Syrphidae		*Tachyporus* spp.		Total Predators	
	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac
Margin	ns	ns	Too few individuals for analysis	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns
Margin*Cut	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns
Distance	ns	ns		ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	**	**	ns	ns	ns	ns
Linear polynomial model	ns	ns		ns	ns	ns	ns	ns	ns	ns	*	ns	**	ns	*	**	ns	ns	ns	ns
Deviations from Linear model	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Distance*Margin	ns	ns		ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	**	ns	ns	ns	*	ns
Linear*Margin model	ns	*		ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	**	*	ns	ns	*	ns
Deviations from Linear*Margin model	ns	ns		ns	*	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns
Distance*Margin*Cut	*	ns		*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Linear*Margin*Cut model	ns	ns		*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Deviations from Linear*Margin*Cut model	*	ns		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 2.7 Sticky trap and D-vac sample analyses results outline for mean trapping dates 5th June and 19th June respectively. * significant at P ≤0.05, ** significant at P ≤0.01, * significant at P ≤0.001. Those in bold are represented graphically.**

Date 4	Cantharidae		Carabidae		Coccinellidae		Dolichopodidae		Empididae		Neuroptera		Linyphiidae		Syrphidae		*Tachyporus* spp.		Total Predators	
	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac
Margin	***	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	**	ns	ns	ns	*	ns	ns	ns
Margin*Cut	**	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
Distance	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*
Linear polynomial model	*	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	*
Deviations from Linear model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns
Distance*Margin	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**
Linear*Margin model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	**
Deviations from Linear*Margin model	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Distance*Margin*Cut	ns	ns	*	ns	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	ns
Linear*Margin*Cut model	ns	ns	Ns	ns	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns
Deviations from Linear*Margin*Cut model	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	*	ns

Table 2.8 Sticky trap and D-vac sample analyses results outline for mean trapping dates 19th June and 25th June respectively. * significant at P ≤0.05, ** significant at P ≤0.01, * significant at P ≤0.001.**

Date 5	Cantharidae		Carabidae		Coccinellidae		Dolichopodidae		Empididae		Neuroptera		Linyphiidae		Syrphidae		*Tachyporus* spp.		Total Predators	
	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac	Sticky	D-vac
Margin	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	*	**	ns
Margin*Cut	ns	*	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
Distance	ns	ns	ns	*	ns	ns	**	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	*
Linear polynomial model	ns	ns	ns	*	ns	ns	**	*	*	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns
Deviations from Linear model	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	*
Distance*Margin	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Linear*Margin model	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
Deviations from Linear*Margin model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Distance*Margin*Cut	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
Linear*Margin*Cut model	*	ns	ns	ns	ns	ns	ns	ns	*	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
Deviations from Linear*Margin*Cut model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 2.9 Sticky trap analysis results outline for mean trapping date 2nd July. * significant at P ≤0.05, ** significant at P ≤0.01, * significant at P ≤0.001.**

Date 6	Cantharidae	Carabidae	Coccinellidae	Dolichopodidae	Empididae	Neuroptera	Linyphiidae	Syrphidae	*Tachyporus* spp.	Total Predators
Margin	ns	**	ns	**	ns	ns	ns	ns	*	ns
Margin*Cut	ns	**	ns	**	ns	ns	ns	ns	*	ns
Distance	*	ns	ns	**	ns	ns	ns	ns	ns	ns
Linear polynomial model	*	ns	ns	**	ns	ns	*	ns	ns	ns
Deviations from Linear model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Distance*Margin	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Linear*Margin model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Deviations from Linear*Margin model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Distance*Margin*Cut	ns	**	ns	**	ns	*	ns	ns	ns	ns
Linear*Margin*Cut model	ns	**	ns	***	ns	*	ns	ns	ns	ns
Deviations from Linear*Margin*Cut model	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

2.3.2.1. Total aphid predators

Looking solely at the effect of the presence of a field margin where there were no interaction effects, the total number of aphid predators caught on sticky traps was significantly greater earlier on in the season (mean date 7th May) where there was a field margin present (Control fields' mean = 0.396 ± 0.111, Margin fields' mean = 0.840 ± 0.111; $F = 8.03_{1,6}$, P = 0.03), however, this was not reflected in numbers of total predators caught by the D-vac suction sampler during mean trapping date 12th May, where there were no differences in numbers of aphid predators caught between margin and control fields (Control fields' mean = 1.294 ± 0.221, Margin fields' mean = 1.025 ± 0.221; $F = 0.74_{1,6}$, P = 0.42).

Using number of taxonomic family groups as an estimate of diversity, greater numbers of aphid predator families were trapped on sticky traps in fields with margin surrounds compared to those without (Control fields' mean = 0.554 ± 0.066, Margin fields' mean = 0.786 ± 0.066; $F = 6.09_{1,6}$, $P < 0.05$) for mean sticky trapping date 7th May but not beyond this date.

2.3.3. The effect of margin disturbance due to cutting on aphid predator groups

The unexpected variable 'Cut' in the analysis during sticky trapping date 3 had an effect on several groups of aerially dispersing aphid predators where comparatively higher or lower numbers of aerially dispersing aphid predators were found at different distances from the field edge in fields whose margins were subject to disturbance. The groups that were affected were the pollen and nectar feeders; Cantharidae and Dolichopodidae caught on sticky traps and Neuroptera caught in D-vac samples; and groups that are known to utilise field margins as an overwintering site such as *Tachyporus* species on sticky traps and Linyphiidae caught in D-vac samples.

2.3.3.1. Linyphiidae

Where there was a surrounding field margin, numbers of Linyphiidae caught on sticky traps were greater across all trapping dates except for mean trapping dates 7th May and 2nd July when there was no difference in the numbers trapped between margin and control fields (Table 2.5 and Table 2.9 respectively). However, numbers of Linyphiidae caught in D-vac samples were significantly higher in fields with margin surrounds for the first trapping date, mean date 12th May, (Control fields' mean = 0.299 ± 0.075, Margin fields' mean = 0.573 ± 0.075; F = $6.63_{1,6}$, P = 0.04).

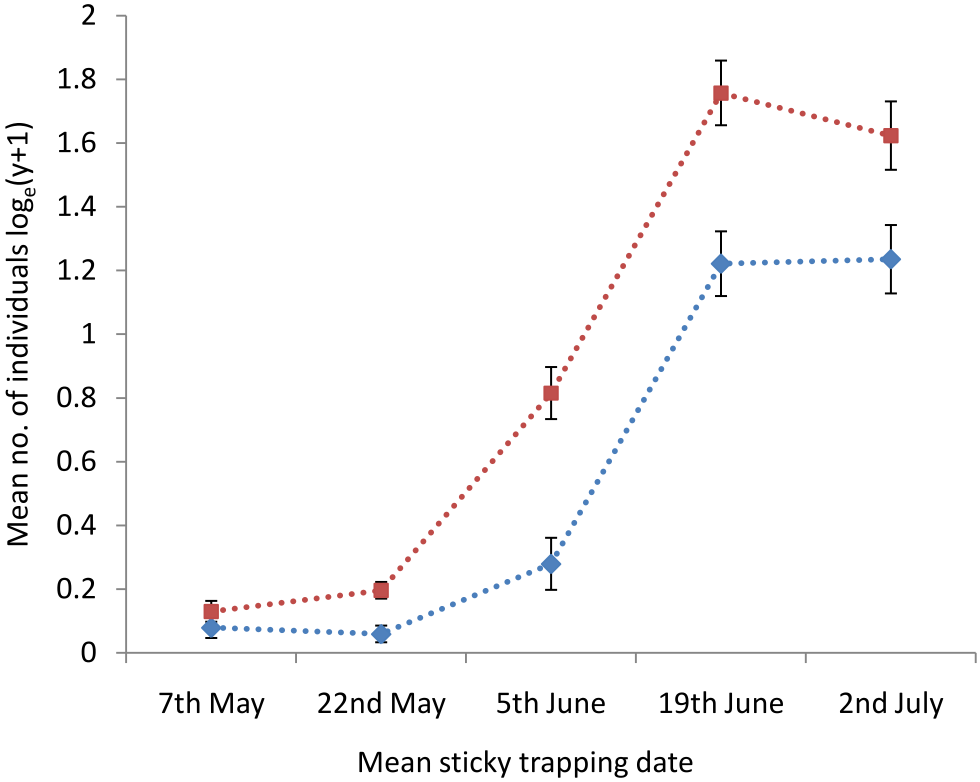


Figure 2.2 Mean numbers of Linyphiidae caught in fields with a margin surround (red squares) compared with fields without a margin (blue diamonds) during all five trapping dates with error bars for the standard error of the mean. Margin and Control means for trapping date 7th May and 2nd July are not statistically significantly different (F = $1.21_{1,6}$, P = 0.31 and F = $6.55_{1,5}$, P=0.05 respectively) but are for the trapping dates 22nd May (F = $13.64_{1,5}$, P = 0.01), 5th June (F = $21.53_{1,5}$, P <0.01) and 19th June (F = $13.93_{1,5}$, P <0.01).

Table 2.10 Means, standard errors, F and P values for Linyphiidae caught in D-vac samples in Margin and Control fields.

Mean date	Margin mean ± S.E.	Control mean ± S.E.	d.f.	F-value	P-value
12th May	0.573 ± 0.075	0.299 ± 0.075	1,6	6.63	0.042*
25th May	0.572 ± 0.125	0.396 ± 0.125	1,5	1.34	0.299
10th June	1.707 ± 0.197	2.034 ± 0.197	1,5	1.91	0.226
25th June	0.897 ± 0.176	0.875 ± 0.176	1,5	0.01	0.935

The effect of margin disturbance on Linyphiidae was in evidence in D-vac samples taken at mean trapping date 25th May, where greater numbers of individuals were found in fields with cut margins (Control fields' mean = 0.396 ± 0.107, Uncut margin fields' mean = 0.272 ± 0.151; Cut margin fields' mean = 0.871 ± 0.151; $F = 7.87_{1,5}$, P = 0.04), however, this effect did not remain and by mean trapping date 10th June no effect of cut margins was detectable in this study. There was an effect on field margin presence on the distribution of Linyphiidae caught in fields during mean D-vac trapping date 10th June where greater numbers were found close to the cropped edge in fields with margins, whereas the reverse was true of those trapped in control fields with fewer close to the cropped edge (Fig. 2.3). This was not a statistically significantly different relationship when distance was considered a categorical variable ($F = 2.38_{2,6.91}$, P = 0.10) but did exhibit statistically significantly distinct first order polynomials contrasts ($F = 4.64_{1,6.91}$, P = 0.04) with distance from the cropped edge with Linyphiidae numbers trapped in margins decreasing further from the cropped edge and those control fields increasing in number from the cropped edge as distance increases. Deviations from the linear model were not significant (F = 0.12, P = 0.73).

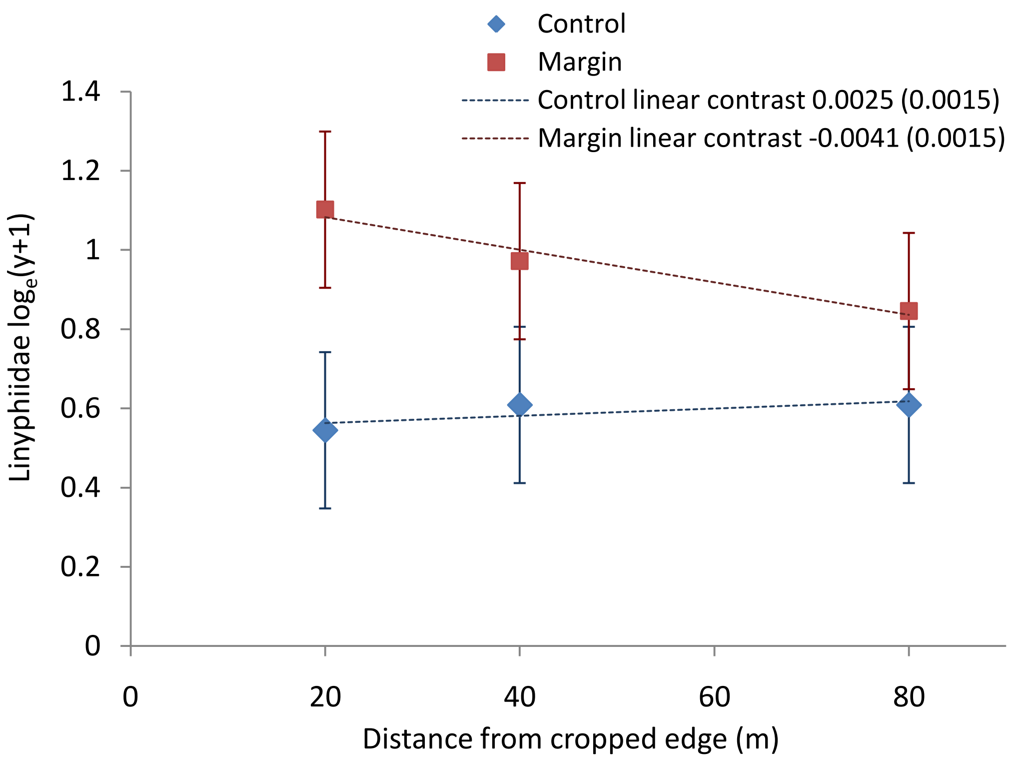


Figure 2.3 Mean numbers and standard errors of Linyphiidae trapped in Margin fields and Control fields D-vac samples at 20m, 40m and 80 from the cropped edge and associated linear contrasts during mean trapping date 10th June. Numbers in parentheses are standard errors for the linear contrasts.

2.3.3.2. Tachyporus *species*

Tachyporus hypnorum, *T. chrysomelinus* and *T. obtusus* comprised 70% of *Tachyporus* spp. on sticky traps and 97% of these three groups in D-vac samples.

Tachyporus spp. showed temporal differences in numbers captured depending on the trapping method (Figure 2.4.)

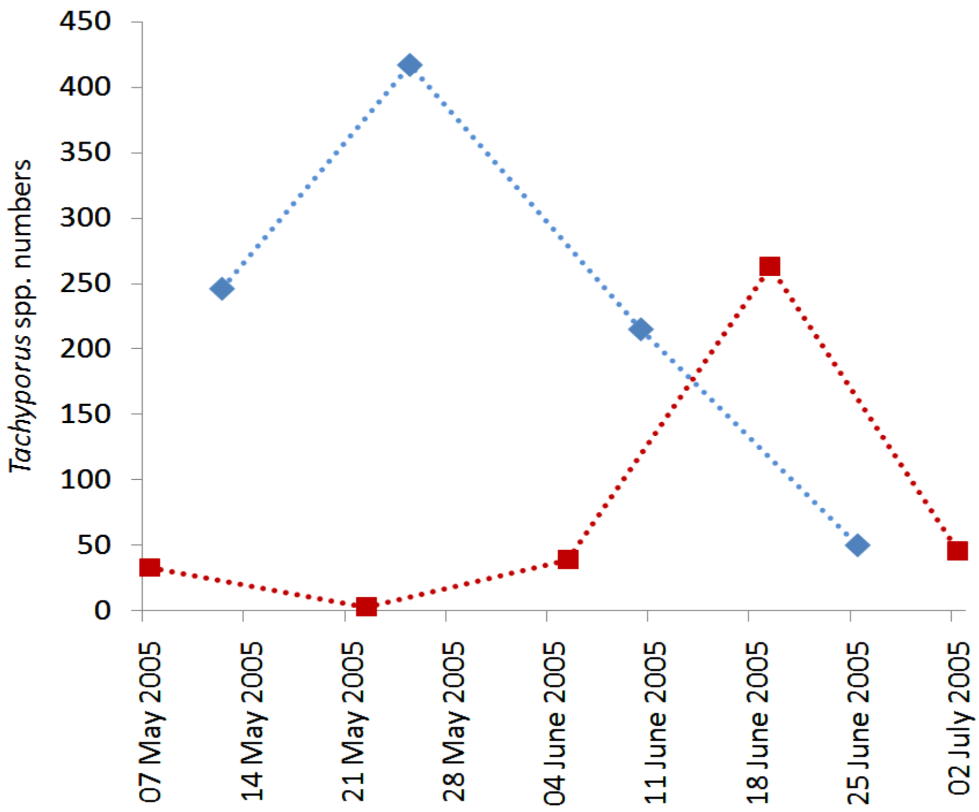


Figure 2.4 Numbers of *Tachyporus* spp. trapped on Sticky traps (red squares) and caught in D-vac samples (blue diamonds) for each of the mean trapping dates throughout the season.

Tachyporus spp. were found in greater numbers in margin fields that had been subject to disturbance by cutting during sticky mean trapping date 5th June (Fig. 2.4) ($F = 7.38_{1,5}$, $P = 0.04$).

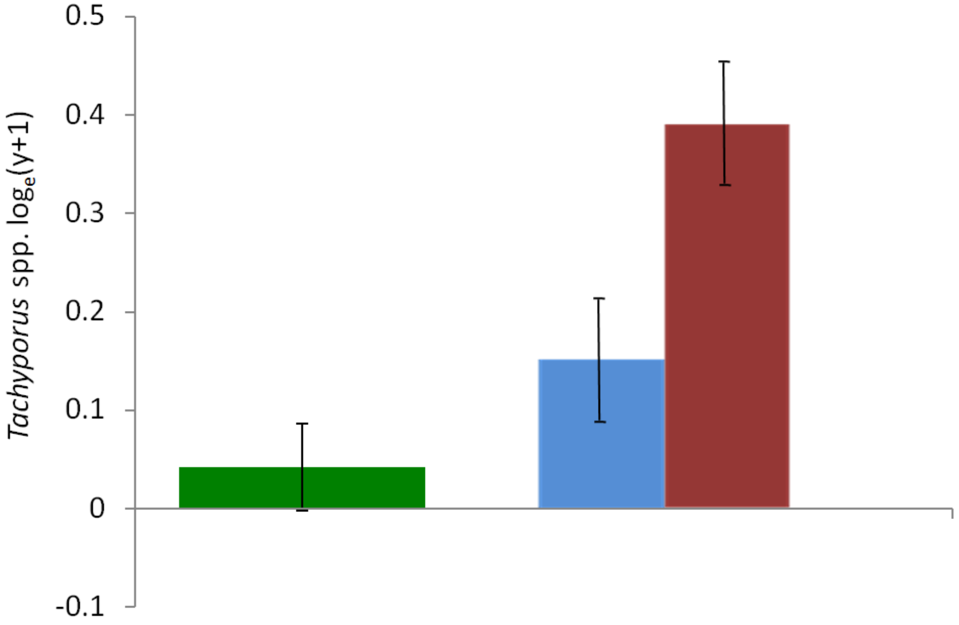


Figure 2.5 Mean count and standard errors of *Tachyporus* spp. trapped on sticky traps during mean trapping date 5th June within Cut (red bars) and Uncut margin fields (blue bars) and control fields (green bars). The width of the bars are proportional to number of sample replicates (Margin cut n = 2, Margin uncut = 2, Control = 4).

Tachyporus species were found in greater numbers in D-vac samples taken in fields without a margin during mean trapping date 25th June (Control fields' mean = 0.334 ± 0.085, Margin fields' mean = 0.017 ± 0.085; $F = 7.02_{1,5}$, $P < 0.05$), no other dates exhibited a difference in numbers of *Tachyporus* species trapped in D-vac samples in fields with and without margins.

2.3.3.3. Empididae

Greater numbers of Empididae were caught in D-vac samples in fields with field margin surrounds during mean trapping date 12th May (Control fields' mean = 0.008 ± 0.013; Margin fields' mean = 0.130 ± 0.013; $F = 46.41_{1,6}$, $P < 0.001$). A linear response of Empididae in control and margin fields was statistically significant with numbers decreasing from 20m to 80m from the cropped edge (Fig. 2.6) in margin fields ($F = 5.18_{2,6}$, $P = 0.03$; Deviations non significant at $F = 1.88$, $P = 0.18$); very few individuals were trapped in Control fields overall.

Sticky traps showed no difference in numbers of Empididae trapped in control fields and those with margins for each trapping date throughout the season.

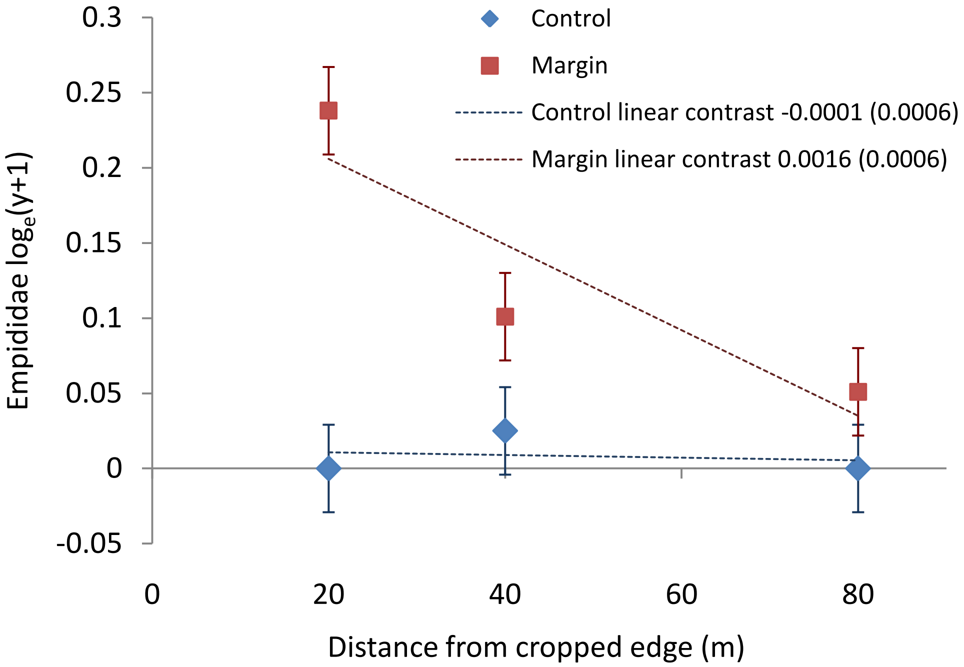


Figure 2.6 Mean numbers and standard errors of Empididae caught in D-vac samples caught during mean trapping date 12th May at the three different distances from the cropped edge in fields (Distance as a categorical factor: F = $3.05_{2,6}$, P = 0.055) with margin surrounds compared to control fields. Numbers in parentheses are standard errors for the linear contrasts.

2.3.3.4. Dolichopodidae

Few Dolichopodidae individuals were captured in both D-vac samples and on Sticky traps during trapping dates 2 (mean trapping dates 7th May and 12th May respectively) and 3 (mean trapping dates 22nd May and 25th May respectively), however, numbers trapped surged during date 4 and subsequently remained high for trapping dates 5 (mean trapping dates 19th June and 25th June respectively) and 6 (sticky traps only for date 6, no D- vac samples were taken, mean trapping date 2nd July). Dolichopodidae were found in greater numbers closer to the margin in D-vac samples and on Sticky traps taken 20m from the cropped edge during mean trapping dates 10th June (Distance: F = $3.77_{2,16}$, P = 0.03; Linear relationship: F = $4.92_{1,16}$, P = 0.03, Deviations from linear model: F = 2.63, P = 0.11) and 19th June (Distance: F =

$5.57_{2,16}$, P <0.01; Linear relationship: F = $10.26_{1,16}$, P <0.01, Deviations from linear model: F = 0.87, P = 0.36) respectively and exhibited statistically significant relationships with distance as a categorical factor and as a linear polynomial variable.

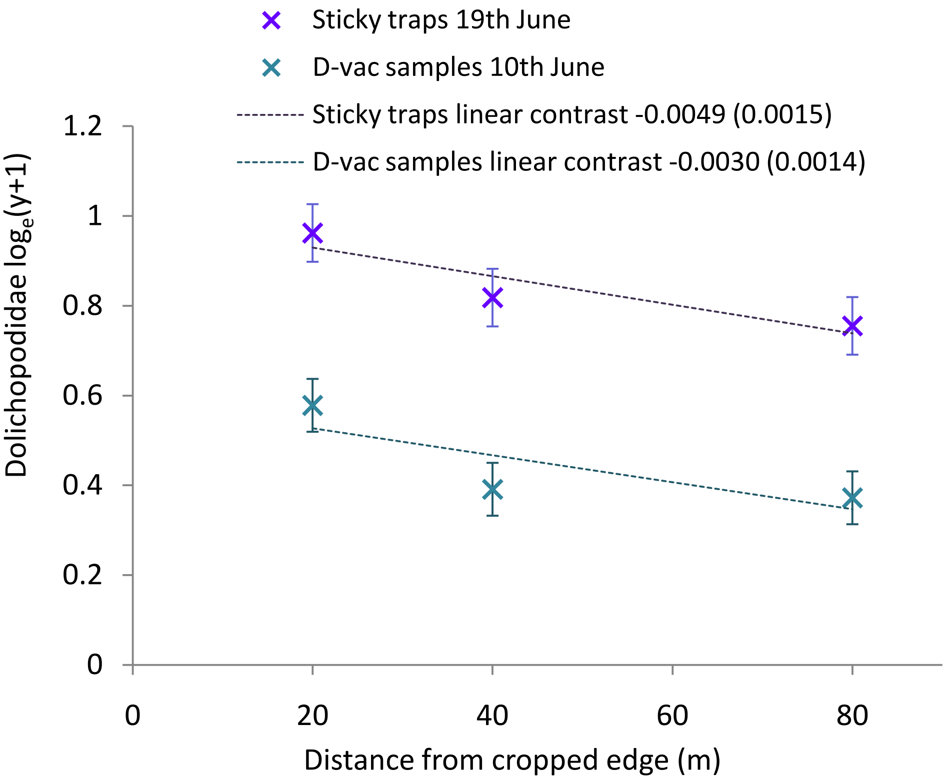


Figure 2.7 Mean numbers and standard errors of Dolichopodidae caught in D-vac samples and on sticky traps for mean trapping dates 10th June and 19th June respectively at three different distances from the cropped edge.

On sticky traps, there were significantly higher numbers of Dolichopodidae trapped in fields that had cut margins, and numbers of individuals decreased in fields with cut margins as distance from the cropped edge increased during mean sticky trapping dates 5th June (Fig. 2.8) and 2nd July (Fig. 2.9) (Distance: F = $7.33_{2,25.49}$, P = 0.001; Linear relationship: F = $12.61_{1,25.49}$, P <0.001, Deviations from linear model: F = 2.09, P = 0.16 and Distance: F = $5.84_{2,14.86}$, P <0.01; Linear relationship: F = $11.61_{1,14.86}$, P = 0.001, Deviations from linear model: F = 0.06, F = 0.806 respectively)

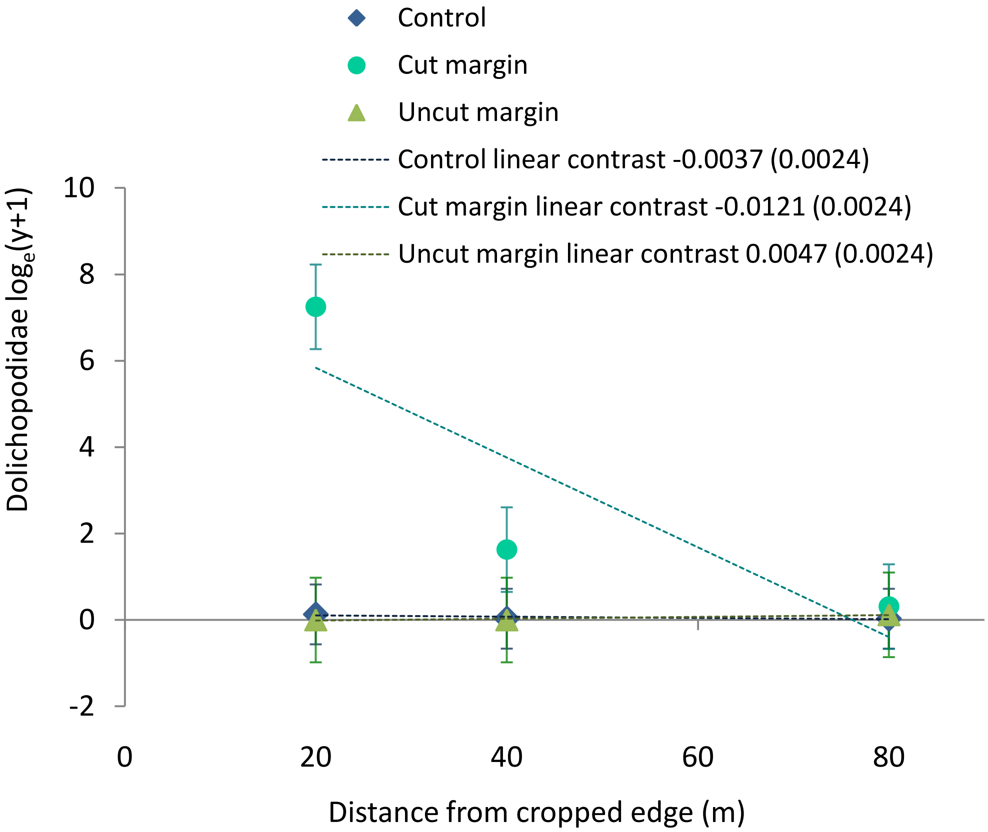


Figure 2.8 Mean numbers of Dolichopodidae trapped on sticky traps at different distances from the cropped edge during mean trapping date 5th June with standard error bars for distance from the cropped edge as a categorical factor. Numbers in parentheses are standard errors for the linear contrasts.

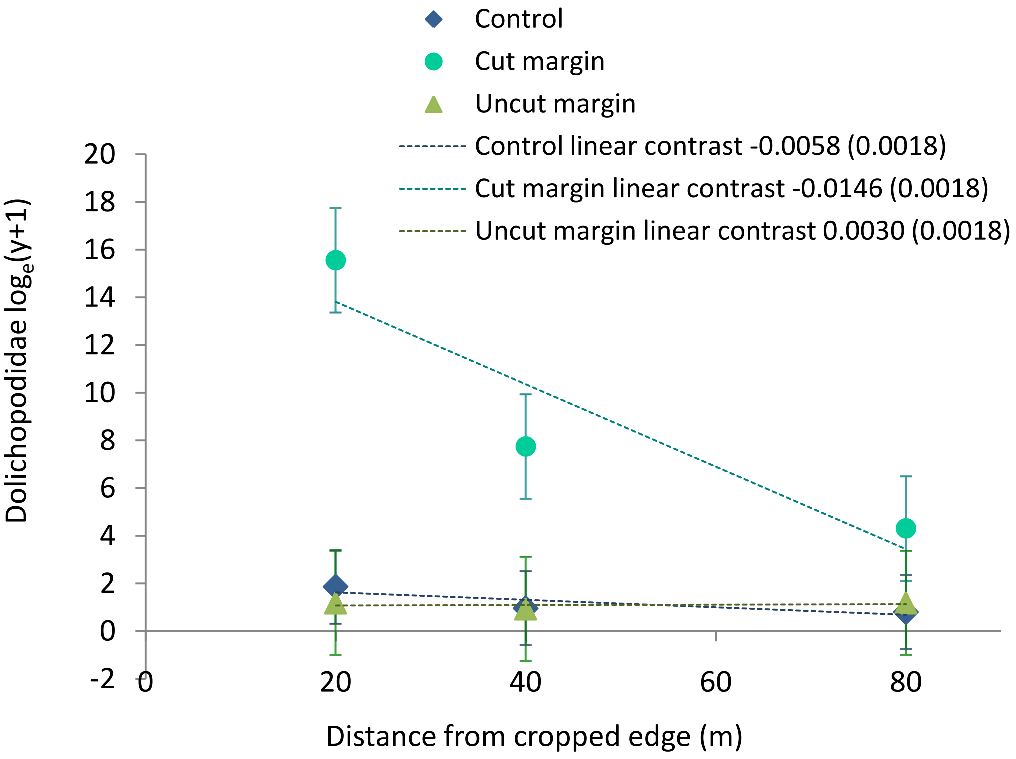


Figure 2.9 Mean numbers of Dolichopodidae trapped on sticky traps at different distances from the cropped edge during mean trapping date 2nd July with standard error bars for distance from the cropped edge as a categorical factor. Numbers in parentheses are standard errors for the linear contrasts.

2.3.3.5. Cantharidae

Numbers of Cantharidae trapped were very low during in both Sticky and D-vac captures for during trapping dates 2 (mean trapping dates 7th May and 12th May respectively) and 3 (mean trapping dates 22nd May and 25th May respectively) (Table 2.4) but numbers trapped increased significantly during date 4 (mean trapping dates 5th June and 10th June respectively) onwards.

Cantharidae exhibited a statistically significant difference in numbers of individuals trapped on sticky traps in fields with cut margins compared to those without for mean trapping date 5th June (Control fields' mean = 0.017 ± 0.009, Uncut margin fields' mean 0.068 ± 0.013, Cut margin fields' mean = 0.142 ± 0.013; $F = 16.27_{1,5}$, P = 0.01) and in D-vac samples taken during mean trapping date 25th June (Control fields' mean = 0.017 ± 0.068, Uncut margin fields' mean 0.645 ± 0.096, Cut margin fields' mean = 0.115 ± 0.096; F = $15.27_{1,5}$, P = 0.01)(Fig. 2.10).

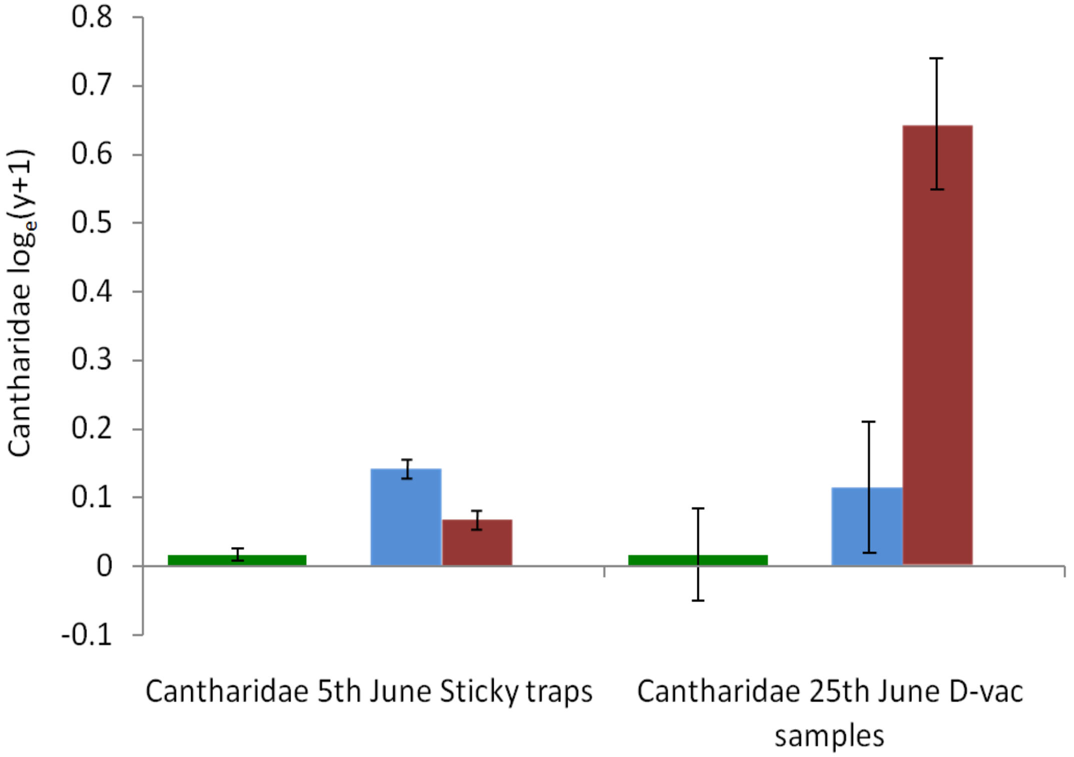


Figure 2.10 Mean count of Cantharidae with standard errors trapped on sticky traps during mean trapping date 5th June and in D-vac samples during mean trapping date 25th June within Cut (red bars) and Uncut margin fields (blue bars) and control fields (green bars). The width of the bars are proportional to number of sample replicates (Margin cut: n = 2, Margin uncut: n = 2, Control: n = 4).

There were also interactions between both the distance from the cropped edge, margin presence and disturbance via cutting during mean sticky trapping date 19th June. Cantharidae on sticky traps were found in similar numbers at all distances in control and fields with intact margins but at far higher numbers at 80m in fields with cut margins (Fig. 2.11)(F = $3.50_{2,6.39}$, P = 0.04). First order polynomial analyses indicated the relationships between Cantharidae caught in fields with cut margins, uncut margins and control fields were significant (Fig. 2.11; F = $6.64_{1,6.39}$, P = 0.01; Deviations F = 0.036, P = 0.553) although there was no significant difference in numbers caught in fields with and without a margin (Control fields' mean = 0.513 ± 0.196, Margin fields' mean = 0.591 ± 0.196; F = $0.08_{1,5}$, P = 0.79).

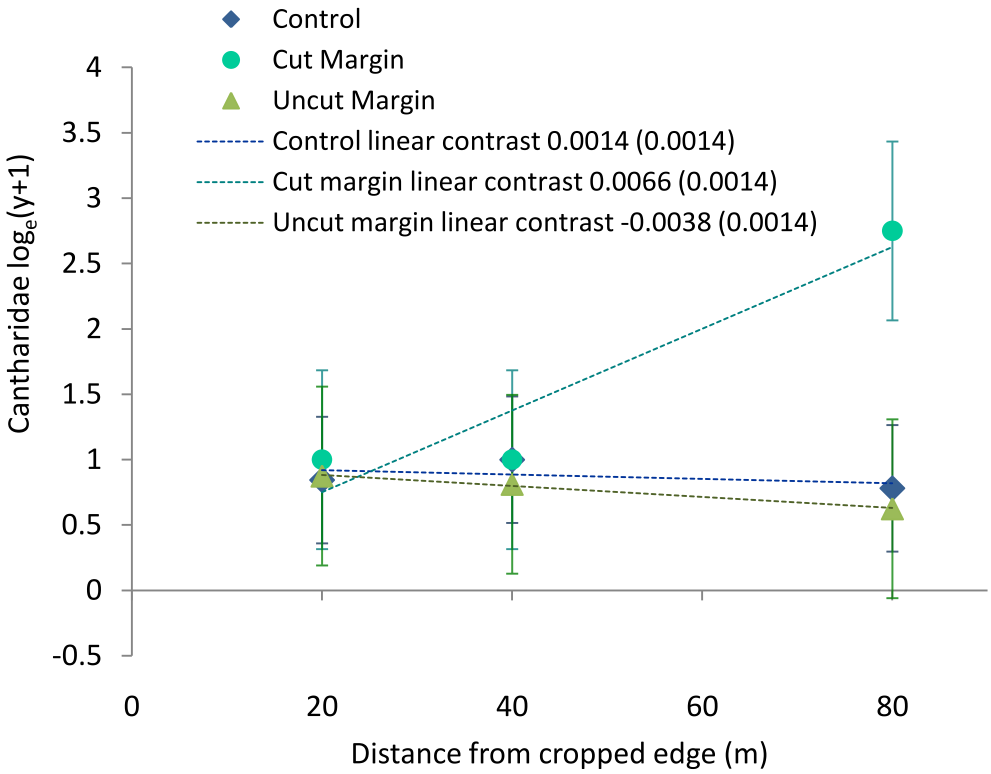


Figure 2.11 Mean numbers and standard errors of Cantharidae trapped in sticky traps at different distances from the cropped edge during mean trapping date 19th June with standard error bars for distance from the cropped edge as a categorical factor. Numbers in parentheses are standard errors for the linear contrasts.

2.3.3.6. Syrphidae

Numbers of Syrphidae trapped decreased throughout the sampling season (Table 2.4), with relatively few caught overall, although both trapping methods showed the same trend of decreasing numbers of Syrphidae trapped.

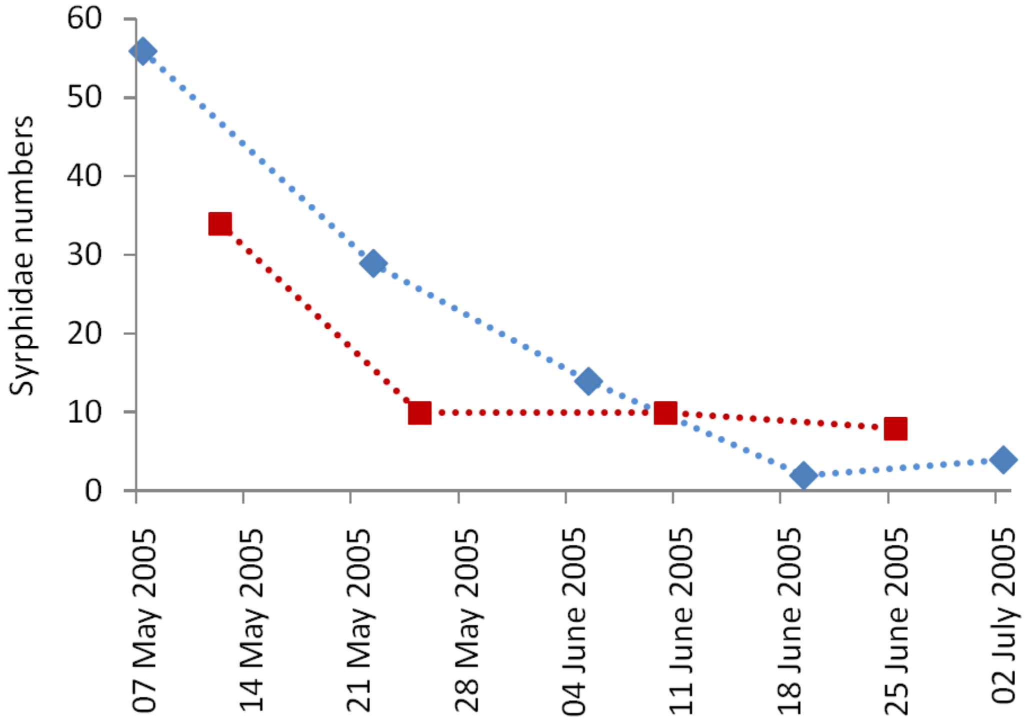


Figure 2.12 Numbers of Syrphidae trapped on Sticky traps (blue diamonds) and caught in D-vac samples (red squares) for each of the mean trapping dates throughout the season.

The presence of a margin seemed to have no effect on numbers trapped with either trapping technique although there was an interaction effect between distance trapped from the cropped edge and margin presence or absence (Fig. 2.13 & Fig. 2.14) during mean sticky trapping dates 22nd May and 5th June ($F = 6.39_{1,9.4}$, $P < 0.01$; $F = 4.24_{1,18.09}$, $P = 0.04$ respectively) with greater numbers of Syrphidae species being captured at 20m from the cropped edge in fields with margin surrounds during mean trapping date 22nd May ($F = 5.07_{2,9.4}$, $P < 0.01$), but this relationship becomes non-significant during mean trapping date 5th June ($F = 0.08_{2,18.1}$, $P = 0.08$) - as numbers of Syrphidae caught decrease.

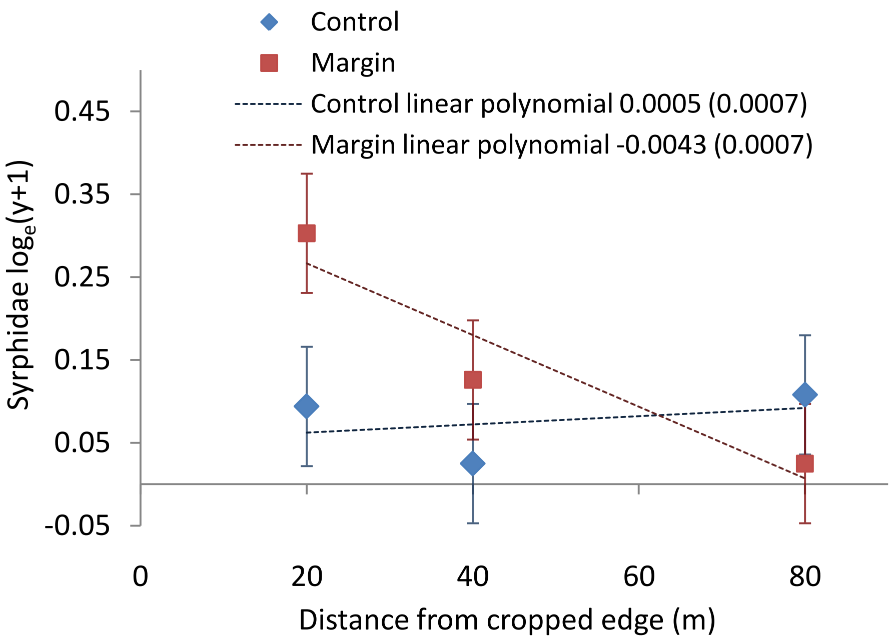


Figure 2.13 Numbers of Syrphidae caught on sticky traps for mean trapping date 22nd May at the three different distances from the cropped edge in fields with margin surrounds compared to control fields with standard error bars for the linear relationship (Distance as a 1st order polynomial relationship: F = $10.12_{1,9.4}$, P <0.01; Deviations from the linear relationship were not significant: F = 0.02, P = 0.89). Numbers in parentheses are standard errors for the linear contrasts.

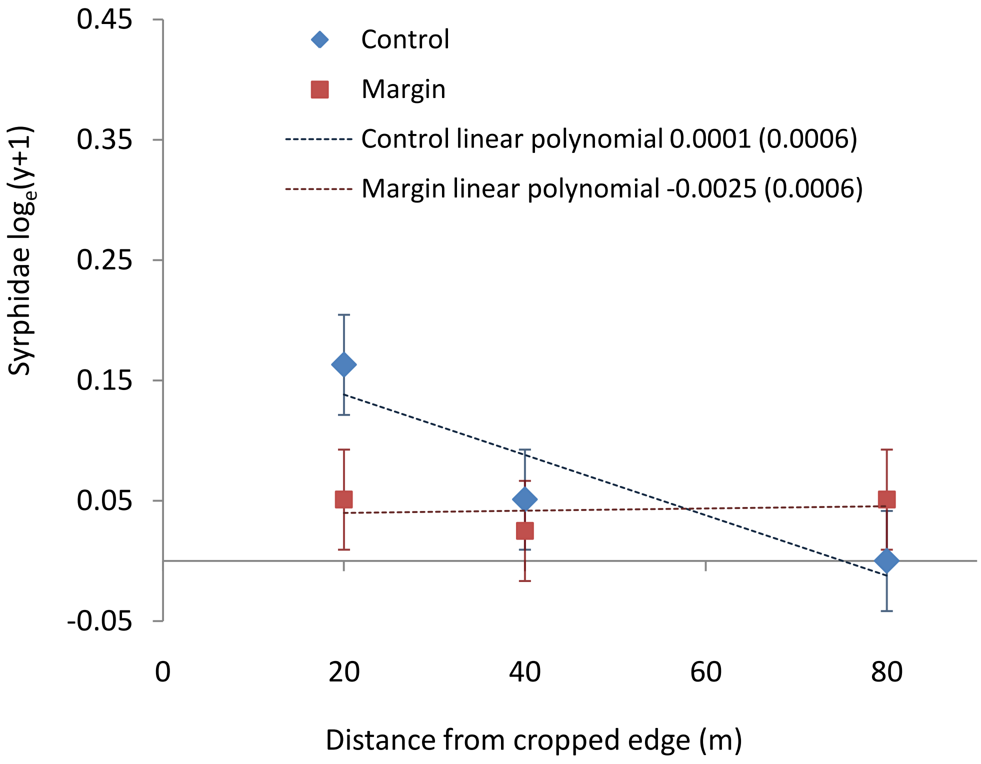


Figure 2.14 Numbers of Syrphidae caught in sticky traps for mean trapping date 5th June at the three different distances from the cropped edge in fields with margin surrounds compared to control fields with standard error bars (Distance as a 1st order polynomial relationship: $F = 4.90_{1,18.09}$, $P = 0.03$; Deviations from the linear relationship were not significant: $F = 0.26$, $P = 0.61$). Numbers in parentheses are standard errors for the linear contrasts.

2.3.3.7. Neuroptera

Very few Neuroptera were trapped in D-vac samples compared with those caught on Sticky traps (total numbers over all dates: 8 in D-vac samples vs. 319 in Sticky traps) but exhibited no response to field margin presence.

2.3.4. Vegetation analyses

(deliberately left blank - see next page)

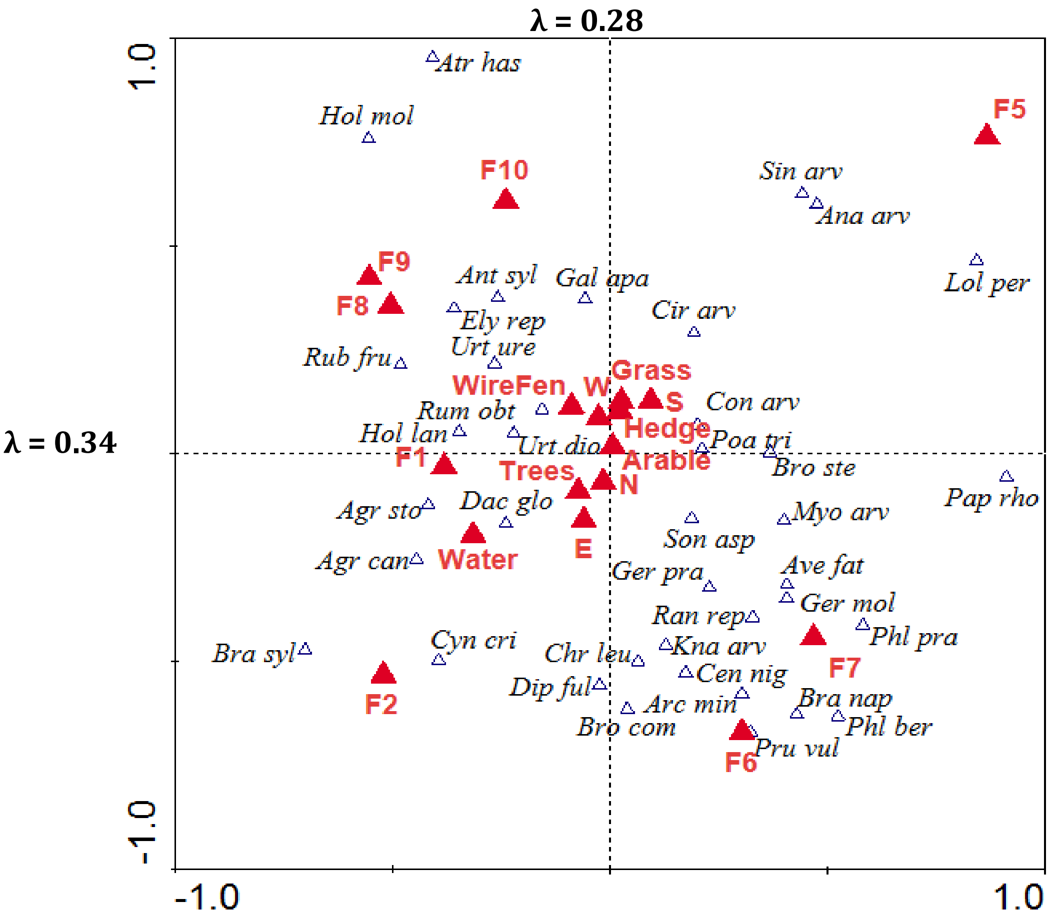


Figure 2.15 Biplot of field margin/boundary (low vegetation) species (fit 10 to 100%) and environmental variables. Plant species are-Agr can: *Agrostis canina*; Agr sto: *Agrostis stolonifera*; Ana arv: *Anagallis arvensis*; Ant syl: *Anthriscus sylvestris*; Arr ela: *Arrhenatherum elatius*; Atr has: *Atriplex hastate*; Arv fat: *Avena fatua*; Bra nap: *Brassica napus*; Bra syl: *Brachypodium sylvaticum*; Bro com: *Bromus commutatus*; Bro ste: *Bromus sterilis*; Cen nig: *Centaurea nigra*; Chr leu: *Chrysanthemum leucanthemum*; Cir arv: *Cirsium arvense*; Con arv: *Convolvulus arvensis*; Cyn cri: *Cynosurus cristatus*; Dac glo: *Dactylis glomerata*; Dip ful: *Dipsacus fullonum*; Ely rep: *Elymus repens*; Gal apa: *Galium aparine*; Ger pra: *Geranium pratense*; Her sph: *Heracleum sphondylium*; Hol lan: *Holcus lanatus*; Hol mol: *Holcus mollis*; Kna arv: *Knautia arvensis*; Lol per: *Lolium perenne*; Myo arv: *Myosotis arvensis*; Pap rho: *Papaver rhoeas*; Phl ber: *Phleum bertolonii*; Phl pra: *Phleum pratense*; Poa ann: *Poa annua*; Poa tri: *Poa trivialis*; Pru vul: *Prunella vulgaris*; Ran rep: *Ranunculus repens*; Rub fru: *Rubus fruticosusm*; Rum obt: *Rumex obtusifolius*; Sin arv: *Sinapis arvensis*; Son asp: *Sonchus asper*; Urt dio: *Urtica dioica*; Urt ure: *Urtica urens*. Environmental variables are: F1: Field 1; F2: Field 2; F5: Field 5; F6: Field 6; F7: Field 7; F8: Field 8; F9: Field 9; F10: Field 10; N: Northern side of the field; E: Eastern side of the field; S: Southern side of the field; W: Western side of the field; Arable: Arable adjacent land; Grass: Grass/Pasture adjacent land; Hedge: Hedge present along field boundary; Trees: Trees present along field boundary; WireFen: Wire fence present along field boundary (where hedges or trees absent).

These results (Figure 2.15) show a difference in plant species present depending on the field margin presence (fields 1,2 6 and 7 had margins) with Axis 1 acting as a division between fields with margins and those without. The side of the field that the samples were collected (Side N, E, S and W) explain very little of the species diversity present and hedge, wire fence, trees and arable land similarly do not affect plant species found in the boundary and field margins. The species with negative values along Axis 1 tend to be species typically found in wildflower meadows (e.g. *Chrysanthemum leucanthemum*; *Centaurea nigra*) whereas species with positive Axis 1 values are commonly arable weed species (e.g. *Urtica dioica*; *Cirsium arvense*), reflecting the difference between fields with sown margins and those without. Despite the margins being sown with seed from a wild meadow, grassy species still pervade and flowering plant abundance was not high.

2.4. **Discussion**

Despite the evidence that many aphid predators are able to fly (see Table 1.1, Chapter 1), studies investigating the effects of semi-natural habitats on aphid predator movements have tended to focus on epigeal predators , e.g. the carabid beetles (Dennis & Fry, 1992; Holland & Luff, 2000; Collins *et al*., 2002; MacLeod *et al*., 2004). This study shows that many groups of aerially dispersing aphid predators, indeed, probably the most important ones in terms of aphid predation (Ellingsen, 1969; Chambers & Adams, 1986; Sunderland *et al*., 1987; Atlihan *et al*., 2004; Freier *et al*., 2007) penetrate fields by flight, or ballooning in the case of Linyphiidae.

The trapping method determined the species composition and numbers of aphid predators dependant on their life history, such as at what time during the season they are more likely to use flight as a mode of transport and movement to floral resources. Sticky traps and D-vac suction traps differ in the way they trap invertebrates, and within the context of this study there are costs and benefits of both methods. Although it was not possible to compare the two trapping methods statistically, table 2.11 provides an overall comparative summary of both methods in the context of numbers of aerially dispersing aphid predators trapped this study and ease of use. The main observation from comparing the two methods directly came from *Tachyporus* spp., Cantharidae and Carabidae. Early on in the season, far more were caught in D-vac samples than on sticky traps. At date 5, however, this trend is reversed with more trapped on sticky traps. From this it can be inferred that *Tachyporus* spp., Cantharidae and some Carabidae are epigeal until early June at which point they are more likely to fly, but also illustrates the differing effectiveness of sticky trapping compared to D-vac suction sampling depending on timing and activity of the invertebrate. The response of *Tachyporus* spp. is discussed in greater depth in section 2.4.3.2. and Cantharidae in 2.4.3.4.

Table 2.11 Comparison of sticky trapping and D-vac suction sampling according to various criteria.

Criteria	Sticky traps	D-vac sampling
Overall effectiveness	Long temporal trapping window encompassing nocturnal, diurnal & crepuscular activity.	Short temporal trapping window, diurnal capture only (in this study). E.g. Very few Neuroptera trapped in D-vacs possibly due to mainly nocturnal flight activity (Lewis & Taylor, 1964). Only captures those species that occur at relatively high densities.
Density measure	Measures activity-density therefore subject to the same problems as pitfall traps (e.g. Southwood, 1978; Topping & Sunderland, 1992). Active fliers more likely to be trapped.	Absolute density measure (Duffey, 1980) but can only cover an extremely small relative area.
Associated problems	Efficacy limited if too many invertebrates are trapped which then cover the sticky area.	Vegetation structure determines efficacy (Hand, 1986), this is not an issue in this study where all samples were taken in wheat fields grown with the same sowing densities and samples taken at similar crop growth stages.
Ease of use	Easy to use, a large number of traps can be set up quickly and sampled at regular intervals. Less dependent on weather, can be used in wet conditions.	Labour intensive. Can only be carried out in dry weather.
Main predator groups caught	Active fliers such as Syrphidae and Neuroptera and ballooning Linyphiidae. Dolichopodidae and Empididae caught in similar numbers to D-vac sampling.	Until mid-June, caught more *Tachyporus* spp. and Carabidae than sticky trapping.

2.4.1. The effect of a 6m florally enhanced field margins on aerially dispersing aphid predators

The presence of a field margin did have an effect on the number of aerially dispersing aphid predators trapped, and/or they influenced aphid predator crop penetration although this varied through the season for different predator groups. Overall, fields with field margin surrounds had significantly greater numbers of aphid predators measured by sticky traps early in the season. The higher numbers of aerially dispersing families trapped in fields with margin surrounds is also likely to be related to the proximity of the overwintering habitat to the fields in which trapping occurred.

The greater numbers of aerially dispersing aphid predators in fields with margin surrounds early on in the season was not attributable to one particular group, but was composed primarily of Empididae (34.6%), Syrphidae (26.0%), *Tachyporus* spp. (15.0%) and Linyphiidae (11.7%). These results indicate that field margins may be important in providing a community of aerially dispersing aphid predator groups early on, when aphid population control is considered to be most effective (Edwards *et al.*, 1979; Chiverton, 1986), rather than the presence of a field margin benefitting a single group or individual species.

An experiment by Holland *et al.* (2008a) that used the same fields as the Chapter 2 study found that aerially dispersing aphid predators were contributing the majority of aphid control but field margins, where present, did not enhance aphid control. However, the study by Holland *et al.* (2008a) commenced on the 6th June 2005, whereas significantly higher total numbers of aerially dispersing predators in fields with margin surrounds in this study were found during early May, when differing rates of aphid predation in fields with and without field margin surrounds would not be detected. Previously, the early emergence of polyphagous predators into winter wheat fields have been considered to provide a significant level of aphid control (Östman *et al.*, 2003) due to the impact they can have on initial aphid population numbers.

The proximity of field margin type habitat has been considered to be important for epigeal predators to encouraging penetration of the crop (Dennis & Fry, 1992; Holland *et al*., 1999; Collins *et al*., 2002), but, here, they are likewise encouraging aerially dispersing aphid predators early in the season, although only when considered as a whole. The presence of field margin habitat has been shown to influence numbers of Syrphidae in adjacent fields (Harwood *et al*., 1994) during the months of summer, although not during early May as shown here. For both *Tachyporus* spp. and Linyphiidae, the higher total of aerially dispersing aphid predators trapped on sticky traps in fields with margin surrounds during mean trapping date 7th May is attributed to the suitability of field margins as non-crop habitat overwintering sites (e.g. Staphylindiae such as *T. hypnorum* and *T. chrysomelinus*: Pfiffner & Luka, 2000; Linyphiidae: Lemke and Poehling, 2002; Overall: Marshall and Moonen, 2002). *Tachyporus* spp. have been well documented as dispersing from field margins in which they overwinter primarily by flight (Coombes & Sotherton, 1984; Petersen, 1999). Very little is known about the possible association of Empididae with field margins and this is investigated further in section 2.4.3.3. These results indicate that field margins may be important in providing a community of aerially dispersing aphid predator groups early in the season rather than the presence of a field margin benefitting a single group or species in particular. As the season progressed, it is possible that dispersal of some groups of aerially dispersing aphid predators leads to a ubiquitous distribution over the landscape (Holland *et al*., 2004) which is undetectable at the single field scale. This will be discussed in more detail in and addressed fully in Chapter 3.

Linyphiidae exhibited a strong response to field margin presence with higher numbers being found in fields with field margin surrounds for three of the five sticky trapping dates. Other groups, such as Cantharidae and *Tachyporus* spp. had significantly greater numbers of individuals trapped during some of the dates in fields with margins. Within all the groups trapped, there were none that the presence of a field margin had a negative effect on their numbers.

2.4.2. Margin cutting

The cutting of the margins during trapping date 2 was unplanned but provided an opportunity to determine its effects on aerially dispersing aphid predators during an important time of many aphid predators' life histories when typically aphid predators are moving into winter wheat fields. Such movement may suppress the initial influx of cereal aphids from surrounding habitat (Bommarco and Fagan 2002).

Margin cutting is often used as a management technique to prevent scrub encroachment (Vickery *et al*., 2002) and therefore encourage biodiversity. However, in studies where cutting has been investigated during the spring/summer months, effects on field margin fauna have been negative. Bell *et al*., (2002) found it reduced *Lepthyphantes tenuis* individuals caught within field margins. The results from this study suggest the disturbance in the field margin 'pushes' Linyphiidae individuals into the adjacent field, since greater numbers were trapped in fields with cut margins compared to those without. This could be beneficial through increasing numbers in the adjacent field and therefore potentially improve aphid control. The removal of inflorescences by cutting has also been shown to reduce numbers of nectar feeding butterflies within margins (Feber *et al*., 1996), again, this study indicates the result is an increase of numbers of the pollen and nectar feeders Cantharidae and Dolichopodidae in adjacent fields. The potential increase in aphid predation as a result remains to be investigated.

2.4.3. Individual group responses to field margin presence and penetration of cropped areas.

2.4.3.1. Linyphiidae

Field margins are considered to be a source habitat for Linyphiidae spiders (Bell *et al*., 2002) and are able to disperse from local areas of high to low population numbers rapidly (Thomas *et al*., 1990). Marshall *et al*. (2006) did not find greater numbers of Linyphiidae in fields with margins although typically field margins do not surround whole fields. Marshall *et al*. (2006), however, did find Linyphiidae spiders were more abundant within the crop area of smaller fields. Within this study it is possible that the presence of margins surrounding the entire treatment fields enhanced the numbers of Linyphiidae trapped within fields with margins to a detectable local effect. This local effect potentially contributed to the greater increase in numbers of Linyphiidae trapped in fields with margin surrounds at the end of May. This is supported by results both directly by Schmidt & Tscharntke (2005), who found Linyphiidae spider abundances were increased by the presence of high percentage areas of non-crop habitat, and within models predicting that small inclusions of non-crop habitat increase the number and persistence of Linyphiidae found in the landscape (Halley *et al.,* 1996).

The differences in numbers of Linyphiidae trapped using the D-vac and on sticky traps are likely to be related to the meteorological conditions. D-vac sampling detected greater numbers of individuals in fields with margin surrounds during the first trapping date, whereas during this time sticky traps were catching low numbers of Linyphiidae. As the season progressed this trend reversed with far greater numbers on sticky traps as meteorological conditions, such as wind speeds less than 3 m s^{-1} (Vugts & van Wingerden, 1976), became more favourable for locomotion by ballooning and therefore more likely for individuals to be caught on sticky traps. The effect of margin disturbance during mean D-vac trapping date 25th May seems to have "pushed" Linyphiidae out into the fields next to the disturbed margins, detected in D-vac samples but not on sticky traps due to the lack of aerial locomotion in evidence during this time.

2.4.3.2. Tachyporus spp.

Tachyporus spp*.* typically overwinter in non-crop habitats such as grassy field edges and hedges (Pedersen *et al.* 1990), but have been shown to have fully dispersed to crop fields by mid-May (Coombes & Sotherton 1986) attributable to their ability to fly. Based on the D-vac sample and sticky trap catches from this study, however, relatively low numbers were caught on sticky traps during mean trapping dates 7th and 22nd May and 5th June but far greater numbers were trapped in D-vac samples *Tachyporus* densities were 2.17 individuals per m^2 during mean D-vac trapping date of 25th May, double that of a study in Germany which found just over 1 per m^2 in winter wheat and beet fields during the same season of study (Markgraf & Basedow, 2002). After this population peak there was an increase in individuals on sticky traps, and a drop in numbers in D-vac samples, possibly as a result of high densities there was an emigration response or lack of prey as *Tachyporus* spp. have a high propensity for aphid consumption (Vickerman *et al*., 1987) and aphid densities within the fields were relatively low. (see Holland *et al*. 2008a; the same fields were used in each of these studies). There was an effect of field margin presence during mean sticky trapping date 5th June when increasing numbers of *Tachyporus* spp. were caught on sticky traps, and significantly higher numbers were trapped in fields with margin surrounds, encouraged further by cutting. The higher numbers of flying *Tachyporus* spp. are likely to be due to the minimum threshold flight temperature being reached (Taylor, 1963). (Petersen, 1999) modelled the sum of day degrees required for *Tachyporus hypnorum* dispersal and found approximately twenty percent of beetles had dispersed based on a sum of day degrees above 14.9 degrees D (based on the sum of day degrees above 12 degrees C and equating to 22 April in Sweden, where the study was conducted) and eighty percent dispersal when the sum of day degrees was 31.1 degrees D (13th May in Sweden). Therefore, the difference in numbers of *Tachyporus* spp. caught in fields with and without margins on mean trapping date 5th June may be a result of increased flight activity of *Tachyporus* spp. from the field margin habitat.

2.4.3.3. Predatory flies: Empididae and Dolichopodidae

Both Dolichopodidae and Empididae species have been overlooked as predators of aphids, although both Empididae (personal obs.) and Dolichopodidae (Ulrich, 2005) do readily predate on aphids. The extremely large densities of these predatory flies, especially around peak aphid population date (e.g. six Empididae individuals and two Dolichopodidae individuals per m^2 during mean D-vac trapping date 25th June) warrants further study of Empididae and Dolichopodidae as entomoghagous pest predators in arable crops.

The high numbers of Dolichopodidae trapped in fields with cut margins is unlikely to be due solely to the disturbance of cut margins, more likely the presence of water bodies close by to fields 1 and 2 that were subject to cutting led to high numbers of water-associated species of Dolichopodidae being trapped (Aquilina *et al*., 2007). Dolichopodidae exhibited a strong association with field edges, as to a lesser extent did Empididae. As a consequence they may fail to penetrate the larger fields. Overall little is known about these two groups and they warrant further investigation (Flückiger & Schmidt 2006).

2.4.3.4. Cantharidae and Syrphidae

Both Cantharidae and Syrphidae utilise pollen and nectar (Cantharidae; Traugott, 2002; Syrphidae: Schnieder, 1969), and both are known for their positive association with flowering plants (Meek *et al.* 2002; Sutherland *et al.* 2001; Cowgill *et al*., 1993a). Syrphidae use visual cues (Bugg, 1992) to locate aphid patches within which to lay their eggs for the aphidophagous larvae to prey upon.

The majority (over 70%) of Cantharidae individuals trapped were *C. lateralis*, a known aphid predator (Landis & van der Werf, 1997) and greater numbers were trapped in fields with margin surrounds in both D-vac samples and on sticky traps, but not for all dates where trapping occurred.

Syrphidae numbers were highest during the first trapping date and decreased as the season progressed possibly due to the low numbers of aphids to be found in fields, however, Syrphidae larvae densities were very high in the fields used in this study (Holland *et al*., 2008a) and would have been able to provide high levels of aphid control (Ankersmit *et al*., 1986). Syrphidae also responded to the presence of field margins, decreasing with distance from the margin but not in the control fields where they exhibited a more uniform distribution but in lower numbers. The further from the field margin that the traps were placed, the fewer Syrphidae individuals were caught, however, Syrphidae individuals caught in control fields showed a uniform distribution as distance from the cropped edge increased. Previously, the Syrphid species *E. balteatus* have been shown to remain close to pollen and nectar sources and are mainly retained in field margin habitat containing flowers (Cowgill *et al.* 1993a; MacLeod, 1999). Additionally Bowie *et al*. (1999) found a similar trend of adult hoverflies trapped at varying distances from a field boundary. By mean sticky trapping date 5th June, however, this trend had reversed, although total numbers of hoverflies trapped had dropped to fourteen from twenty-nine.

2.4.3.5. Neuroptera

Neuroptera, although highly aphidophagous (Stelzl & Devetak, 1999) and attracted to large patches of flowering plants (Villenave *et al.* 2006), did not demonstrate any differences in numbers whether a field margin was present or not. Sticky trapping rather than D-vac suction sampling was a more effective way of capturing the neuropteran *C. carnea*; the only species of Neuroptera captured in this study. Sweep also may be more appropriate for species occurring at low densities.

2.4.4. Field boundary flora

The presence of field margins surrounding fields 1, 2, 6 and 7 affected the floral composition at the field edge with species usually associated with wild meadows being present. This was clearly shown by the division of fields with and without sown field margins along Axis 1 in Figure 2.15. The CANOCO CCA analysis was carried out with the primary objective to determine if any other environmental variables that are known to affect particular groups of aerially dispersing aphid predators, such as hedges (e.g. Asteraki *et al*., 1995), trees (e.g. Wratten *et al*., 2003b), wire fence lines (e.g. Griffiths *et al*., 2000) and water (e.g. Aquilina *et al*., 2007) were in proximity to the fields which could affect the predators trapped within them and be wrongly attributed to a field margin effect. The vegetation analysis showed this was not the case of the environmental variables tested, except for ‘water’ which was associated mainly with fields 1 and 2 due to the proximity of a water body. Interestingly, the side of the field that the vegetation was surveyed, described by the variables N, E, S and W, also did not seem to affect the plant species or abundance overall, although aspect would be expected to have an effect (Le Coeur *et al*., 1997), whereas it would be expected that habitat boundaries facing different directions may exhibit a different range of invertebrate species and abundance (Sarthou *et al*., 2005) and subsequently the predators found within them may vary

(Dennis *et al*., 1994; De Cauwer *et al*., 2006). The differences exhibited due to field margin presence was clearly a factor that had far greater influence on the plant species present than the side of the field that the species sampling was carried out. Overall the vegetation composition had no impact instead the aerially dispersing aphid predator response was driven by the presence or absence of a field margin surround.

2.4.5. Summary

Early seasonal movement of flying aphid predators may be underestimated and, until now, the majority of research on predation of colonising aphids has been attributed to epigeal polyphagous predators. Both Schmidt *et al*. (2003) and Holland *et al*. (2008a) found that predators that could access aphid colonies aerially have the greatest effect on reducing aphid populations, although Holland *et al*. (2008a) found no difference in predation levels of flying aphid predators when margins were present compared to fields without margins; the same fields as used in this study. Field margin disturbance affects the numbers of predators found in adjacent fields and the penetration of fields up to 80m by some aerially dispersing aphid predators may pose a problem. Sticky trapping would seem the best option for trapping aerially dispersing aphid predators where a choice must be made between the two strategies.

2.4.6. Further work

Many agricultural invertebrate studies are conducted at the single field scale. For invertebrates that can disperse, either by active flying, such as Syrphidae, or by using the wind as a mode of transport, such as Linyphiidae, the single field scale may not be large enough to discover their dispersion patterns. Although the study carried out in 2005 showed the presence of field margins to have a significant effect on some groups, each field was considered as a single unit. When considering aerially dispersing aphid predators the question of "grain size" arises (Mayer & Cameron, 2003) due to the distance that aerially dispersing invertebrates can cover and studies at landscape scale levels are necessary to discover how field margins can affect aerially dispersing aphid predators and therefore a suitable pest management strategy can be devised (Irwin, 1999). This leads on to the next chapter looking at the effect of field margin density at the landscape scale.

Chapter 3

Do higher proportional areas of uncropped land (primarily composed of field margin habitat) surrounding winter wheat fields increase the number of aerially dispersing aphid predators within them and thereby levels of aphid control?

3.1. **Introduction**

3.1.1. From single field to landscape scale

In agricultural systems predatory invertebrates have been mainly studied at the field scale but landscape scale studies are becoming increasingly common as it is realised that the impacts of semi-natural habitats exert their influence at wider scales. Several landscape scale studies have been carried out on a number of aphid enemies, both epigeal (e.g. Holland *et al*., 2005; Schmidt *et al*., 2005) and flying (e.g. Thies *et al*., 2005; Haenke *et al*., 2009), but drawing succinct conclusions between quantity of semi-natural habitat and resulting impact on pest populations has not been straightforward (see Griffiths *et al*., 2008 for a detailed review). At the single field scale it is easier to detect the influence of a habitat manipulation in a replicated study. In landscape scale studies a greater number of factors, due to study area size, can potentially exert an influence on the enemies and pests in question and replication becomes difficult (Cao *et al*., 2002). Knowing the range and timing of movement of both pests and their predators are, however, key to the development of successful integrated pest management (IPM) strategies (Aylor & Irwin, 1999). It is also necessary to select the resolution and maximum study size area carefully so as to reflect the range of the organism in question and limit the influence that the scale of choice can potentially have on the results of the study itself (Mayer & Cameron, 2003). The aerially dispersing aphid predators within arable ecosystems have dispersal ranges that vary widely, from up to 30 km travel in a single day by Linyphiidae (Thomas *et al*., 2003) to locally focussed movements of Syrphidae (Bowie *et al*., 1999). The decision to implement and manipulate field margin type habitat, however, occurs at farm scales, since this is a factor that can be influenced and investigated with relative ease, this is the appropriate landscape scale size for this study.

3.1.2. Potential differing temporal responses related to predator life history and behaviour

There is likely to be a difference in the way that aphid predators with varying life histories and methods of field margin utilisation respond to the proportional area of field margin habitat depending on their dispersal habits (Jauker *et al.*, 2009) over the short and long term:

1. *Long term temporal response*

A higher proportional area of field margin type habitats over several years could increase aphid predator numbers due to habitat resource provisioning (Denys & Tscharntke, 2002). This has been shown by beetle banks with numbers of aphid predator species increasing within them over several years (MacLeod *et al*., 2004), and predator numbers increasing where beetle banks are present during the summer season in adjacent fields (Prasad & Snyder, 2006). An incentive to leave the beetle bank and move into adjacent fields is usually needed and the requirement for food may be a driving factor (Frampton *et al*., 1995).

2. *Short term temporal response*

During the spring/summer season the predator species utilising the field margin, for example, for overwintering habitat, pollen and nectar (where in existence) or for alternative prey, and would not be expected to exhibit a large scale response to the proportional area of field margin habitat. For example, the hoverfly *Episyrphus balteatus*, conducts foraging flights during the warmer months to both collect food and search for aphid colonies within which females lay their eggs (Almohamad *et al.*, 2009) and the flight distances seem to be localised during this seasonal time period (Lovei, 1993; Wratten *et al.*, 2003b). Other species of invertebrates that also utilise pollen during the warmer months, such as bees (Greenleaf *et al.*, 2007; Steffan-Dewenter & Tscharntke, 1999) and parasitoids (Roschewitz *et al.*, 2005) have also been shown to have relatively contracted dispersal scales.

It is possible that these temporal variations in behaviour of aerially dispersing aphid predators influence the spatial scale to which the predator responds assuming predators follow the time/diffusion model response.

3.1.3. Potential differing spatial responses related to predator life history and behaviour

An increase in the proportional area of field margin habitat would be expected to benefit all aphid predator species numbers by increasing the area of sites and resources for both overwintering predators and those that use pollen and nectar as a food resource. An increased proportional area of field margins will also improve the chance that a field margin will occur in local proximity to a field in which control is required. The way in which predators respond may vary according to the resource they are utilising. Aerially dispersing aphid predators that use field margins as sites for a longer term (multi-year) overwintering strategy are likely to have a functional response area larger than those of pollen and nectar feeders who, it is anticipated, have a short term strategy of small scale 'shuttle' movements between the resource and the crop in which control is required.

One of the commonest aphid predators found occurring in grassy field margins are from the genus *Tachyporus*, (e.g. *Tachyporus hypnorum*; Dennis *et al.*, 1994; Griffiths *et al*., 2000) and they were shown to exist in greater numbers in fields with field margin surrounds (Oaten *et al.*, 2007). At larger scales than a single field, greater numbers of *Tachyporus* spp. would be expected to be found in areas that have higher densities of field margin surrounds. However, the spatial limit of this potential relationship is unknown. *Tachyporus* spp. are known to disperse by flight (Markgraf & Basedow, 2002), but extrapolating information from Petersen (1999) and Coombes & Sotherton, (1986) it is likely to be a seasonal response rather than a continuous foraging behaviour.

The trophic level that an organism functions at is also not necessarily an indicator of the spatial scale that is recognised (Thies *et al.*, 2003), but body size may be a guide (Roland & Taylor, 1997 & Schweiger *et al.*, 2005). The lack of a scale indicator makes it necessary to carry out post experimental analyses of response spatial scales as it not known *a priori*, nor can be estimated, at which spatial scales the habitat manipulation is likely to result in a functional response. This method of determining the scale of functional areas is becoming more common and has been carried out with success in several studies already mentioned (Steffan-Dewenter *et al.*, 2002; Thies *et al.*, 2003; Kleijn & van Langevelde, 2006) and others involving other farmland insects (e.g. butterflies: Bergman *et al.*, 2004).

3.1.4. Other managed uncropped land

As outlined in section 1.5.1., there are typically other types of managed uncropped habitat in UK arable farmland that may potentially have similar effects on aerially dispersing aphid predators that field margins do. Previous studies have used percentage area of total uncropped land as an explanatory variable (e.g. Steffan-Dewenter *et al*., 2002; Thies *et al*., 2003, 2005), but this may not be a reflection on the amount of uncropped land within the area that is actively managed as part of an agri-environment process. The main groups of predators identified in this study are potentially manipulated through the provisioning of field margin-like habitats (see section 1.5.2, table 1.1), so the proportional areas of these habitats should have detectable effects where they exist.

3.1.5. Hypothesis, objectives and aims.

Hypothesis:

Higher proportional areas of uncropped land (primarily composed of field margin habitat) surrounding winter wheat fields increase the number of aerially dispersing aphid predators within them and thereby levels of aphid control.

Objectives:

1. Determine the response for the key groups of aphid predators.
2. Assess the optimum functional landscape scale *a posteri* for each predator group.
3. Determine whether proportional area of field margin or field margin proximity is a better measure of explaining aerial aphid predator dispersal from field margins.
4. Assess the effect of the proportional area of field margin habitat on overall predation of cereal aphids by aerially dispersing predators.

Aim: Determine whether higher densities the proportional areas of uncropped land (primarily composed of field margin habitat) surrounding winter wheat fields increases the number of aerially dispersing aphid predators and thereby levels of aphid control.

3.2. **Methodology**

3.2.1. Aerially dispersing aphid predators trapped on sticky traps

This study was carried out in twelve fields of winter wheat located in Dorset and Hampshire, England. Fields were selected in order to provide a range of field margin densities surrounding them, due to these criteria fields were spaced at least 1.8km apart except for two fields that were 0.6km distant from each other. Each area surrounding the fields had varying densities of field margin. In each of the twelve fields, termed 'target' fields, the perimeter of the cropped area was mapped using GPS and a 40m buffer area determined inside the cropped area using GIS software, MapInfo v8.0. The length of this '40m interior perimeter' was calculated and this value divided by eight. Sticky traps, consisting of A4 sized acetate coated in Tangletrap (The Tanglefoot Co., Grand Rapids, Michigan, USA) an odourless sticky insect trapping gel, wrapped around 2 litre clear plastic bottles, were then positioned at eight equally spaced intervals along the interior perimeter (see Fig 3.1).

Sticky traps were run weekly for ten weeks starting at the end of April. Since trapping was carried out continuously the traps were positioned with the bottom edge 20cm from the top of the crop so the traps did not interfere with the spray boom during crop spraying. No insecticides were used in the winter wheat fields in which the traps were located for the duration of the study, but winter wheat growth regulator and herbicides, where necessary, were applied.

Sticky traps brought in from the field were stored at -40 degrees C and aphid predators captured on them were later identified and recorded.

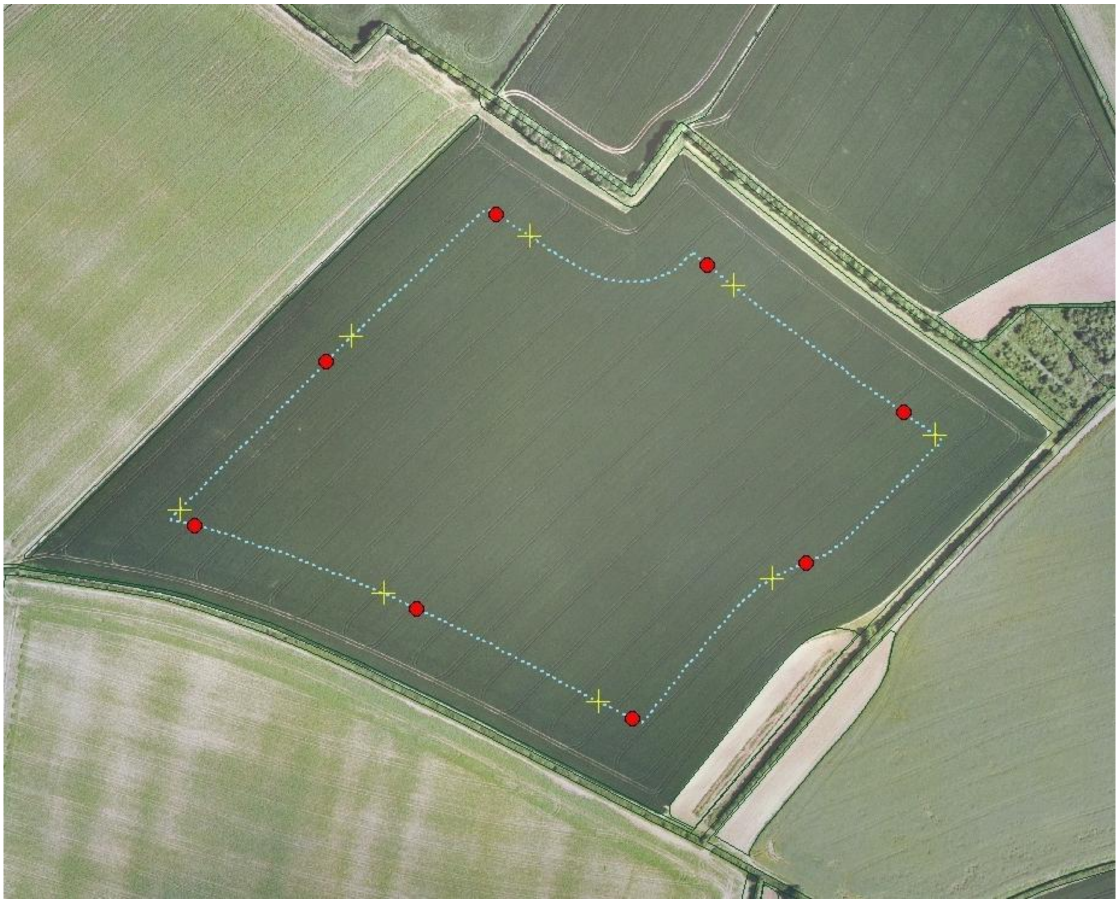


Figure 3.1. Diagram showing one of the fields used in this study. The dark green area shows the cropped area of the field which was mapped using GPS. The light blue line show the inner perimeter situated 40m from the edge of the cropped area. The red dots indicate the location of each sticky trap. Trap plants (see section 3.2.2) were located 20m clockwise along the interior perimeter and are shown as yellow crosses in this diagram.

3.2.2. The indirect effect of the proportional area of field margin habitat on artificial aphid populations

In order to determine if aphid predation by aerially dispersing predators was determined by field margin the proportional area of field margin habitat, artificial local populations of aphids were created 20m, in a clockwise direction, from each of the sticky traps in the twelve fields (see Fig. 3.1 for trap plant locations).

Aphids of the species *Sitobion avenae* were reared in controlled conditions, free from predators and parasitoids, on young winter wheat plants (aphid host plants) for a month prior to the experiment. Trap plants were grown by planting 20-25 wheat seeds in 152mm diameter plastic plant pot located in a polytunnel designed to be impervious to external invertebrates. On day seventeen post planting, the plants were thinned to ten seedlings and taken out into six of the twelve fields together with the artificially reared *S. avenae* packed separately. Once in the field 100 mixed instar *S. avenae* were counted on the leaves of aphid host plants and these leaves were cut off and draped over the trap plant. The crop around the trap plant was cut in a 50cm radius to ensure aphids could not crawl from the trap plant to surrounding wheat plants. Each trap plant pot was placed in a 5cm deep saucer containing a litre of water. This ensured the trap plant soil remained moist whilst deterring ground-dwelling aphid predators from reaching the aphids on the trap plants. Each trap plant was watered every 3-4 days to ensure a constant water supply for the growing wheat plants and ensure access to the trap plant by terrestrial invertebrates was limited. On day eighteen post planting, the trap plants were set up in the six remaining fields following the above methodology.

Using the day the plants were put out in the field as zero, the aphids that remained on the trap plants were counted at days 3, 8, 10, 14 and 22 (Julian days). Counting between days 14 and 22 was hampered by rainfall.

3.2.3. Calculating habitat areas.

Areas of different habitat types were mapped using GIS mapping software MapInfo v8.0, using information taken from aerial photographs, farmer interviews and farm records. Areas of cropped land were mapped and total areas calculated for each buffer zone. The area of non-cropped land was calculated by using the total buffer area minus any areas classified as crop, urban (including gardens) or water. All areas were mapped to a fine resolution (<0.5m) and assigned a habitat classification. In addition to habitat classifications at the field level, within field habitats were also identified and mapped. These features were classified according to their type as shown in table 3.1.

The term “field margin” consisted of the categories listed in table 3.1.

Table 3.1 Field margin classifications used to determine field margin type habitat proportional area

Width	Type
2m	Grass margin
4m	Grass margin
10m	Grass margin
12m	Grass margin
20m	Wildflower strips
2m	Florally enhanced margins
2m	Natural regeneration strips
3m (approximately)	Beetle banks
Variable	Wildflower and sown grass mix
Variable	Wild bird mix strips

Although not all of these categories would be considered field margins in the strictest sense, they can be regarded as having field margin attributes. For example, "beetle banks" are not considered a field margin but are essentially a field margin flanked on either side by crop. They were designed to provide overwintering sites to the centre of large fields (Thomas *et al*., 1991), reducing the distance aphid predators need to travel from the overwintering site and to potentially provide aphid control mid-field (Collins *et al*., 2002). This has been discussed in more detail in section 1.5.2.

The locations of field margins and the length of time that they had been in place were determined through farmer interviews and copies of their maps submitted to the Rural Payments Agency for the purpose of agri-environment scheme payments. Aerial photographs were utilised as well as ground truthing, where necessary, to ensure field margin types, locations and areas were accurate.

Each of the traps was buffered in MapInfo to obtain a series of concentric areas surrounding the central target field (see Fig. 3.2 for an example) using buffer radii of 50m, 100m, 250m, 500m, 750m and 1000m. Each of the buffer areas were analysed separately and the field margin area within calculated and divided by the total buffer area to give a value of field margin area in m^2 per hectare for every buffer in each field. This methodology of calculating habitat areas was repeated using aphid trap plants as the central points.

In addition to field margin area, field margin proximity was also calculated for each trap and each aphid plant location. Field margin proximity was measured as the distance to the closest field margin in meters for each trap or pot plant location.

Figure 3.2 An example of one of the fields used in this study as shown in MapInfo v8.0. The red dots in the target field represent the location of each of the eight sticky traps. The yellow crosses indicate where the wheat pot plants inoculated with aphids were

placed. The dotted red lines shows the buffer areas for each of the six radii. Aphid pot buffer radii are not shown.

Although the inclusion of fields in this study were determined on the basis of a varying levels of proportional area of field margin habitat between fields, other factors were also calculated. These were: total non-crop area, hedge proportional area and the proportional area of trees. These factors were measured to see if the proportional area of field margin habitat was confounded with the habitat variables listed above which could be considered to potentially affect numbers of some aerially dispersing aphid predators.

3.2.4. Statistical analyses

3.2.4.1. Field margin areas and other habitat correlations

To determine if the proportional area of field margin habitat was correlated with other landscape factors, general linear models were carried out (for each buffer radius separately) between the proportional area of field margin habitat and percentage non-crop habitat, tree cover and hedge proportional area. Other variables were not included due to overparameterization, but these three variables were considered to be of greater importance in potentially both affecting flying aphid predator numbers and potentially also autocorrelating with the proportional area of field margin habitat. Variations in percentage crop habitat have been shown to affect numbers of Linyphiidae (Schmidt et al., 2005) and cereal aphid parasitoids (Thies et al., 2005). Trees may act as barriers to movement of aerial predators (e.g. hoverflies: Wratten et al., 2003b) and hedges used for overwintering and breeding of carabid beetles (Holland & Luff, 2000).

3.2.4.2. Aphid predator response to field margin area analyses

Mean numbers of aphid predators from the groups Cantharidae, Coccinellidae, Dolichopodidae, Empididae, Linyphiidae, Neuroptera and predatory Staphylinidae were summed across all ten dates. Groups were chosen on the basis that they had been trapped in high enough numbers to enable meaningful analysis. Shapiro-Wilk non-normality tests and normality plots of invertebrate data confirmed that transformation was not necessary. Using R version 2.9.2, each of the group values were regressed against the proportional area of field margin habitat in m2 per hectare for buffers of radius's 50m, 100m, 250m, 500m, 750m and 1000m around the target fields. Adjusted r2 values obtained for each regression were plotted against each buffer radius to determine which scale best describes the relationship observed for each group (van Langevelde, 2000; Steffan-Dewenter et al. 2002). At 500m, 750m the buffer areas for two fields overlapped so aphid predator numbers were meaned across the two fields and plotted against the proportional area of field margin habitat for the combined buffer areas and an n of 11. At 1000m two pairs of fields both had overlapping buffer areas so again, aphid predator numbers were meaned as well as field margin areas. This reduced n to 10. (Table 3.2)

Table 3.2 number of data points used in the analysis for each buffer radius.

Buffer radius	50m	100m	250m	500m	750m	1000m
N	12	12	12	11	11	10

3.2.4.3. Aphid predator response to field margin proximity analyses

To determine if proximity to field margin was a significant factor in the number of aphid predators trapped in the target fields, the distance (in m) to the closest field margin was calculated for each trapping point within each field using Vertical Mapper (version 3.1) within MapInfo v8.0. The effect of field margin proximity on numbers of groups of flying predators was investigated using linear mixed effects models using the method of residual maximum likelihood (REML). Field margin proximity was assessed after adjusting for field by fitting the following model in Genstat (version 12.1.0): fixed effects = distance to closest field margin, random effects = field.

3.2.4.4. Aphid pot population response to field margin area

Percent aphid population changes were calculated between each count date for each aphid pot population. This percentage population change was then analysed to determine if the area of field margin surrounding the target field in which the aphid pot populations were located, were correlated with aphid population change. A repeated measures REML was conducted (in Genstat version 12.1.0) with fixed effects = field margin area and random effects = field*date. The date used was the mean Julian day (with the day the pots were put out set as zero) between the two dates used to calculate percentage population change. A separate REML analysis was carried out for each buffer.

3.2.4.5. Aphid pot population responses to field margin proximity

Aphid population response was calculated as the percentage difference between aphid population numbers for each pot between each successive date.

To test the effect of field margin proximity on aphid pot populations over time accounting for the field within which the pots were located, a repeated measures REML was carried out by fitting the following model in Genstat (version 12.1.0): fixed effects = distance to closest field margin, random effects = Julian date*field.

3.3. **Results**

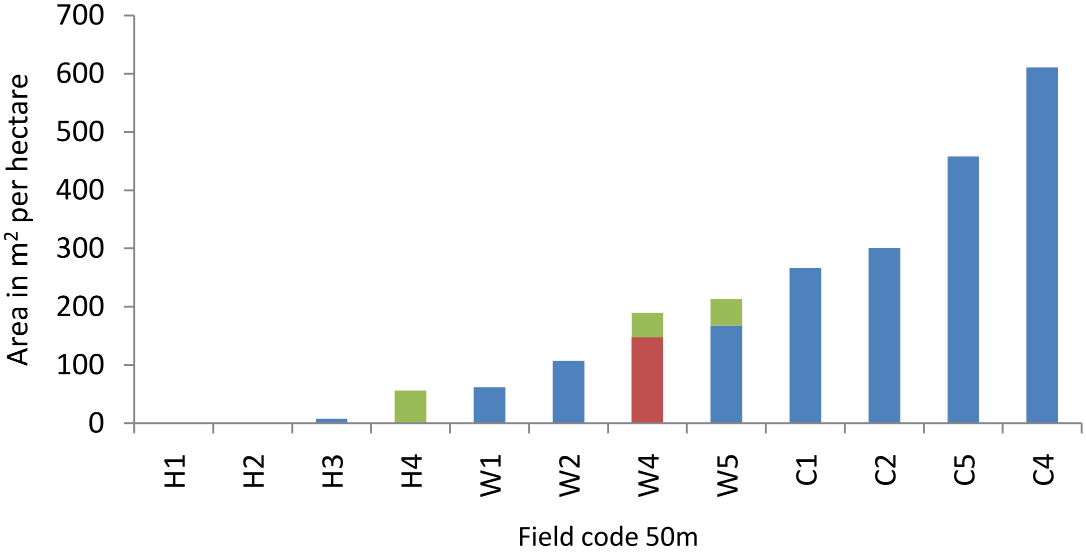
A breakdown of total numbers of aerially dispersing aphid predators trapped on the sticky traps for each trapping date is given in table 3.3.

Table 3.3 Total numbers of aerially dispersing aphid predator groups caught on the sticky traps for each of the ten trapping dates.

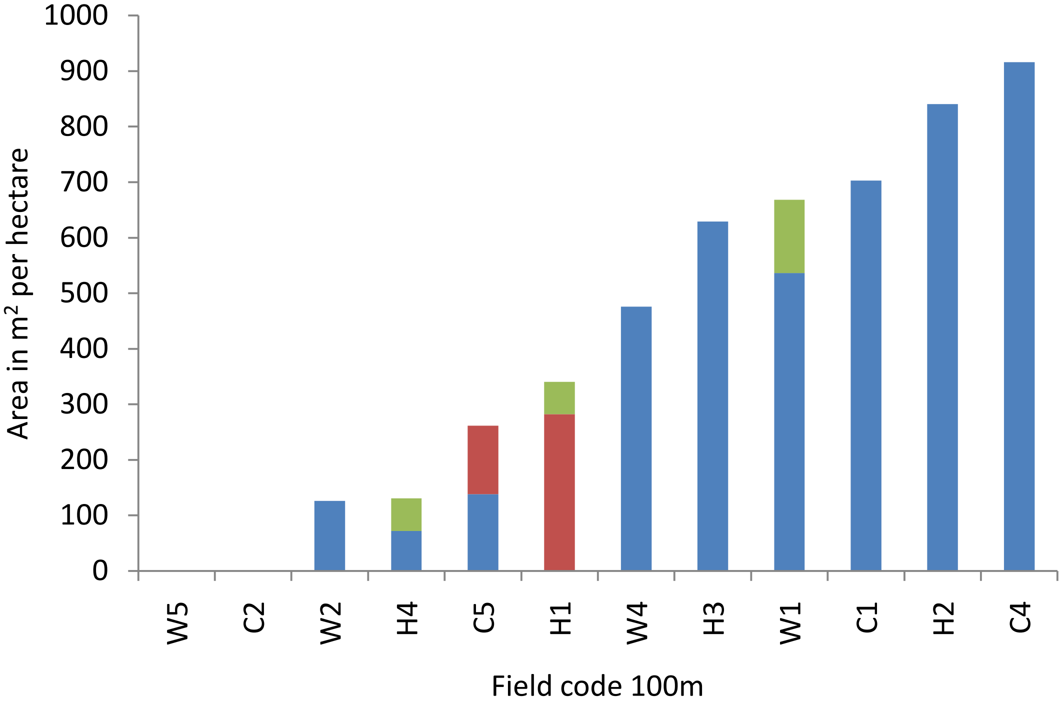
Date	Cantharidae	Carabidae	Coccinellidae	Dolichopodidae	Empididae	Predaceous *Tachyporus spp.*	Linyphiididae	Neuroptera	Syrphidae
3rd May – 10th May	0	8	10	1	37	128	34	3	132
10th May – 17th May	0	7	7	0	23	72	15	0	207
17th May – 24th May	1	0	0	0	46	0	6	0	217
24th May – 31st May	5	1	5	37	50	91	56	4	64
31st May – 7th Jun	33	7	89	23	30	349	192	1	21
7th Jun – 14th Jun	65	7	33	96	48	48	379	220	14
14th Jun – 21st Jun	84	3	17	214	232	38	332	347	16
21st Jun – 28th Jun	77	4	10	434	386	19	611	247	25
28th Jun – 5th Jul	191	5	39	618	102	45	343	106	34
5th Jul – 11th Jul	48	2	18	359	135	17	530	58	327
Sum over all dates	504	44	228	1782	1089	807	2498	986	1057

Predators that responded to field margins at the single field scale (see Chapter 2) were tested against the proportional area of field margin habitat at six landscape scales; Cantharidae, predaceous *Tachyporus spp.* (comprising of *T. hypnorum, T. chrysomelinus* and *T. obtusus*), Empididae and Linyphiidae. Other aerially dispersing aphid predators were not analysed due to increased model overparameterization (Aebischer, 2008, pers. comm.). Generalized linear model analyses were carried out to determine if other habitat types within the study areas were correlated with the proportional area of field margin habitat so field margins could not be said to be solely responsible for correlations with the aphid predator groups.

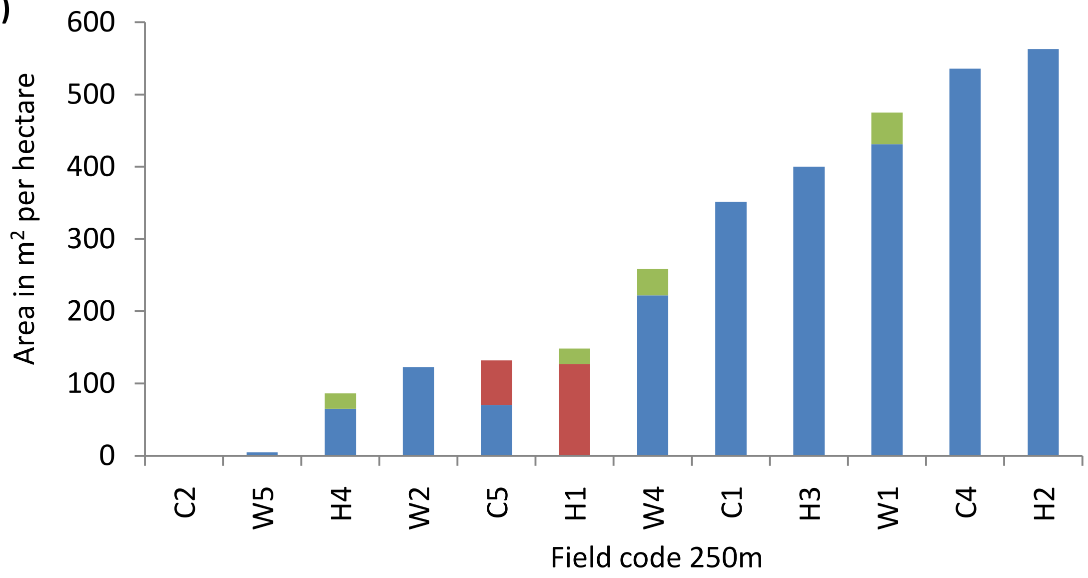
A)



B)

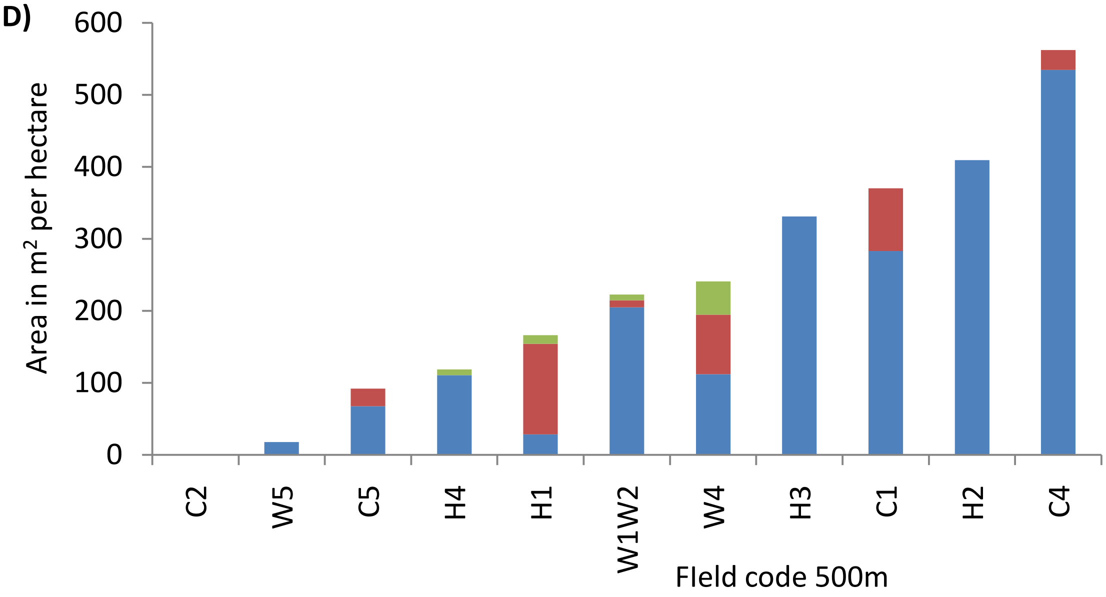


C)

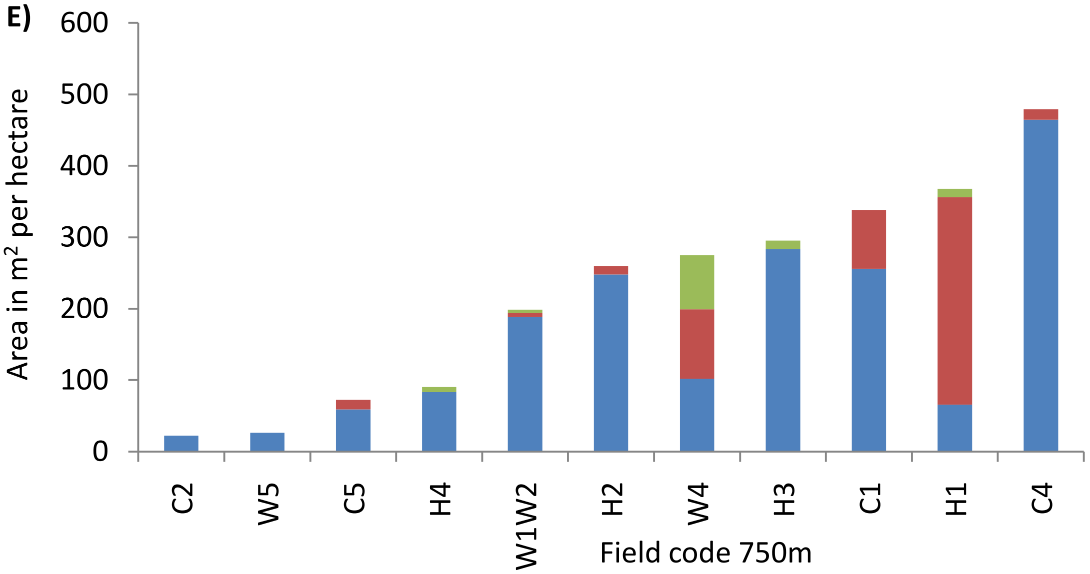


600
500
400
300
200
100
0
Area in m² per hectare
C2
W5
H4
W2
C5
H1
W4
C1
H3
W1
C4
H2
Field code 250m

D)



600
500
400
300
200
100
0
Area in m² per hectare
C2
W5
C5
H4
H1
W1W2
W4
H3
C1
H2
C4
FIeld code 500m



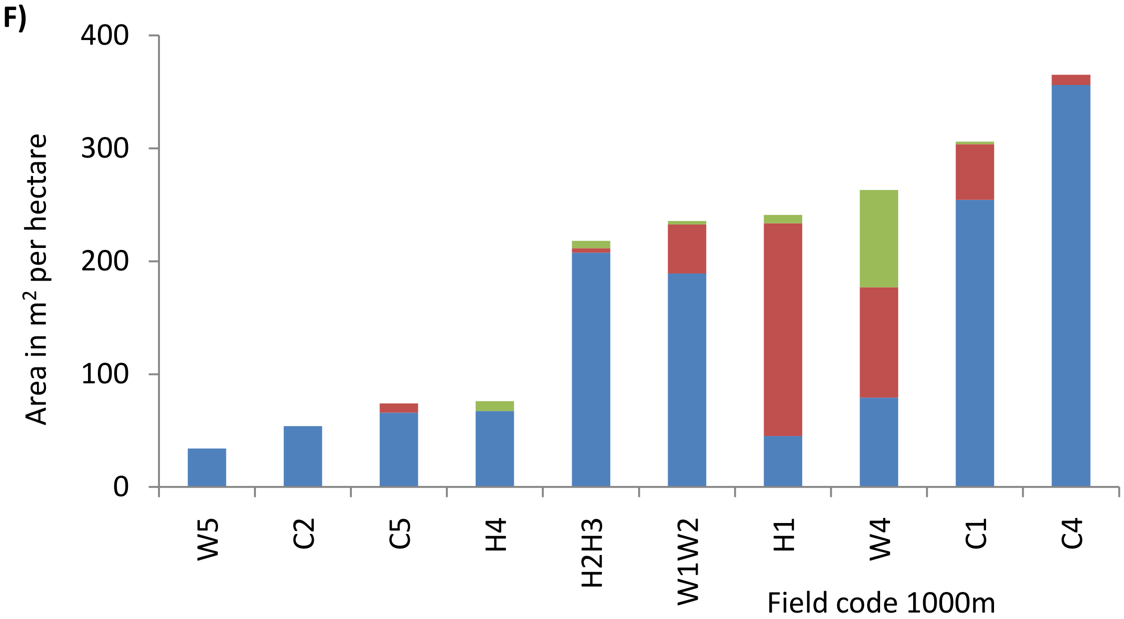


Figure 3.3 Relative proportions of field margins when divided into three types. Blue represents grassy margins/areas, red bars are field margins/areas with a floral component and green bars are beetle banks. A) 50m buffer radius (n = 12); B) 100m buffer radius (n = 12); C) 250m buffer radius (n = 12); D) 500m buffer radius (n = 11); E) 750m buffer radius (n = 11) and F) 1000m buffer radius (n = 10). Fields are ordered by field margin area per m^2 ascending. See table 3.4 for how the field margin types were categorised.

All buffer radiuses had variable field margin areas over the range of 12 fields (Figure 3.3). All five graphs show the majority of field margins were of the grassy type (see table 3.4 for categorisation of field margin types into these three groups).

Table 3.4 Classification of field margins into three groups based on their properties.

Grassy margins/areas	Florally enhanced margins/areas	Beetle banks
10m grass margins	20m wildflower strips	Beetle banks
2m grass margins	2m florally enhanced margins	
12m grass margins	6m florally enhanced margins	
2m natural regeneration strips	Wildflower and grass sown mix	
4m grass margins		
4m natural regeneration strips		
6m grass margins		
Wild bird mix strips		

3.3.1. Correlations between the proportional area of field margin habitat and other habitat variables

General linear models carried out between the proportional area of margin and percentage non-crop habitat, the proportional area of trees and the proportional area of hedges demonstrated autocorrelation between total proportional area of field margin habitat and percentage non-crop habitat at the 50m buffer radius only (table 3.5). The same model was applied to habitat densities of buffer radii 100m, 250m, 500m, 750m and 1000m and all results from these models were non-significant indicating no autocorrelation between the proportional area of field margin habitat and the other habitat variable measurements. The very high level of correlation at the 50m radius between the proportional area of field margin habitat and percentage uncropped land is due to, on average, 48% of uncropped land being field margin (this percentage is taken from the mean across all twelve fields for simplicity). The likelihood of non-crop habitat consisting of field margin in such close proximity of the sticky traps is high, hence the autocorrelation. At the next spatial scale (100m), the radii encompasses a large enough area for other non –crop habitat to form the majority (average across all 12 fields was greater than 72%) of non-crop habitat present, and for the other, larger, buffer radii.

Table 3.5 GLM results between the proportional area of field margin habitat (measured in m^2 per hectare) and three other habitat variables for 50m buffer radius (* = significant at <0.001 level).**

50m buffer radius (overall r^2 = 0.83, n = 12)	**Parameter**	**Standard error**	**t -value**	**P –valve**
Intercept	-46.959	63.561	-0.739	0.481
Hedges (m^2/hectare)	-0.097	0.616	-0.158	0.879
Trees (m^2/hectare)	-0.099	0.131	-0.755	0.472
Uncropped land (percentage)	71.664	13.242	5.412	<0.001***

3.3.2. The effect of proportional area of field margin habitat on flying aphid predators

A total of 492 aphid predating Cantharidae were captured in this study. Most were of the species *Cantharis lateralis* (Löbner & Hartwig, 1994) but aphid predating *Cantharis nigrians* (Vickerman and Sunderland, 1975) and *Rhagonycha fulva* (Harizanova, 1995) were also trapped. A total of 806 predaceous *Tachyporus spp*. (composing of 69% *T. hypnorum*, 18% *T. chrysomelinus* and 13% *T. obtusus*), 1087 Empididae and 2492 Linyphiidae were trapped in all twelve study fields over the 10 trapping dates. Simple regressions between the proportional area of field margin habitat and numbers of aphid predators trapped revealed significant correlations between numbers of Cantharidae and the proportional area of field margin habitat at spatial scales of 100m and 250m radii (Table 3.6). The Pearson product-moment correlation coefficient, *r*, at which the relationship was best described (250m) showed Cantharidae demonstrated a negative response to the proportional area of field margin habitat (Fig. 3.4).

Table 3.6 Correlation coefficients (*r*), coefficients of determination (r^2) and P- values (P) for each of the simple regressions for the four predator groups at all spatial scales regressed against the proportional area of field margin habitat. * = P <0.05; ** = P <0.01.

Predator group		**Scale**					
		50m	**100m**	**250m**	**500m**	**750m**	**1000m**
Cantharidae	*r*	-0.315	-0.651	-0.705	-0.564	0.509	-0.432
	r^2	0.098	0.424	0.497	0.318	0.259	0.186
	P	0.319	0.022*	0.010**	0.071	0.110	0.213
Predaceous *Tachyporus spp.*	*r*	0.368	0.388	0.404	0.659	0.729	0.758
	r^2	0.135	0.150	0.163	0.434	0.532	0.574
	P	0.239	0.212	0.193	0.027*	0.011*	0.011*
Empididae	*r*	-0.091	0.311	0.354	0.144	-0.169	-0.120
	r^2	0.008	0.096	0.125	0.020	0.028	0.014
	P	0.779	0.325	0.259	0.673	0.619	0.741
Linyphiidae	*r*	-0.137	-0.473	-0.436	-0.298	-0.299	-0.313
	r^2	0.018	0.223	0.190	0.088	0.089	0.097
	P	0.670	0.120	0.156	0.374	0.372	0.379

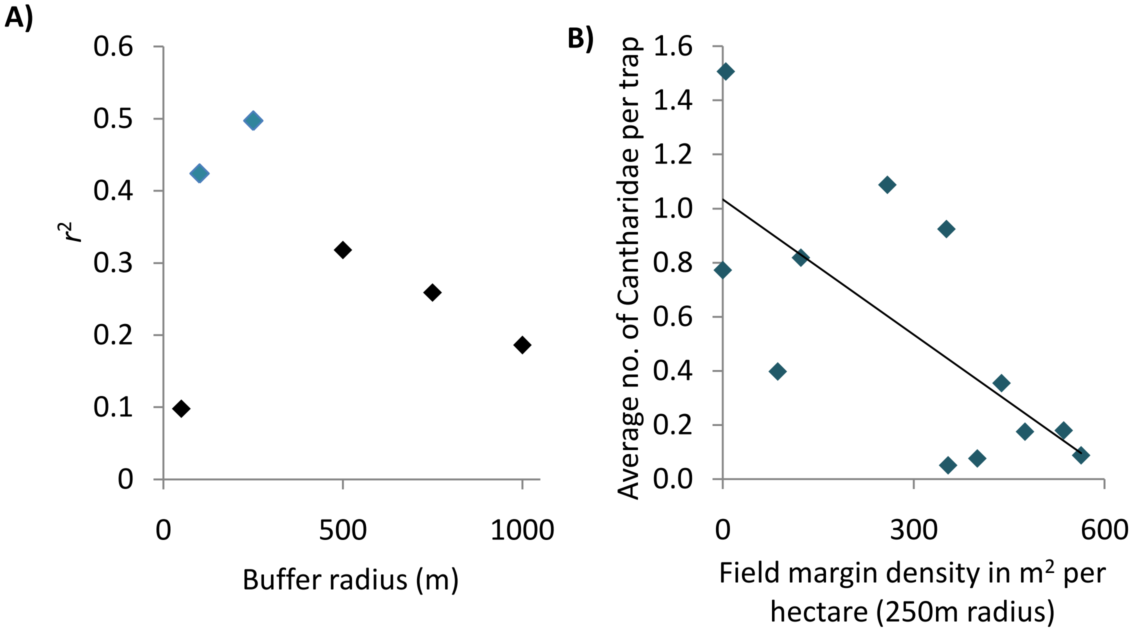


Figure 3.4 Correlations between the proportional area of field margin habitat (in m^2 per hectare) on numbers of Cantharidae for each spatial scale from 50m to 1000m. A) shows r^2 values for each of the simple regressions (see also table 3.6), blue coloured points indiciate a significant relationship at the 95% level. B) shows the relationship between Cantharidae numbers and field margin denisty for the regression at which the r^2 value is at it's highest; 250m. Equation for regression slope in B): $y = -0.0017x + 1.034$.

Cantharidae demonstrated the strongest relationship with the proportional area of field margin habitat at the 250m scale, although at 100m scale it was still statistically significant. The relationship observed for Cantharidae was a negative one; as the proportional area of field margin habitat increased the numbers of Cantharidae captured over the season decreased.

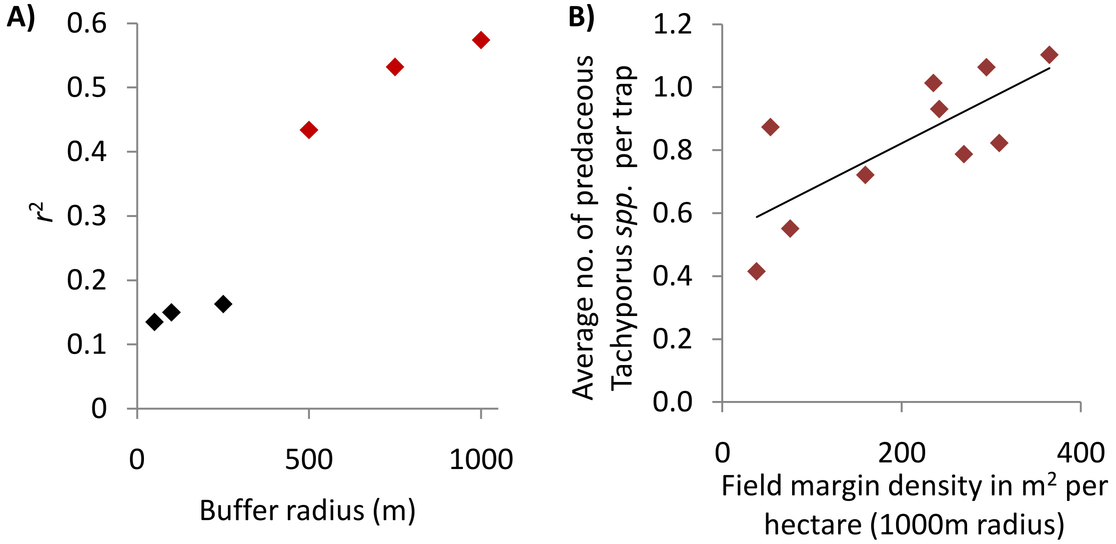


Figure 3.5 Correlations between field margin the proportional area of field margin habitat (in m^2 per hectare) on numbers of predaceous *Tachyporus* spp. for each spatial scale from 50m to 1000m. A) shows r^2 values for each of the simple regressions (see also table 3.6), red coloured points indiciate a significant relationship at the 95% level. B) shows the relationship between predaceous *Tachyporus* spp. numbers and field margin density for the regression at which the r^2 value is at it's highest; 1000m. Equation for regression slope in B): y = 0.0014x + 0.533.

Predaceous Tachyporus spp. numbers were significantly affected by the proportional area of field margin habitat at spatial distances of 500m, 750m and 1000m (Table 3.6). The relationship was at its strongest at 1000m radius. The relationship was a positive one; as the proportional area of field margin habitat increased so did the number of predaceous *Tachyporus* spp. found in the target fields.

Neither Linyphiidae nor Empididae exhibited any relationship between the proportional area of field margin habitat and numbers of individual predators trapped in each of the target fields at any spatial scale.

3.3.3. Correlations between field margin density on aphid pot populations

Aphid pot populations were unaffected by the proportional area of field margin habitat. There was a general decrease over time on numbers of aphids present on the plants (Table 3.7). The presence of rainfall post Julian day 14 hindered the aphid count results as cereal aphids are affected by rainfall which dislodges them from the plant (Winder, 1990). Even up to this date, however, aphid pot populations varied greatly within fields, with some pot populations increasing rapidly and others not surviving. Table 3.8 shows the lack of a detectable relationship between field margin as a proportional area and changes in aphid pot populations between counts.

Table 3.7 Mean number of aphids remaining on potted wheat plants on each Julian day by field. †Julian day 22 was not included in analyses due to high rainfall between Julian day 14 and 22

Field code	Julian day				
	3	8	10	14	22†
C1	53.1 ± 4.4	45.3 ± 8.2	41.9 ± 6.1	27.5 ±7.4	0.5 ±0.4
C2	67.1 ± 6.4	42.3 ± 9.2	45.9 ± 11.0	38.4 ± 10.6	0.5 ± 0.5
C4	48.6 ± 7.6	25.3 ± 6.1	27.0 ± 7.6	35.8 ± 11.4	6.0 ± 2.1
C5	57.8 ±5.8	45.5 ± 7.5	33.0 ± 8.7	17.9 ± 5.9	1.5 ± 1.1
H1	57.6 ± 7.9	50.1 ± 9.0	41.0 ± 9.3	32.0 ± 14.2	1.0 ± 0.5
H2	60.3 ± 6.1	52.8 ± 6.6	47.3 ± 11.9	19.5 ± 10.5	0.5 ± 0.5
H3	63.3 ± 7.1	56.2 ± 12.6	67.2 ± 14.8	61.3 ± 33.0	2.3 ± 1.4
H4	56.4 ± 4.3	43.9 ± 6.2	39.0 ± 6.0	21.8 ± 4.0	0.9 ± 0.5
W1	51.8 ± 6.0	77.1 ± 12.0	82.4 ± 16.5	50.8 ± 17.5	0.6 ± 0.5
W2	47.3 ± 7.0	46.4 ± 6.0	44.0 ± 4.0	31.7 ± 7.5	0.1 ± 0.1
W4	47.1 ± 7.8	34.5 ± 7.7	45.9 ± 7.6	34.8 ± 11.4	2.0 ± 0.7
W5	54.0 ± 8.5	38.9 ± 11.3	29.0 ± 10.2	19.1 ± 7.7	1.9 ± 1.2

Table 3.8 Results of repeated measures REML analyses on aphid population responses' (as a percentage) dependent on field margin area for each buffer radius. * = P <0.05.

Buffer radius	Explanatory	Wald statistic (n =384, 1 d.f.); X^2 probability
	Date	6.14; 0.016*
50m	Margin area	0.00; 0.986
	Date*Margin area	0.02; 0.886
	Date	6.13; 0.016*
100m	Margin area	0.03; 0.885
	Date*Margin area	0.00; 0.989
	Date	6.14; 0.016*
250m	Margin area	1.80; 0.972
	Date*Margin area	0.01; 0.909
	Date	5.33; 0.024*
500m	Margin area	0.01; 0.930
	Date*Margin area	0.06; 0.802
	Date	5.33; 0.024*
750m	Margin area	0.03; 0.888
	Date*Margin area	0.07; 0.787
	Date	4.17; 0.046*
1000m	Margin area	1.00; 0.769
	Date*Margin area	0.03; 0.857

3.3.4. Field margin proximity and aphid predators

Field margin proximity and aphid predator relationships were tested using REML models (section 3.4.4.2). Of the four predator groups tested (the same groups as tested in section 3.2.2) only Cantharidae exhibited a statistically significant response to field margin proximity (table 3.9). The estimated field margin effect of -0.013 (table 3.9) for Cantharidae indicates a negative response to field margin proximity when the effect of field is taken into account. So where the field margin distance increased, fewer Cantharidae were caught over the ten week trapping season.

Table 3.9 Results of REML analyses on the abundance of aphid predators as a response to distance from closest field margin. ** indicates X^2 probability significant at less than 1% probability level.

Predator group	Wald statistic (n = 96, 1 d.f.); X^2 probability	Estimated effects ± S.E.	
		Constant	Field Margin
Cantharidae	8.31; 0.005**	5.344 ± 1.889	-0.013 ± 0.005
Predaceous *Tachyporus spp.*	0.91; 0.354	8.521 ± 0.671	-0.003 ± 0.003
Empididae	0.39; 0.535	11.480 ± 2.386	-0.005 ± 0.007
Linyphiidae	0.39; 0.537	26.52 ± 3.165	0.006 ± 0.010

3.3.5. The effect of field margin proximity on aphid pot populations

There was no effect of field margin proximity on aphid pot populations. Again, aphid populations were not accurately measureable after Julian day 14 and were subject to large within-field variation. Table 3.10 shows the lack of a relationship between field margin proximity and the percentage difference of aphid pot populations between fields depending on the proportional area of field margins surrounding each field.

Table 3.10 Results of repeated measures REML analysis on percentage population differences between aphid numbers for each date response to distance from closest field margin. * indicates X^2 probability significant at less than 5% probability level.

Fixed effect	Wald statistic (n =384, 1 d.f.); X^2 probability	Estimated effects of fixed effects ± S.E. (Constant = 44.61 ± 1.785)
FM Distance	0.34; 0.617	-0.002 ± 0.008
Julian day	6.19; 0.015*	-2.053 ± 0.450
FM Distance & Julian day interaction	0.03; 0.860	-0.002 ± 0.002

3.4. **Discussion**

In this study, whether the proportional area of field margin habitat had an effect on aerially dispersing aphid predators and their aphid prey was examined, and, where possible, assessed over what spatial scales any effects on predators were occurring. Field margin habitat expressed as a proportional area had an effect on some of the key aphid predator species (section 3.4.1), and Cantharidae exhibited a slight negative response to field margin proximity (section 3.3.5). Field margins were determined as the sole contributor to varying key aphid predator numbers where affected, and this is discussed in detail in section 3.4.1.

3.4.1. Key aphid predator responses

The four key aphid predators for which the effect of field margin densities were examined were: Cantharidae, Empididae, Linyphiidae, and *Tachyporus* spp. Both the groups Cantharidae and *Tachyporus* spp. responded to the proportional area of field margin habitat, although in different ways, but neither Linyphiidae nor Empididae exhibited a response.

3.4.1.1. Cantharidae

Cantharis lateralis, the Cantharidae species most common in this study, have been seen to consume aphids in the field (Landis & van der Werf, 2007) and also, when trapped in winter wheat fields, have been proven to have consumed aphids in the majority of specimens trapped (Löbner & Hartwig, 1999). Cantharidae utilise pollen and nectar as a means of food and have been shown to be found in greater numbers in field margins that contain floral resources (Meek *et al*., 2002).

Within this study there was a very low percentage of field margins that were categorised as pollen and nectar mixes, or those that contained wildflowers, for example, at the 250m buffer radius only two of the twelve areas had field margins that were categorised as having a sown floral component. Despite this, Cantharidae still exhibited strong correlations to field margins as a whole. ‘Grassy’ field margins in themselves, through being an undisturbed habitat, are, however, more likely to contain some wildflowers, even if very low in number, that Cantharidae could potentially utilise (Critchley *et al*., 2006). Additionally, the provisioning of a field margin creates a buffer between within-crop processes and boundaries, such as hedgerows, increasing the presence of floral resources (Marshall *et al*., 2006) and providing a reservoir of alternative prey Meek *et al*., 2002).

The negative response of Cantharidae to the proportional area of field margin habitat was not predicted. The response of aphid enemies that use pollen and nectar as a resource would be expected to be localised as generally it is assumed that the enemies would disperse into the crop and return to a pollen and nectar resource when required. 'Spillover effects', or similar, are not well studied with respect to agricultural invertebrates (Rand *et al*., 2006) and, where they have been studied, the focus tends to be on primarily generalist predators' movements from overwintering sites (Sotherton, 1984, 1985; Wallin, 1985; Coombes & Sotherton, 1986; Holland *et al*., 1999; Denys & Tscharntke, 2002; Bonmarco & Fagan, 2002, Holland *et al*., 2008a). Few studies look at two-way movement to determine the overall population net effect between non-crop habitat and cropped fields (see Duelli *et al*., 1990) so it is unknown to what extent there is an attractant effect of non-crop habitats 'pulling in' beneficial predators from the fields. Sutherland *et al*., (2001) noted that the hoverfly, *Episyrphus balteatus*, whose larvae are aphidophagous, demonstrated a very positive association with wildflower habitat set up to encourage conservation biocontrol, and was rarely seen in the crop. Similarly, Kleijn & van Langevelde (2006) found greater numbers of species of hoverflies in areas with high numbers of flower abundance, but the sampling for this study was conducted in the boundaries themselves and not in cropped fields. Within this study it would seem that the presence of field margins draw cantharids away from the cropped habitat within which control is required.

3.4.1.2. Tachyporus *spp.*

Tachyporus spp. typically overwinter in extraneous grassy strip areas (Sotherton, 1984; Thomas *et al*., 1991) and have been shown to use field margins as an overwintering site (Pfiffner & Luka, 2000; Pywell *et al*., 2005), but also fly readily (Pedersen, 1990; Markgraf and Basedow, 2002). Through dispersal work, it was concluded that they disperse rapidly into fields in spring, primarily by flight (Coombes & Sotherton, 1986; Pedersen, 1990, 1999) but have also shown to exist in air columns at 200m altitude (Chapman *et al*., 2004). Previous studies looking at *Tachyporus* spp. dispersal have been at the single field scale. This study is the first to show that habitat manipulations exert a response in *Tachyporus* spp. populations over a far greater distance than has previously been considered. The high level of correlation observed between *Tachyporus* spp. and the proportional area of field margin habitat at the 1000m buffer radius (in this study on average encompassing an area 415 hectares in size) questions whether *Tachyporus* spp. respond to the proportional area of field margin habitat at a greater scale than present in this study. Previous work on *Tachyporus* spp. have conceded that they readily fly, but the use of flight interception traps as an alternative to pitfall traps is not common (Pedersen, 1990; Markgraf and Basedow, 2002). This study shows sticky traps are a suitable method for trapping *Tachyporus* spp. and provide more information on their movement than pitfall traps which focus on trapping beetles during relatively small scale localised dispersal (the largest area investigated using pitfall trapping was 64ha; Holland *et al*., 2005). As well as the large landscape area that *Tachyporus* spp. are shown to be influenced by, the response that they have to the proportional area of field margin habitat is a positive one. The average farm size that was encountered in conducting this study, including farms adjacent to those in which the target fields belonged, was far less than the average value of the 1000m buffer radius area (490 ha). As a result, the implementation of field margin habitats in neighbouring farms will have an effect on the numbers of *Tachyporus* spp. found in the farm being considered.

3.4.1.3. ***Empididae***

Empididae, despite being affected by the presence of a field margin in Chapter 2, showed no response to the varying proportional area of field margin habitat in this study. Empididae were not identified to species level so those species that feed on floral resources were not separated out from those that do not. In Chapter 2 it could be perceived that the florally enhanced field margins were in close proximity to the field in which trapping occurred, so attracting floral feeding Empididae species. Empididae are generalist predators and consume a wide range of arthropods as well as existing in many different types of habitat, therefore the lack of an effect on the proportional area of field margin habitat at the landscape scale is not surprising. Results from this study could be improved if solely flower-feeding species were identified, however, the lack of information on species that utilise floral resources and the huge number of species existing in general (worldwide estimate of 7,500 species: Cumming, 2006) and emerging from winter wheat fields (Jones, 1976) would make this task extremely difficult as yet. The low levels of florally enhanced habitat present in the landscapes could also compromise the result. Despite the lack of response detected by Empididae to the proportional area of field margin habitat at the landscape scale, the relatively large numbers present during the time aphid population increases and peak density still makes them potentially important aphid population suppressors.

3.4.1.4. Linyphiidae

Linyphiidae did not exhibit a significant response to the proportional area of field margin habitat at any of the spatial scales measured, despite the increase of Linyphiidae trapped in fields with field margin surrounds in Chapter 2 and the suitability of field margins as a source for Linyphiidae (Bell *et al*., 2002). Previously Schmidt *et al*. (2005) found Linyphiidae to exhibit positive correlations between percentage semi-natural habitat surrounding winter wheat fields, but only at landscape radii of 1060m and above; this size of area is just beyond the maximum of 1000m radii in this study. Schmidt *et al*. (2005) used the measure of non-crop habitat as a predictor of Linyphiidae abundance, which encompasses non-margin type habitats that Linyphiidae utilise such as grassland (Thomas & Jepson, 1999). Schmidt *et al*. (2005) also measured Linyphiidae density using a distance method, where as the sticky traps used in this study, as mentioned previously; act as a measure of activity-density. Linyphiidae dispersal by ballooning (Thomas, 1996) is known to be affected by several factors, such as disturbance (Halley *et al*., 1996), organic farming (Schmidt *et al*., 2005), meteorological conditions (Reynolds *et al*., 2007 and references within), and prey availability (Weyman & Jepson, 1994) and type of habitat from which dispersal is occurring (Thomas, 1996). Linyphiidae, due to their method of dispersal, seem to be affected by the presence of field margin type habitat at local scales (Chapter 2; Lemke & Poehling, 1997; Marshall *et al*., 2006) but beyond this, other, different factors such as alternative non-crop habitat may play a greater role in determining numbers in winter wheat fields.

3.4.2. Life history affects response scales to the proportional area of field margin habitat

The two aphid predator groups that were shown to be influenced by field margin area were not similarly collective in their response, which related to how they utilise field margin habitats. The two aphid predators that demonstrated a response to field margin the proportional area of field margin habitat differed in both the scale and type of relationship at which the proportional area of field margin habitat affected them. *Tachyporus* spp. (primarily composed of *T. hypnorum*) responded at a large scale of 1000m radius. Cantharidae were the other group to exhibit a relationship, but the relationship was fairly local and a negative one. The reaction of *Tachyporus* spp. to the proportional area of field margin habitat is likely to be a longer-term and at a large scale effect due to the time it takes to build up populations within suitable overwintering habitat; typically 1-2 years (Thomas *et al*., 1991; Thomas & Marshall, 1999; MacLeod *et al*., 2004). Cantharidae responded to the proportional area of field margin habitat at smaller spatial scales as they are influenced by ephemeral floral resources and therefore the response is likely to be a short term one. More research over several years is needed to clarify the potentially differing temporal responses to the proportional area of field margin habitat.

The lack of a response of aphid pot populations to the proportional area of field margin habitat may be due to several reasons. Aphid populations respond differently to many factors other than just the presence of predators (Dixon, 1977), although attempts were made to minimise the effects of differing soil and wheat types and growth stages through the use of trap plants. Also, the presence of artificially created 'islands' of high aphid populations in the field may have been encountered by a few predators with the capability to consume high numbers of aphids in a short space of time (e.g. *Adalia bipunctata* consumption rates; see Ellingsen, 1969) whereas other pot populations may not have been found. Overall the variability in the technique used in this study in an open system may have been subject to too many uncontrollable within field variables.

3.4.3. Non-crop habitat, hedges, field margins and landscape context

There were no correlations between field margins and non-crop habitat (at least at 100m buffer radius and above), tree cover and hedge area. This allowed conclusions based solely on field margins to be drawn. Previously, hedges were shown to be useful as overwintering sites for predatory Carabidae (Fournier & Loreau, 1999), can be a source of floral resources for hoverflies (Rothary, 1994) and have been shown to support high populations of predators although those that are able to fly are not present in large numbers (Pollard & Holland, 2006). Species of aphid predators that utilise hedges typically are of the Carabidae and Staphylinidae families and, in the study carried out by Pywell *et al*. (2005) there was not a preference for hedgerows over field margins by the two most abundant *Tachyporus* spp. in this study: *T. hypnorum* and *T. chrysomelinus*. Overall, in this study, field margins are of a greater benefit to enhancing numbers of aerially dispersing aphid predators that utilise field margins as an overwintering habitat.

The lack of any relationship between the area of non-crop habitat and numbers of aphid predators or predation is in contrast to previous work. Landscape scale studies are now fairly regularly carried out in which variable percentages of non-crop area is used as a determinant of landscape complexity and the subsequent effects examined on pest enemies (Steffan-Derwenter *et al*., 2002; Thies *et al*., 2003; Kruess *et al*., 2003; Theis *et al*., 2005; Roschenwitz *et al*., 2005; Clough *et al*., 2007). The quality of tracts of non–cropped land is also often overlooked. It is worth focussing research efforts into determining the locations and quality of habitat manipulations that can actually be implemented by farmers and landowners. Some studies state that the greatest positive effects on pest enemies are obtained when manipulations are placed in the simplest landscapes (Thies & Tscharntke, 1999; Östman *et al*., 2001; Tscharntke *et al*., 2002). As indicated in section 3.4.3.1, this requires co-ordination and knowledge on the habitats that will provide the greatest benefits to the predators being considered (Roschenwitz *et al*., 2005; Kleijn & van Langevelde, 2006).

The use of the proportional area of field margin habitat in this study as a potential causative effect in numbers of aerially dispersing aphid predators is unique since previous studies have used overall landscape complexity, generally measured as percentage arable land within a specified area, rather than a specific habitat type (e.g. Thies *et al.*, 2003; 2005). Field margins, or field margin type habitat such as beetle banks, are habitat types that have been shown to increase numbers of some aphid predators in adjacent fields (Collins *et al.*, 2002; Oaten *et al.*, 2007; Chapter 2), whereas other habitat types present in the UK landscape have not been evaluated in terms of providing aphid predators in winter wheat fields in the vicinity. The inclusion of 'untested' habitat types in landscape analyses may dilute any effect, if present, and is likely to account for the lack of correlations between all non-crop habitat and aerially dispersing aphid predators at scales of 100m and above. The results, especially for *Tachyporus* spp., iterate how important a network of field margin habitat throughout the landscape can be in potentially influencing numbers of aphid enemies in winter wheat fields.

3.4.4. Field margin proximity & variability

Field margin proximity was only found to be a factor in determining numbers of cantharids in winter wheat fields. At the spatial scales in this study, greater than the single field scale, field margin area seemed more important than proximity. Haenke *et al*., (2009) found a positive correlation between Syrphid abundance and flower densities; a similar relationship is likely to occur between area of overwintering habitat and numbers of overwintering predators.

The lack of variability in types of margin implemented on arable farms is also likely to be a decision based on economics. The cost of sowing grassy field margins is considerably lower than that of florally enhanced margins and this is reflected in the higher proportions of grass dominated field margins that surrounded the target fields, additionally, pollen and nectar areas require more regular sowing to prevent deterioration to grassy areas, unless managed correctly. The low prevalence of beetle banks is also fairly surprising considering the positive research that has been conducted concluding that they can be useful as a means of indirect pest control (Collins *et al.*, 2002) through the habitat provisioning for overwintering beetles (Thomas *et al.*, 1991; MacLeod *et al.*, 2004), although beetle banks are not common throughout England (Boatman *et al*., 2007). The very low percentage of field margin area that was composed of florally enhanced areas is likely to affect the types of aerially dispersing aphid predators trapped in this study, with fewer aphid predators that consume pollen and nectar being present. With so few farms having sown floral resources around them nationally (Boatman *et al*., 2007) even at the 1000m buffer radius, the investigation of solely florally enhanced resources or partitioning of field margin types could not be conducted.

3.4.5. Conclusions

This study is the first to detect a link between the proportional area of field margin habitat and numbers of *Tachyporus* spp. and highlights the necessity of agri-environment schemes to consider areas larger than farm scale when implementing IPM strategies. The potential of field margins to act as a sink for Cantharidae may limit their usage when considered as a pest control measure.

Chapter 4

Do aerially dispersing aphid predators utilise field margin resources directly and subsequently move into adjacent winter wheat fields?

4.1. **Introduction**

4.1.1. The effects of a floral field strip on aphid predator distributions

In previous chapters it has been shown that the presence of a field margin can significantly increase numbers of aphid predators in target fields at the local field scale, but at larger scales the proportional area of field margin habitat may have either a source or sink effect depending on the life history and ecology of the aphid predator in question. A local scale study was carried out examining how the presence of a floral field margin affected the distribution of aphid predators in adjacent fields and examined the direct use of a floral field margin by the Syrphid *Episyrphus balteatus*, whose larvae are aphidophagous.

4.1.2. Aphid and predator distributions

Aphids were found to be heterogeneously distributed within cereal crops, located in patches of higher density with few in the gaps between, but patches were dynamic through the season (Winder *et al.*, 1999). If a predator or predators are to respond rapidly, both temporarily and spatially, to reduce the aphid population before wheat damage occurs then they must be able to respond to these dynamic aphid patches (Bugg, 1992). The potential fast response of aerially dispersing aphid predators to aphid population patches makes them ideal for aphid control but, as seen previously, the presence of a field margin may present both a cost, by acting as a sink, and a benefit, by acting as a source of aphid predators. The majority of field margin habitats established under agri-environment schemes in England are comprised of grass margins (Boatman *et al.*, 2007), but pollen and nectar strips are an option within the Entry Level Scheme and Higher Level Scheme and aim to provide resources for a "range of nectar feeding insects, including butterflies and bumblebees" (DEFRA Handbook, UK, 2008). Many aerially dispersing aphid predators have been shown to use floral resources in field margins, through the identification of specific pollen species in the guts of insects tested, e.g. Hoverflies (Wratten *et al.*, 1995 & 2003; Bowie *et al.*, 1999) and marking techniques e.g. a range of predator species (Long, 1998). Additionally, the presence of floral resources has been shown to increase the numbers of some aerially dispersing aphid predator species in the vicinity (Harwood *et al.*, 1994) although a direct link between the utilisation of field margins and subsequent aphid control in adjacent cropped fields has not been proven (Wäckers *et al.*, 2006). The additional pollen and nectar resources may attract other natural enemies that can consume pollen and/or nectar e.g. Cantharidae and Empididae. Cantharidae are known to consume both pollen and nectar (Meek *et al.*, 2002; Traugott, 2003) but also prey upon aphids (Vickerman & Sutherland, 1975; Sutherland *et al.*, 1987; Landis & Van der Werf, 1997) and a selection of Empididae are also known to consume both nectar and invertebrate prey (Burkhill, 1946; Chvála, 1994; Preston-Mafham, 1999) but the effect that this has on their distribution and dispersal from the resource is not known. The floral enhanced field margins may also support an abundance of alternative prey for these predatory natural enemies. Previous studies on the effect of wildflower strips have tended to focus on hoverflies and have been mixed in their results. It is accepted that floral resources can enhance both the number of species and individual numbers of aphidophagous hoverflies (Cowgill, 1993a; Hickman & Wratten, 1996; Sutherland *et al.*, 2001), especially number of individuals of *E. balteatus* (MacLeod, 1999) which is the most numerous species of Syrphidae present in UK arable ecosystems (Dean, 1982; Chambers & Adams, 1986) but their subsequent distribution and movement into the crop is not clear. Very few studies have examined the effect of floral field margins on other aphid predators (Marshall & Moonen, 2002; Oaten *et al.*, 2007), and the subsequently the spatial distributions of aphid predators in the presence of a floral resource are not known.

Spatial distributions of predators in response to prey clustering can be used to determine the response of a predator to its aphid prey and subsequent potential value (Winder *et al.* 2005). Since aphid clusters in winter wheat are relatively immobile compared with their free ranging predators, their clusters can be mapped and compared with those of the predators, accounting for a time lag (Winder *et al.*, 2001; Sih, 1984). Using Spatial Analysis by Distance IndicEs (SADIE), developed by Perry (1995; see also Perry, 1998), geostatistical associations can be determined for predator and prey counts in clustered ecological count data where low numbers are likely to be recorded and gaps and patches are likely to be dynamic (Perry, 1996).

Previous studies using this statistical technique have shown that the polyphagous predatory beetle, *Pterostichus melanarius*, despite not relying solely on aphids for food, exhibited a positive association to aphid population clusters, allowing for a time lag (Winder *et al.* 2001). This technique also allows the effect of field boundaries to be taken into consideration when interpreting the results (Holland *et al.*, 2005).

4.1.3. Invertebrate marking techniques

Despite convincing evidence that field margin habitats do provide a resource for aphid predators, and can help to increase numbers of them where they are required, there is still little evidence proving a direct trophic link although this has been attempted through the use of mark-recapture methods. Various methods have been used with different levels of success and often involve physically marking the external surface of the insect with paint or dye (e.g. Narisu & Schell, 1999; Lavandero *et al.*, 2004), or etching the chintinous surface of the insect to provide a visually distinctive mark (Griffiths *et al*, 2001). These techniques suffer from the disadvantage of only proving that the invertebrate was in that specific location at that time. They also cannot provide information about the invertebrates' use of resources unless the animal's diet is then investigated using ELISA or molecular techniques. In addition, these techniques often require manipulation of the invertebrate in question which has often led to concerns over a resultant modification of behaviour and associated reduced survivorship and fitness costs either through the markers' visual appearance or effect of handling (Salazar *et al.*, 1997). Due to the numbers of invertebrates often required to ensure recapture of marked individuals, these techniques are also usually labour intensive (Hagler & Jackson, 2001).

The use of invertebrate "chemoprints" can be used to determine the origin of the invertebrate (e.g. Bowden *et al.*, 1985). This involves measuring levels and subsequent ratios of trace elements within an organism and using these ratios to determine origins. This method can be manipulated by artificially raising the level of a trace element through liquid application onto the resource area and detecting the subsequent raised levels in invertebrates that have used the resources either directly, such through feeding on the vegetation sprayed, or indirectly, through preying on marked organisms. The element rubidium was first suggested by Berry (1972) as a "self-marker" and has remained the elemental marker of choice since it is easy to use as a salt (rubidium chloride) and the methods of detection, usually using a method of Atomic absorption spectrophotometry (AAS), are sensitive enough to pick up elevated levels that confer no disadvantage to the invertebrates' fecundity, longevity or behaviour (Polavarapu *et al.*, 1992; van Steenwyk *et al.*, 1992; Qureshi *et al.*, 2004 and Pickett *et al.*, 2004). Organisms pick up rubidium through consuming rubidium chloride. Rubidium is analogous to potassium and replaces some of the potassium in the tissues of the organism. Once exposure to rubidium ceases the extra rubidium is excreted and levels of rubidium in the organism return to normal levels. This can create a problem for rubidium marking studies since the excretion of rubidium is dependent on the metabolism and feeding rate between invertebrate individuals as well as between species (Long, 1998). This limits the length of time that field studies can be carried out for without obtaining false negative readings due to prior expulsion of rubidium from the invertebrates' tissues.

For this study rubidium chloride was a suitable identifier since it can be used to mark many individuals at once, is not especially labour intensive and proves actual utilisation of the resource (in this case a pollen and nectar field margin), whilst natural behaviour, longevity and fecundity are unaffected. In particular, it was a requirement that the insects used were already present in the field and were not being reared, marked and released due to the effect this could have on dispersal mapping. The temporal aspect was also anticipated not to be problematic as local field scale movements that occur over a few days were being measured rather than long term, large scale movements.

Previously, rubidium chloride has been tested for its efficacy as a marker of aphids and their enemies both in the laboratory, including aphids of the species *Acyrthosiphon pisum* (Frazer & Raworth, 1974), *Myzus persicae* and *Macrosiphum euphorbiae* (Guillebeau *et al.*, 1993) and parasitoids of *Sitobion avenae*, *Aphidius* *rhopalosiphi* (Mutatori *et al.*, 2005). In the field it has been used to mark parasitoids (Fernandes *et al.*, 1997 and Scarratt *et al.*, 2008) and a range of predators (Long, 1998 and Prasfika, 2004), but its use to mark and evaluate the use of non-crop habitats by natural enemies is still in its infancy. This study is the first time that rubidium chloride's suitability has been tested to mark hoverflies of the species *E. balteatus*[1] and the Coccinellid *Adalia bipunctata* and also the first step in using such a marker to evaluate the effectiveness of pollen and nectar mixes at providing resources for aphid predators.

The hoverfly, *E. balteatus*, was chosen as the study species as it has a life history suited to examining it's movements between a floral strip and surrounding cereal fields using rubidium chloride as marker for several reasons:

- The adults are solely pollen and nectar feeders (Stubbs & Falk, 2002) and the females especially require pollen and nectar for egg development (Schneider, 1969) so consume pollen and nectar around the time of aphid population growth in order to maximise their reproductive success.

- Females search for aphid colonies within which to lay their eggs (Scholz & Poehling, 2000).

- Hoverfly larvae have been shown to be voracious aphid predators (Tenhumberg & Poehling, 1995) and therefore are able to control aphid population outbreaks if they exist in large enough numbers (Chambers & Adams, 1986) so can be considered to be extremely useful as an aphid control measure.

4.1.4. Hypothesis, objectives and aims.

Hypothesis:

Aerially dispersing aphid predators utilise field margin resources directly and subsequently move into adjacent winter wheat fields.

---

[1] Long, 1998, may have marked Syrphidae of the species *Episyrphus balteatus* but this is not referred to in the text, only species belonging to the genus *Toxomerus*.

Objectives:

1. Determine if rubidium chloride can be used successfully under field conditions to mark aphid predators that either i) feed on aphids directly such as *A. bipunctata* or ii) rely on floral resources to maximise production of aphidophagous larvae, such as *E. balteatus.*

2. Examine the movements of *E. balteatus* post feeding on rubidium labelled forage plants and subsequent dispersal into adjacent cereal fields.

3. Examine the spatio-temporal distributions of aerially dispersing aphid predators in the presence of a sown pollen and nectar field margin and relate their distribution to that of aphids within the cereal crop.

Aims:

Determine whether rubidium chloride can be used successfully in an open system to mark aphid predators.

Determine whether the presence of a floral field margin affects the distribution of aerially dispersing aphid predators and if pollen and nectar resources in field margins are utilised by aerially dispersing aphid predators.

4.2. **Methodology**

4.2.1. Rubidium marking - Pilot study

A 6m wide sown flower-rich margin was selected that had been sown with:

5% certified common bentgrass (*Agrostis capillaries*)
10% certified crested dogstail (*Cynosurus cristatus*)
20% certified smaller catstail (*Phleum bertolonii*)
15% certified sheep's fescue (*Festuca ovina*)
20% certified red fescue (*Festuca rubra*)
20% certified smooth meadow grass (*Poa pratensis*)
2% lesser knapweed (*Centaurea nigra*)
1% field scabious (*Knautia arvensis*)
1% self heal (*Prunella vulgaris*)
1% yarrow (*Achillea millefolium*)
1% ox-eye daisy (*Chrysanthemum leucanthemum*)
1% lady's bedstraw (*Galium verum*)
1% meadow buttercup (*Ranunculus acris*)
1% sorrel (*Rumex acetosella*)
1% wild carrot (*Daucus carota*) (Cotswolds seeds, Gloucestershire, UK)

On the floristically enhanced field margin thirty cages were set up, spaced at 5m apart, during early June 2008. Each cage consisted of a plastic ring, 1m in diameter, which was dug into the soil surface, ensuring minimal disturbance to the area inside the ring, and any gaps were filled with damped calcium bentonite to ensure a seal and stopping entry and exit of any invertebrates. A cylindrical net tent was attached to the ring using tape and extended upwards to a height of approximately 1.2m. The net was sealed at the top to a central cane post pushed into the earth to create an enclosed cage. Each cage was hand searched and any large invertebrates removed. Fifteen of the cages were selected at random to be sprayed with 87ml (a ten second spray) of 3000ppm rubidium chloride solution (the treatment) and the other fifteen with 87ml of distilled water (the control). After spraying, three two-spot ladybirds, *A. bipunctata,* and four recently hatched hoverflies, *E. balteatus*, both species purchased from Koppert UK Ltd., were released into each cage. Releasing them post spray helped to prevent them from picking up the mark solely through external contact. After 72 hours the enclosures were hand searched and any *A. bipunctata* and/or *E. balteatus* found were pootered and placed in individual tubes and returned to the lab in a coolbox. Once back at the lab they were immediately frozen to -20 deg C. and subsequently processed and analysed for the presence of rubidium using a flame emission atomic absorption spectrophotometer (FE-AAS) (see section 4.2.3).

4.2.2. Rubidium marking – large scale field study

4.2.2.1. Predator sampling

The main study was carried out at Benham Drove Farm, Nether Wallop, UK (51°08′12.90″N, 1°36′34.82″W). The site consisted of a sown pollen and nectar strip 10m wide and 0.5km long (total area 0.5 hectares) directly adjacent to a winter wheat field (Figure 4.2). This was sown as part of the Higher Level Scheme (DEFRA website, Environmental Stewardship Handbook, 2005; see Chapter 1, section 1.5.1). The area was mapped using a Trimble Explorer 3C handheld GPS device accurate to 0.5m and subsequently a grid of 77 sticky trap stations were located in the cropped area of the winter wheat field and close by (Figure 4.2) each trap being located 60m from the other. Each sticky trap station consisted of two 360 degree clear sticky traps (32 x 21 cm) above crop level orientated in along a north-south line, but due to low numbers of aphid predators trapped on them during dates 1 and 2, during trapping date 3 and 4, a yellow sticky trap (20 x 40 cm) was also attached to the central posts of each trapping station. The yellow sticky traps were located below the top of the crop to ensure they were only visible to aerial fauna that came within approximately 3-5m of the trapping station. This was to ensure that any insects attracted by the yellow colour were not artificially attracted from other areas, especially by the yellow traps located next to the pollen and nectar strip, but were attracted to the trap as they flew within a 3-4m radius of the yellow sticky traps. All aphid predators were identified on all the sticky traps. Table 4.1 shows the aphid count, rubidium spraying and trapping timetable for this study.

Table 4.1 Aphid counts, rubidium chloride spray and trapping timetable

Date	Action
23rd June	First rubidium chloride spray on pollen and nectar strip
24th June	Date 1 cylindrical sticky traps set
25th June	Date 1 Aphid count
28th June	Date 1 cylindrical sticky traps collected, date 2 traps set
30th June	Date 2 Aphid count
2nd July	Date 2 traps collected
13th July	Second rubidium chloride spray on pollen and nectar strip
14th July	Date 3 cylindrical and yellow sticky traps set
16th July	Date 3 Aphid count
18th July	Date 3 cylindrical sticky traps collected, date 4 traps set
22nd July	Date 4 traps collected

The pollen and nectar strip was sown with the following species:

20% Meadow fescue (*Festuca pratensis*)
20% Creeping red fescue (*Festuca rubra*)
10% Cocksfoot (*Dactylis glomerata*)
10% Timothy (*Phleum pratense*)
15% Tall fescue (*Festuca arundinacea*)
5% Smooth stalk meadow grass (*Poa pratensis*)
3% Red clover (*Trifolium pretense*)
5% Sainfoin (*Onobychis viciaefolia*)
3% Alsike clover (*Trifolium hybridum*)
3% Birds foot trefoil (*Lotus corniculatus*)
3% Black medick (*Medicago lupulina*)
3% Common vetch (*Vicia sativa*)

4.2.2.2. Vegetation sampling

Vegetation sampling was carried on the 11th July 2008 to determine the number and species of plants flowering during trapping. This consisted of identifying and counting the number of flowers (or flower heads) of each species within a $1m^2$ quadrat placed at 10m intervals along the length of the floral strip, but randomly positioned width ways across the strip. The same flower sampling technique was carried out for the other habitats surrounding the field which included a beetle bank and field boundaries. This was to assess the attractiveness of habitats other than the floral strip to flower feeding aphid predators.

4.2.2.3. Aphid counts

Aphid counts were carried out during three of the four trapping dates. At each of the trapping points 25 tillers of wheat were selected at random in a 5m radius of the trapping station. Numbers of each species of aphid (*S. avenae*, *M. dirhodum*, or *R. padi*) were counted and their location on the tiller (ear, flag leaf, or lower) were recorded. Alate aphids were indicated, as were parasitized aphids as far as it was possible to determine. Aphid counts were pooled across the 25 tillers at each point for analysis.

Figure 4.1 Photograph showing a single trapping station, there are two yellow sticky traps per trap, one is the other side of the central post facing in the opposite direction.

4.2.2.4. Rubidium spraying and trapping timetable

2g per litre of powdered rubidium chloride (RbCl) was added to 125 litres of reverse osmosis water to give a 2000ppm RbCl concentrate and the 125 litres sprayed evenly over the 0.5 hectare pollen and nectar block using a handheld backpack sprayer with a 1m boom configured to spray an area 1.5m wide with no spray overlap. The concentrations of 1000ppm and 2000ppm of rubidium chloride have previously been shown to be suitable for marking parasitoids in the field (Scarratt *et al.*, 2008), so it was assumed from the very high rubidium levels in the invertebrates from the pilot study that a concentration of 2000ppm would be more than adequate. Spraying was conducted during suitably calm, dry meteorological conditions in the evening to prevent excessive evaporation of the solution and to maximise the potential for the sprayed plants to absorb and translocate the rubidium in the rubidium chloride solution. The day after spraying the sticky traps were operated for a period of 12 days, replacing the traps with fresh ones at 4-day intervals. All traps were frozen as soon as possible after collection to kill and preserve the invertebrates on them. Due to time and economic constraints it was decided to focus on just the hoverflies trapped on the yellow traps during trapping date 3 and analyse them for rubidium. As higher numbers of *E. balteatus* were caught than predicted, each yellow trap was divided into two and only *E. balteatus* caught on the upper half of the trap sexed. Fifty percent of the sexed females were subsequently analysed for the presence of rubidium. In the case of decimals, the number was randomly rounded up or down.

Flower heads and leaves closest to the flower head of the clover species *T. hybridum* were collected at random points along the sprayed pollen and nectar block during dates 13th July (pre-rubidium spray) and post spray on 14th, 18th and 21st July. The rubidium content of *Trifolium hybridum* was chosen as greater numbers of inflorescences were present during invertebrate trapping than any other species (see section 4.2.2.2). Clover samples were washed and separated into flowers and leaves. They were then processed following the protocol in section 2.2.3., but post drying were crushed and weighed to give a total dry weight per sample of approximately 10.0 mg. Ten samples of each type were analysed.

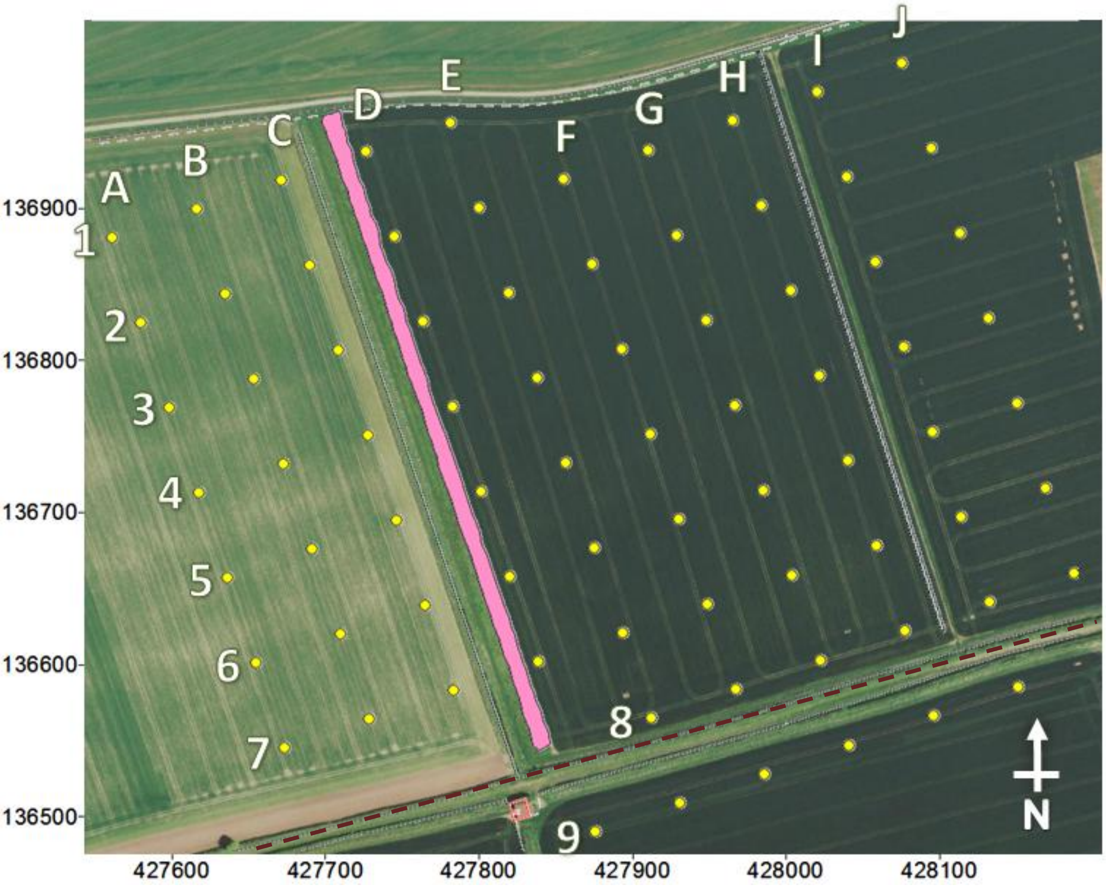


Figure 4.2 Map of the site and sticky trap stations (yellow dots). The 500m by 10m wide floral strip is indicated in pink and the beetle bank in dark turquoise. A farm track with large hedges either side runs along the bottom of the image with one row of traps to the south of the track (indicated by the maroon dashed line). All dark green fields are winter wheat and the lighter green field to the left is winter barley. This aerial photo was taken pre crop maturation at near the beginning of the season. The numbers that run along the left-hand side and along the bottom are the British National Grid co-ordinates for the site, other letters and numbers are trapping station identifiers.

4.2.3. Rubidium analysis

Rubidium analyses were carried out on both the *A. bipunctata* and *E. balteatus* from the pilot study and female *E. balteatus* from the main study. In addition, clover leaf and flower samples were taken at random from the pollen and nectar strip in the main study to examine the concentration of rubidium in them.

Forty-three *E. balteatus* were obtained from sticky traps used in another study at around the same time but the control sticky traps were located approximately seventy miles away from the main study site. Control clover samples were also taken from a different site on the same farm. For the pilot study, the rubidium levels of the *A. bipunctata* and *E. balteatus* from the control tents were used to determine a baseline rubidium concentration for each species.

Insect/plant digestions and rubidium analyses were carried out using the following protocol: Hoverflies were removed from the sticky traps and rinsed in Histo-Clear II (Agar scientific, Essex, UK) followed by 98% ethanol to ensure complete removal of the sticky substance and external rubidium mark, all other samples were rinsed thoroughly with reverse osmosis water to remove any external rubidium marker. The samples were then dried for 48 hours in a drying oven at 60 deg C and subsequently weighed. Each sample was digested in 150 µL HNO_3 for 24 hours at 30 deg C. and 150µL of 30% H_2O_2 solution added and maintained at 30 deg C for 24 hours to complete the digestion. Each sample was then diluted in 2.1mL of MilliQ water to give a total solution volume of 2.4mL in order to have enough fluid for analysis. Digested samples were then run through an Atomic Absorption Spectrophotometer (Varian Spectra AA200) with a rubidium lamp with an absporption wavelength of 780nm. Rubidium standards of 0.0, 0.2, 0.5, 0.7, 1 and 5ppm were used for calibration; these were obtained through dilutions of 1000ppm of trace analysis grade rubidium chloride solution (ICP ARISTAR, VWR Scientific, UK). The GF-AAS was set for a pre- rinse time of 5 seconds and a read time of 5 seconds. Recalibration of the AAS occurred every 10-15 samples using the standards. The parts per million values were divided by their dry weight to give a rubidium concentration in µg for each sample.

4.2.4. Statistical analyses

4.2.4.1. Pilot study

Firstly Welch's two-sample t-tests (due to unequal sample sizes) were carried out on rubidium concentrations measured in µg per insect ($\log_e$ transformed + 1) for both *A. bipunctata* and *E. balteatus* recaptured in control and rubidium chloride treated tents. These were to determine if there was a significant difference in rubidium concentrations between treatment and control individuals. Secondly, threshold levels of rubidium concentrations were calculated from insects recaptured in the control tents to determine the percentage of individuals that were successfully marked. An individual insect was considered marked if its rubidium concentration exceeded the mean plus three standard deviations of the concentrations of rubidium in the controls. This is the standard procedure to obtain a rubidium concentration threshold (Stimmann, 1974).

4.2.4.2. Large field scale study: Aphid predator distributions

SADIE analyses were used to determine if there were significant levels of patchiness in the distributions of aphid predators. Subsequently red-blue SADIE plots were also used to determine if there were significant associations or dissociations between aphids and aphid predators. To allow for the effect of a time lag between prey location and potential consumption, aphid numbers for dates 1 and 3 were compared with predator numbers for dates 2 and 4 respectively.

SADIE analyses were carried out on individual data sets to determine spatial distributions and subsequently associations were run between the cluster indices data to determine the spatial similarity between data sets.

SADIE red-blue analyses (single data set counts) identify areas of patch clustering using the positive index v_i and its associated probability P_i, and gap clustering using the negative index v_j and its associated probability P_j. Values around unity indicate random distributions. Positive values, where $v_i > 1.5$, indicate patches where clusters are one and a half times greater than that expected from a random arrangement of counts, and negative values $v_j < -1.5$, indicate patches where clusters are one and half times fewer than expected from a random arrangement of counts.

Distribution maps of red-blue SADIE single data analyses were created using Surfer for Windows Version 6.04 (Golden Software Inc., Golden, Colorado, USA). To determine if two data sets are statistically correlated, correlation coefficients, X, were determined between clustering indices of the two data sets being considered (methodology described in Perry and Dixon, 2002). X significance was determined through values obtained from a randomisation test (X_{rand}) that also provided a P_D

value via Dutilleul (1993) adjustment procedure. Positive coefficients indicate spatial association, negative coefficients; spatial dissociation. X and P_D values at less than the 5% statistically probability interval were considered significant. ($P_D < 0.025$ or $P_D > 0.975$)

4.2.4.3. Large scale field study: rubidium marking thresholds and subsequent dispersal and distribution

The forty-three control *E. balteatus* samples were meaned and a threshold value of rubidium concentration in µg per hoverfly calculated. All *E. balteatus* rubidium values in µg per hoverfly from the main study were compared to this value and those that exceeded it were considered to be successfully marked. The overall spatial pattern of marked *E. balteatus* was analysed to determine if there was a significant level of clustering using SADIE.

SADIE analysis was used to analyse the spatial distribution of marked hoverflies. The numbers of marked hoverflies were converted to proportions at each date with the denominator being the number of unmarked female hoverflies trapped on the analogous yellow stick trap. Since SADIE has been developed specifically for count data (Perry, 1995) and not for data that have been transformed through the usual methods ($\log_{10}$, arcsine square root etc.), the marked/total hoverfly proportions were multiplied by 100 to give whole integer data (Conrad, personal communication, 2008). Data were then analysed using SADIE in the usual way. It should be noted that it does not matter what order of magnitude the data are multiplied by, the ability of SADIE red-blue to detect clusters does not change (Conrad, personal communication, 2008).

4.3. **Results**

4.3.1. Rubidium marking pilot study

Both t-tests between rubidium levels in control and rubidium exposed *E. balteatus* and *A. bipunctata* were significant at the 95% confidence level (*E. balteatus*: t = -15.03, df = 8.10, P<0.001; *A. bipunctata* t = -4.73, df = 9.87, P<0.001 on $\log_e+1$ transformed data). All of the hoverflies exposed to rubidium were marked beyond the threshold value of 2.212 µg per individual (Mean of 0.628 plus 3* the standard deviation value of 0.528) and contained, on average, one hundred and forty times more rubidium than those in from the control. Of the *A. bipunctata*, nine of the ten individuals exposed to rubidium were marked beyond the rubidium threshold level of 3.742 µg per individual (Mean of 0.913 plus 3* the standard deviation value of 0.943) and, of those successfully marked, contained, on average, one hundred and fifty times more rubidium than those from the control tents.

4.3.2. Main study: Spatial distributions of aphids and their predators

There were very high numbers of Empididae, Dolichopodidae, alate aphids and Syrphidae caught on bottle traps and even greater numbers of Empididae, Dolichopodidae and Syrphidae on yellow sticky traps. Table 4.2 shows numbers trapped by date and insect family for both cylindrical (A) and yellow (B) sticky traps.

Aphids were not counted on yellow traps due to separate within field counts and both alate and wingless morphs being caught on them since the traps were located below the crop canopy.

Table 4.2 Total numbers of each group of flying aphid predators trapped on cylindrical sticky traps (A) and yellow sticky traps (B) for each trapping date.

A

Cylindrical sticky traps	**1**	**2**	**3**	**4**
Cantharidae	2	3	40	15
Dolichopodidae	116	117	194	134
Empididae	313	295	183	226
Female *E. balteatus*	22	6	281	322
Male *E. balteatus*	0	1	247	211
Female Syrphidae other than *E. balteatus*	45	31	42	102
Male Syrphidae other than *E. balteatus*	7	3	36	60
Alate Aphididae	1428	3541	1010	719
Tachyporus spp.	12	23	9	20

B

Yellow traps	**3**	**4**
Cantharidae	138	49
Dolichopodidae	596	595
Empididae	4241	4641
Female *E. balteatus*	1728	945
Male *E. balteatus*	1308	641
Female Syrphidae other than *E. balteatus*	0	0
Male Syrphidae other than *E. balteatus*	0	0
Tachyporus spp.	3	2

4.3.2.1. Aphids

All SADIE red-blue analyses demonstrated patchy distributions when trapped above the crop (cylindrical sticky traps) but only date 2 aphid tiller counts demonstrated a patchy distribution (Table 4.3). Despite the lack of significant patchy distributions demonstrated by date 1 and date 3 aphid tiller counts, it was considered useful to determine if significant associations existed between aphid tiller counts and those trapped on cylindrical sticky traps.

Table 4.3 Results from SADIE single association tests for aphids trapped on cylindrical sticky traps and yellow sticky traps for each date of trapping. *P* * <0.05; *P* ** <0.01; *P* * <0.001.**

	Aphid tiller counts			Cylindrical sticky trap counts			
	Date 1	Date 2	Date 3	Date 1	Date 2	Date 3	Date 4
I_a	1.245	1.619	1.132	1.562	2.231	1.663	1.390
P	0.08	<0.01**	0.20	<0.01**	<0.001***	<0.01**	0.03*

SADIE association tests were carried out between aphid counts and alate aphids found on the cylindrical sticky traps for each of the three dates (date 4 has no analogous aphid count). Although few aphids were found through assessing their numbers on the wheat tillers, their spatial distribution was strongly associated with that determined from the cylindrical sticky traps (Table 4.5). The size of the clusters, however, was much smaller for the tiller counts as opposed to those determined from the bottle traps (Table 4.4) indicating that the latter may be a more effective way of determining the extent spatial distributions of aphid numbers, when relatively low, in cereal crops.

Table 4.4. Total numbers of aphids counted in the crop on the tillers and numbers of alate aphids trapped on cylindrical sticky traps.

Aphid count dates	Count	Aphid sticky trap dates	Alate count
25th June	248	28th June	1428
30th June	84	2nd July	3541
16th June	23	18th July	1010
n/a	n/a	22nd July	719

Table 4.5. Association indices between aphids counted in the crop and aphids trapped on cylindrical traps for each of the three trapping dates. (P_D * <0.025 or >0.975; P_D ** <0.01 or >0.99; P_D * <0.001 or >0.999).**

Counts		Sticky traps	X	P_D
Count 1 all aphids	vs.	Date 1 Cylindrical sticky traps all aphids	0.501	<0.001***
Count 2 all aphids	vs.	Date 2 Cylindrical sticky traps all aphids	0.568	<0.001***
Count 3 all aphids	vs.	Date 3 Cylindrical sticky traps all aphids	0.400	<0.001***

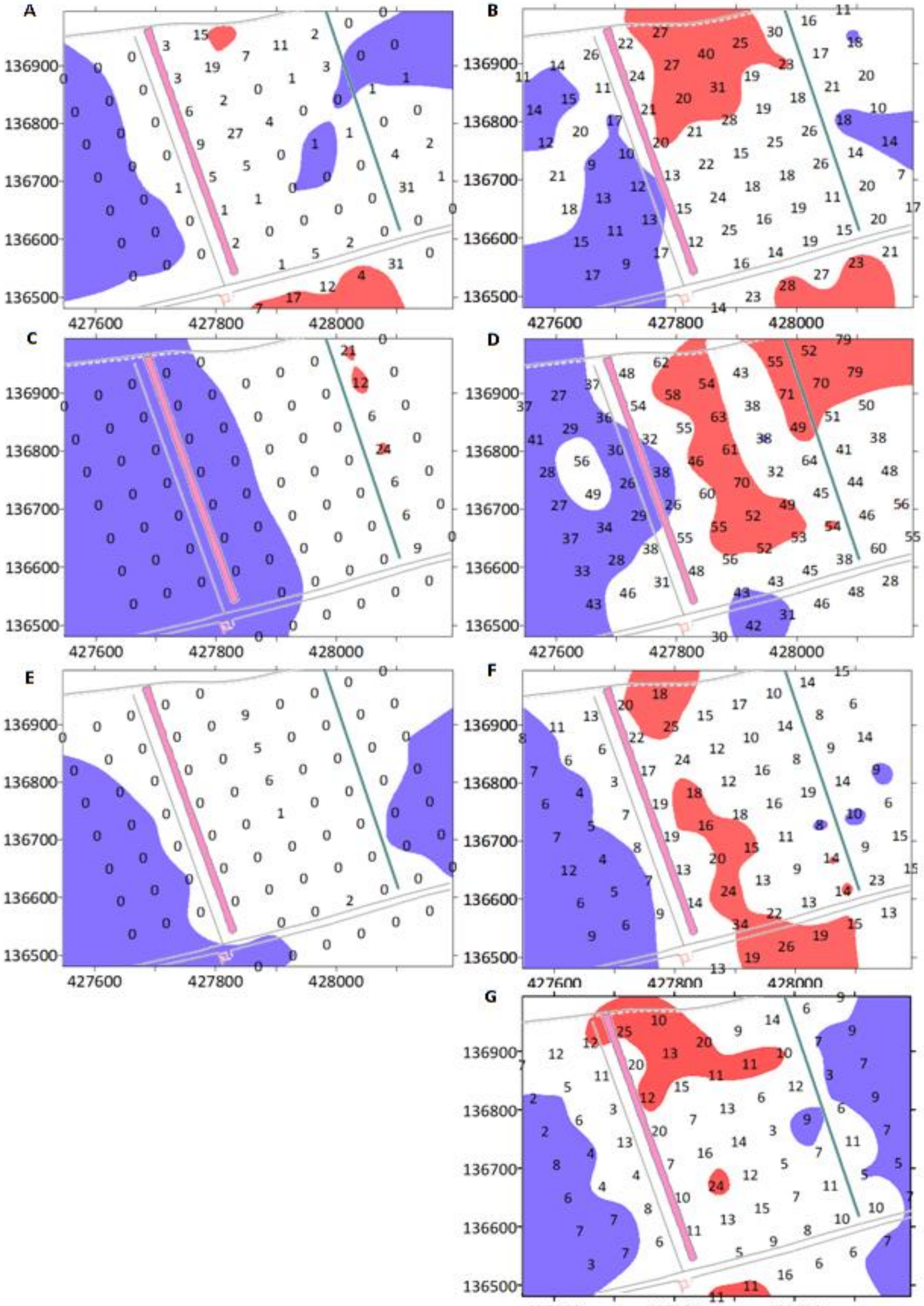


Figure 4.3 SADIE red-blue plot maps of cluster indices for date 1,2 and 3 aphid counts (maps A, C and E respectively) and date 1,2,3 and 4 alate aphids caught on cylindrical sticky traps (maps B, D, F and G respectively). The maps indicate areas of high counts,

patches, in red where $v_i > 1.5$ and low counts, gaps, in blue where $v_j < -1.5$. The white areas indicate where aphid counts are effectively random. The numbers show the raw counts at each trapping station point.

Primarily considering the aphids caught on cylindrical sticky traps, there were few in the spring barley field to the west of the pollen and nectar strip (Figure 4.3; B, D, F and G), but clusters of aphids existed in the centre of the winter wheat field, particularly during date 2. Numbers of aphids trapped next to the pollen and nectar strip were lower than in the adjacent trap rows (rows E and F) during dates 2 and 3 but not during date 4 where higher numbers were caught in trap row D than the rest of the field.

4.3.2.2. Empididae

Empididae demonstrated different distributions and numbers caught depending on the trapping methodology. Yellow sticky traps caught more Empididae than the cylindrical traps. Empididae trapped on yellow traps demonstrated a significant heterogeneous distribution for both dates but only those trapped during date 2 on the cylindrical traps had a significant heterogeneous distribution (Table 4.6). Looking at the numbers trapped using yellow sticky traps, the highest numbers of Empididae were caught in traps in row "D" next to the floral strip during date 4 and along this same row in date 3 and along the row of traps to the south of the winter wheat field. Both these distributions suggest a utilisation of the pollen and/or nectar present in the floral strip and the field boundary/ hedgerow floral resources.

Table 4.6 shows results from SADIE single association tests for Empididae trapped on cylindrical sticky traps and yellow sticky traps for each date of trapping. *P* * <0.05; *P* ** <0.01; *P* * <0.001.**

	Cylindrical trap counts				Yellow trap counts	
	Date 1	Date 2	Date 3	Date 4	Date 3	Date 4
I_a	1.200	1.890	0.805	0.930	2.050	1.625
P	0.11	<0.001***	0.93	0.60	<0.001***	<0.01**

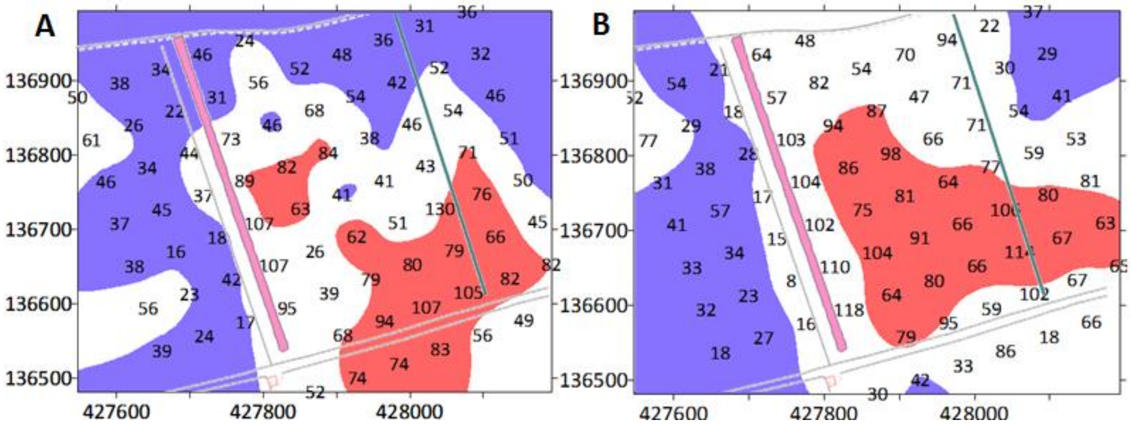


Figure 4.4 Contour maps of cluster indices for Empididae numbers caught on yellow sticky traps for dates 3 (A) and 4 (B). The maps indicate areas of high counts, patches, in red where $v_i > 1.5$ and low counts, gaps, in blue where $v_j < -1.5$. The white areas indicate where Empdidae counts are effectively random. The numbers show the raw counts at each trapping station point.

SADIE association tests carried out between aphid numbers obtained for count date 3 and cylindrical sticky trap numbers for dates 3 and 4 (Table 4.6) showed positive associations with yellow sticky traps Empididae for four of the six association tests.

Table 4.7 SADIE association statistics for tests between aphids and Empididae. (P_D * <0.025 or >0.975; P_D ** <0.01 or >0.99; P_D * <0.001 or >0.999; ns = not significant at 5% and above level). The letters correspond to the associations represented in map form in Figure 4.4.**

			Yellow sticky trap Empididae		
	Date		3		4
Aphid count	3	**A**	$X = 0.160$ $P_D = 0.108$ ns	**B**	$X = 0.364$ $P_D = 0.002$ **
Cylindrical sticky trap aphids	3	**C**	$X = 0.365$ $P_D < 0.001$ ***	**D**	$X = 0.485$ $P_D < 0.001$ ***
	4	**E**	$X = 0.149$ $P_D = 0.091$ ns	**F**	$X = 0.286$ $P_D = 0.006$ **

As well as significant associations existing between alate aphids (cylindrical sticky traps) and Empididae when the same dates are compared directly, there are also significant associations between date 3 aphid counts and alate aphids when compared to Empididae trapped on yellow traps during date 4, indicating a lag response of Empididae to aphid numbers over a relatively short time frame of four days.

The highest associations between alate aphids and Empididae occurs primarily in the centre of the main wheat field, and in the barley field, although the large blocks of dark green in the barley field are somewhat due to the traps being mapped on the diagonal and the plot extrapolating further west of row A (see Figure 4.5) than data exists for.

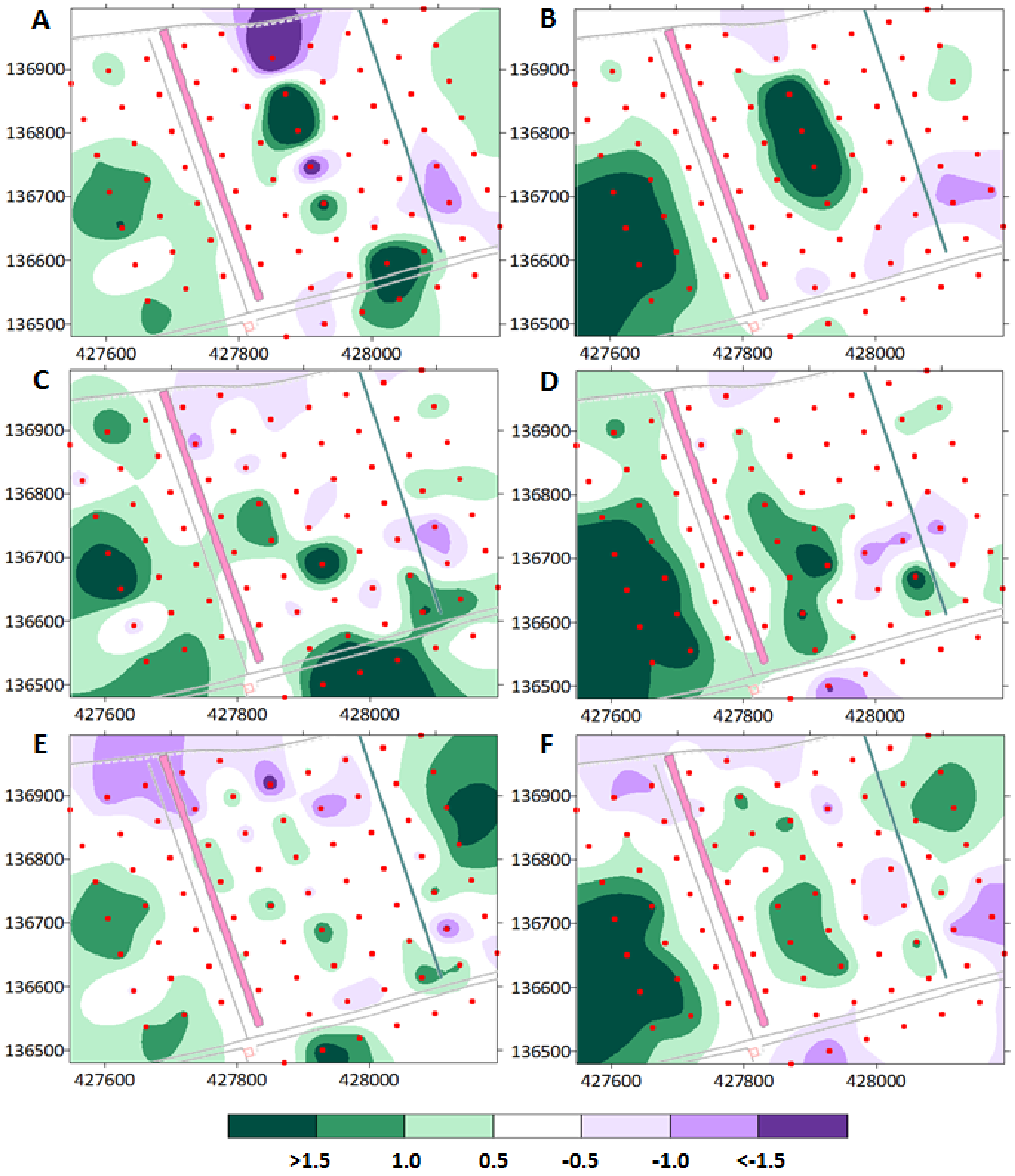


Figure 4.5 Local association plots for both alate aphids and terrestrial aphids compared to distributions of Empididae. This figure is linked to Table 4.7 above which shows the statistics and significance for each of the six associations. The legend shows *X*p at each point and the resultant association order of magnitude. Green plots show positive associations, purple, negative associations. White space indicates unity.

Mapping the association values (similar to the methodology used in Winder *et al.*, 2001) between Empididae and aphids at each date revealed that the strength of associations depended on temporal proximity of aphids to Empididae. Despite only four association plots being carried out between yellow sticky trap Empididae and cylindrical sticky traps aphids, there seems to be a strong indication that Empididae spatial patterns follow those of aphids (Figure 4.6; A). This pattern also occurs when Empididae cylindrical trap data are analysed, but with fewer significant associations. Although it must be noted that there was an increased length of time between dates 2 and 3 than between 1 and 2 and 3 and 4 which would potentially dilute a temporal effect between dates 1 & 2 and 3 & 4.

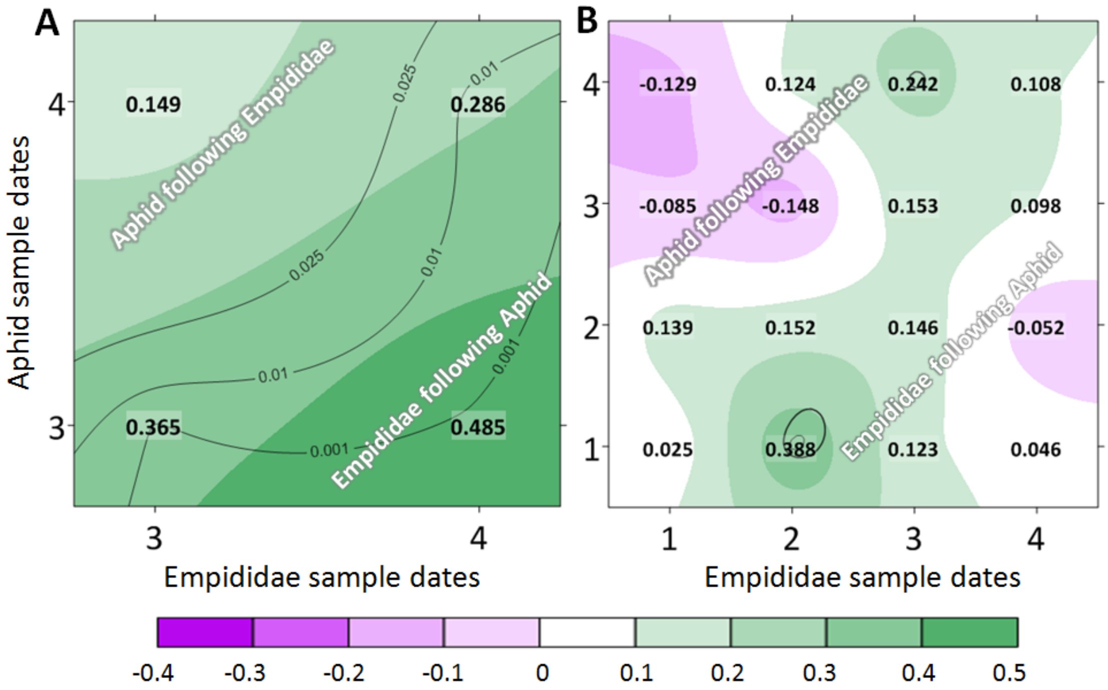


Figure 4.6 Contour maps of SADIE association values between sample dates for yellow sticky trap Empididae and cylindrical sticky trap aphid captures (A) and cylindrical sticky trap Empididae and aphid captures (B). Green areas show positive association values, purple; dissociative values for unlagged (main diagonal) and lagged (above and below main diagonal) association tests. Contour lines indicate P-values.

4.3.2.3. Syrphidae

Syrphidae adults were divided into male and female individuals primarily to determine the movements of the egg laying females. Syrphidae were split into *E. balteatus* individuals and other Syrphidae.

Syrphidae other than *E. balteatus* (composed of the species *Sphaerophoria scripta*, *Metasyrphus corollae* and *Melanostoma* spp.) were trapped on cylindrical sticky traps but not on yellow traps. Females were analysed for their distributions within the study area. On cylindrical traps during dates 1 and 2 they exhibited significantly patchy distributions (I_a = 1.532, P<0.01 and I_a = 1.368, P = 0.03 respectively) but not during dates 3 and 4 (I_a = 1.224, P = 0.09 and I_a = 0.843, P = 0.85 respectively), although the patch clusters do not exist around the pollen and nectar strip area (Figure 4.7; A and B). *E. balteatus* are, however, the focus for this study due to the large numbers trapped and considered importance as aphid predators.

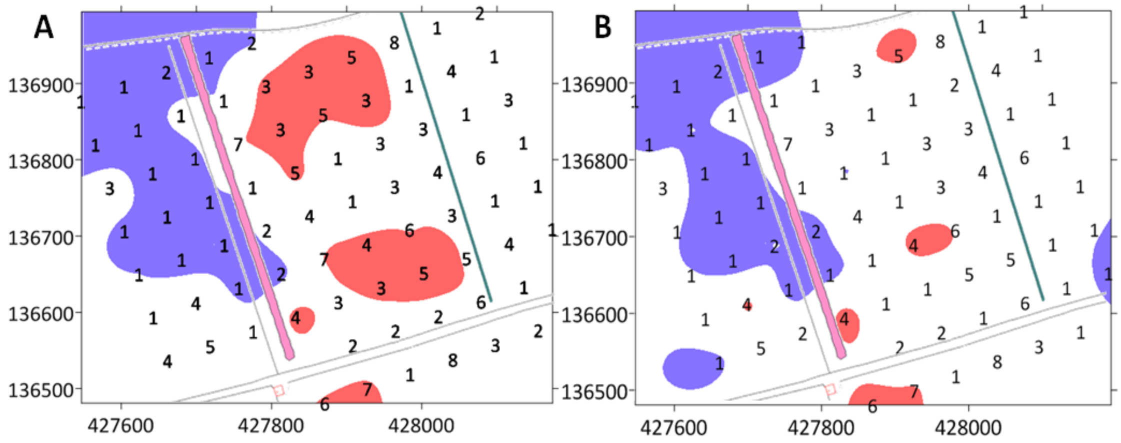


Figure 4.7 SADIE red-blue plot maps of cluster indices for date 1 (A) and 2 (B) cylindrical trap Syrphidae other than *E. balteatus*. The maps indicate areas of high counts, patches, in red where v_i > 1.5 and low counts, gaps, in blue where v_j < -1.5. The white areas indicate where aphid counts are effectively random. The numbers show the raw counts at each trapping station point.

During dates 1 and 2, the cylindrical sticky traps caught few *E. balteatus* overall but by dates 3 and 4, hundreds of individuals were caught on yellow sticky traps as well as cylindrical traps (Table 4.2). SADIE red-blue analyses carried out for female hoverflies caught on bottles during dates 1 and 2 did not demonstrate significantly clustered distributions (I_a = 1.123, P = 0.19 and I_a = 0.902, P = 0.68 respectively) but significant patchy distributions were found during date 3 and date 4 (Table 4.8). The distribution and density of *E. balteatus* did not seem to be influenced by the presence of the pollen and nectar block since higher numbers did not seem to occur in close proximity. Additionally the distribution of *E. balteatus* numbers did not remain the same between dates 3 and 4,

Table 4.8 SADIE red blue analyses and association analyses for female and total *E. balteatus* caught on cylindrical and yellow sticky traps during dates 3 and 4. For red-blue single cluster analysis : *P* * <0.05; *P* ** <0.01; *P* * <0.001. For association analyses: P_D * <0.025 or >0.975; P_D ** <0.01 or >0.99; P_D *** <0.001 or >0.999; ns = not significant at 5% and above level. The letters correspond to the respective contour map in Figure 4.8.**

Cylindrical trap counts		*vs.*	Yellow trap counts		X	P_D
A All *E. balteatus* date 3			**B** All *E. balteatus* date 3		-0.164	0.922
$I_a = 1.917$	$P<0.001$***		$I_a = 1.435$	$P = 0.02$*		
C All *E. balteatus* date 4			**D** All *E. balteatus* date 4		0.409	<0.001***
$I_a = 2.109$	$P<0.001$***		$I_a = 2.046$	$P<0.001$***		
E Female *E. balteatus* date 3			**F** Female *E. balteatus* date 3		0.005	0.484
$I_a = 1.913$	$P<0.001$***		$I_a = 1.460$	$P = 0.02$*		
G Female *E. balteatus* date 4			**H** Female *E. balteatus* date 4		0.340	<0.001***
$I_a = 2.107$	$P<0.001$***		$I_a = 1.967$	$P<0.001$***		

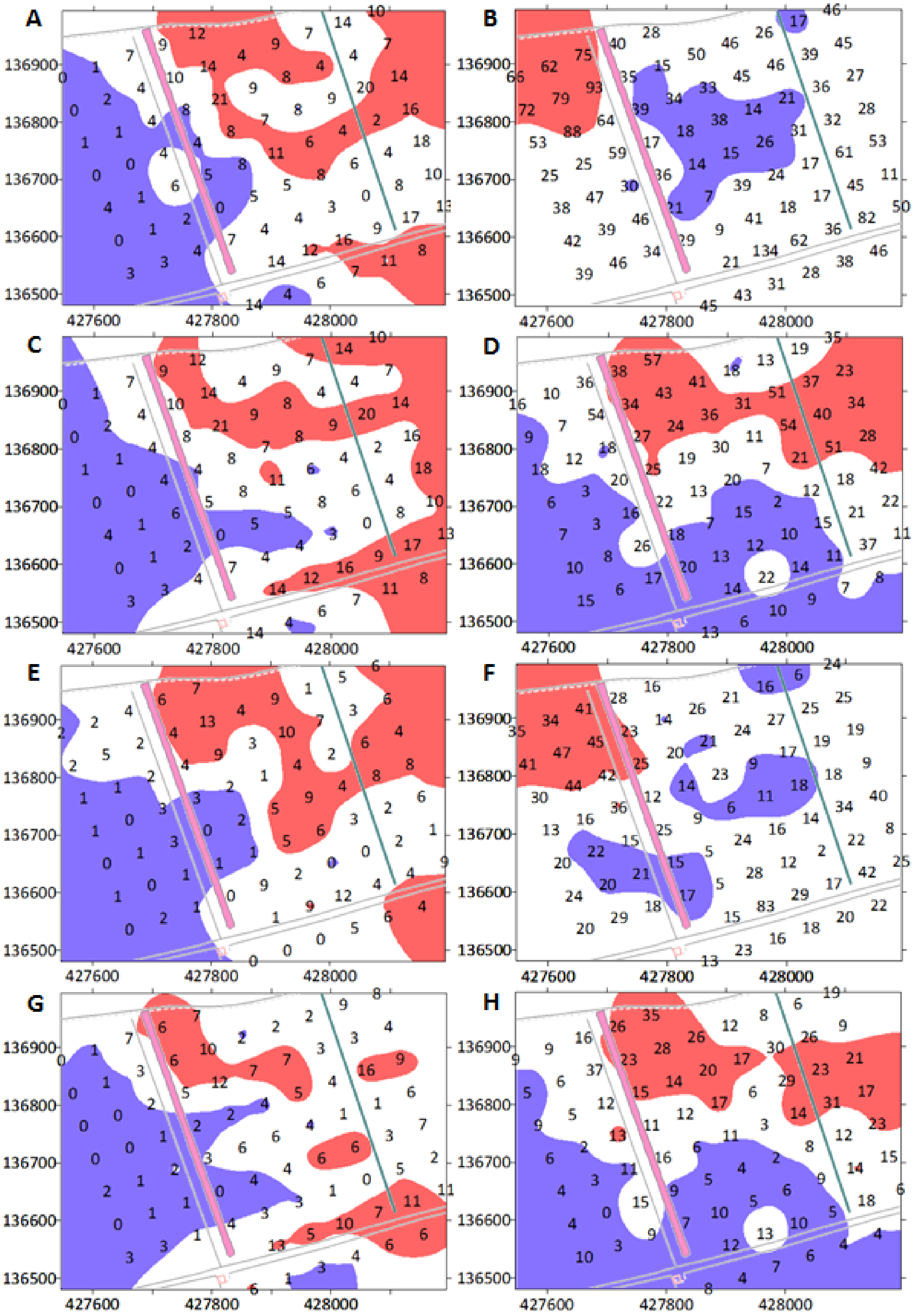


Figure 4.8 Contour maps of cluster indices for total and female *E. balteatus* numbers caught on yellow sticky traps and cylindrical traps for dates 3 and 4. At each trapping point the numbers of individuals trapped are shown. Figure identifiers correspond to

those in Table 4.8. The maps indicate areas of high counts, patches, in red where v_i > 1.5 and low counts, gaps, in blue where v_j < -1.5. The white areas indicate where aphid counts are effectively random. The numbers show the raw counts at each trapping station point.

The distributions of female and male *E. balteatus* on yellow traps and cylindrical sticky traps were highly significantly associated (yellow traps date 3: $X = 0.516$, $P_D < 0.001$; yellow traps date 4: $X = 0.7262$, $P_D < 0.001$ and cylindrical traps date 3: $X = 0.417$, $P_D < 0.001$, cylindrical traps date 4: $X = 0.405$, $P_D < 0.001$). Analyses between females and males on cylindrical sticky traps were not carried out for dates 1 and 2 due to either zero or very low numbers of male *E. balteatus* trapped during this time (Table 4.2; A). There were no associations of total cylindrical *E. balteatus* trapped between either aphid counts (date 1: $X = 0.094$, $P_D = 0.219$; date 2: $X = 0.319$, $P_D = 0.089$) or alate aphids (date 1: $X = 0.057$, $P_D = 0.317$; date 2: $X = 0.029$, $P_D = 0.410$) on cylindrical sticky traps for dates 1 and 2 but significant disassociation between total *E. balteatus* numbers caught on yellow traps during date 3 and both aphid counts ($X = -0.331$, $P_D = 0.994$; Fig 4.9; A) and alate aphids trapped on cylindrical sticky traps ($X = -0.349$, $P_D = 0.998$; Fig 4.9; B) although no significant associations were observed between aphids and solely female *E. balteatus* (counts date 3: $X = -0.102$, $P_D = 0.771$ and alate aphids date 3: $X = -0.219$, $P_D = 0.968$). The date 3 disassociations occur primarily in the centre of the field where *E. balteatus* numbers are low but alate aphid numbers are high.

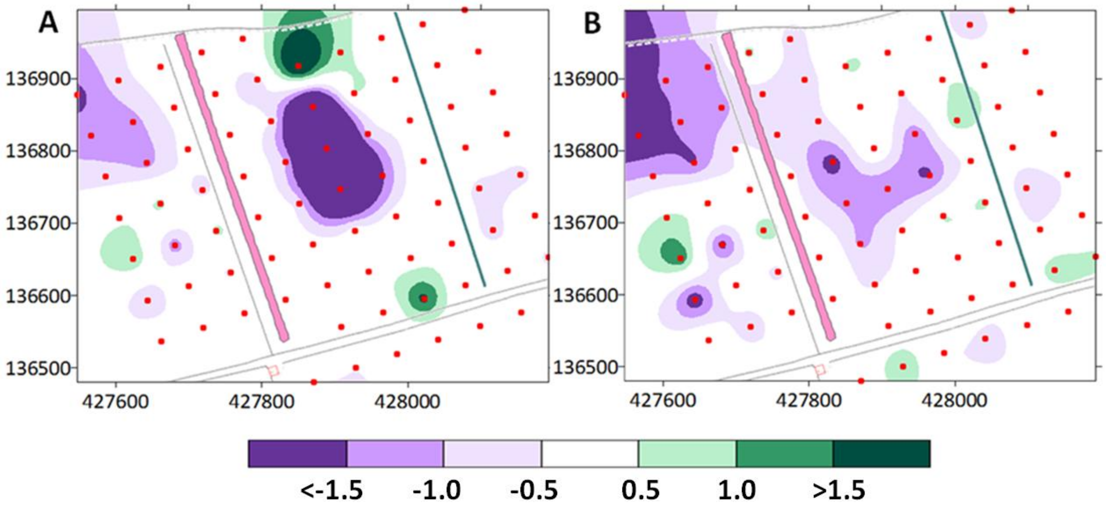


Figure 4.9 Local association plots for total *E. balteatus* trapped on yellow traps compared to aphid count distributions during date 3 (A) and total *E. balteatus* trapped on yellow traps compared to alate aphids trapped on cylindrical sticky traps also during date 3 (B). Both associations were significantly negative.

Mapping the association values (as in Figure 4.6 and similar to the methodology used in Winder *et al.*, 2001) between *E. balteatus* and aphids showed associations were not strong between alate aphids and yellow trapped *E. balteatus* and significant disassociation occurred during date 3, the distribution of which is shown in Figure 4.9. *E. balteatus* numbers were low in the centre of the wheat field, where aphid numbers were high.

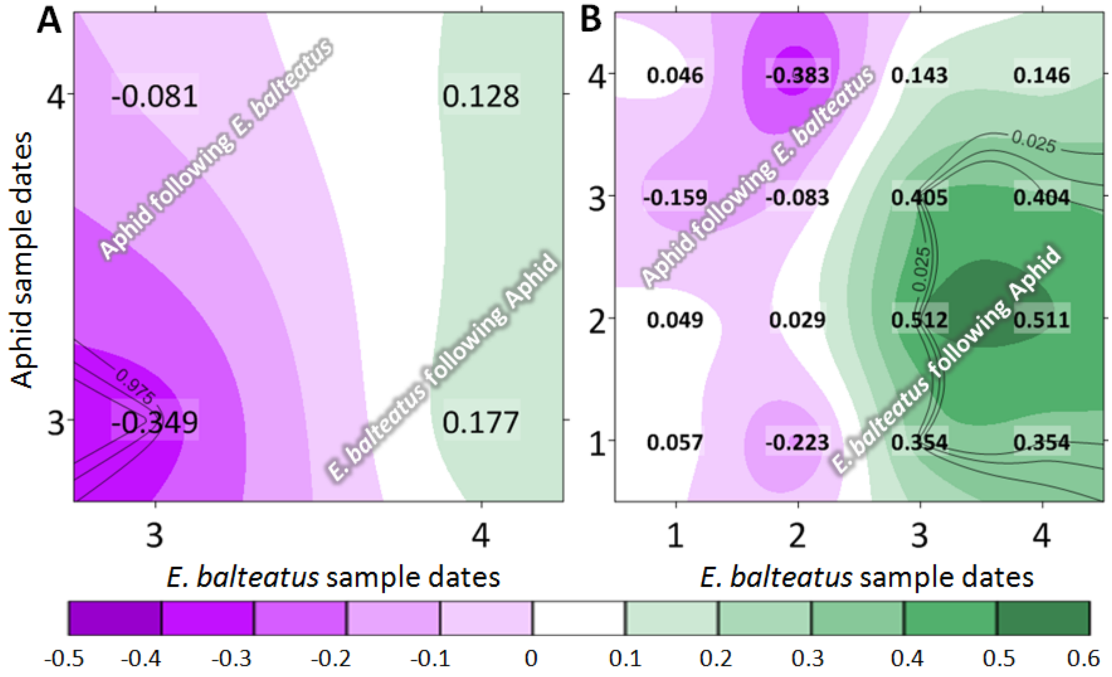


Figure 4.10 Contour maps of SADIE association values between sample dates for yellow sticky trap *E. balteatus* and cylindrical sticky trap aphid captures (A) and cylindrical sticky trap *E. balteatus* and aphid captures (B). Green areas show positive association values, purple; dissociative values for unlagged (main diagonal) and lagged (above and below main diagonal) association tests. Contour lines indicate P-values. It must be noted that there was significant dissociation between *E. balteatus* numbers during date 2 and cylindrical sticky trap aphids during date (P_D = 0.999) although this is not particularly clear in diagram B.

Associations were not particularly strong between *E. balteatus* and alate aphids during dates 1 and 2, although dissociative, however, significant associations existed between *E. balteatus* and aphids during dates 3 and 4. Figure 4.10 B seems to show a negative association where the aphid follows *E. balteatus* temporally but an association effect where *E. balteatus* follow the aphid distributions temporally. The extended time lag of 12 days between trapping during dates 2 and 3 seems to have created a divide between dissociation and association of the two populations.

4.3.2.4. Dolichopodidae

Dolichopodidae were found to display heterogeneous distributions on cylindrical sticky traps during date 2 and on yellow sticky traps on both dates 3 and 4, but not otherwise (Table 4.9).

Table 4.9 SADIE red blue analyses for Dolichopodidae trapped on cylindrical and yellow sticky traps for each trapping date * <0.05; *P* ** <0.01; *P* * <0.001.**

	Cylindrical trap counts				Yellow trap counts	
Date	1	2	3	4	3	4
I_a	0.921	1.574	0.777	0.979	1.545	1.341
P	0.65	<0.01**	0.97	0.48	<0.01**	0.04*

SADIE associations carried out between alate aphids and Dolichopodidae caught on both cylindrical and yellow sticky traps are shown in Table 4.10. All associations were not significant at the 5% level except for Dolichopodidae on yellow traps and alate aphids during date 3 where there was a significant disassociation.

Table 4.10 SADIE association analyses between Dolichopodidae and alate aphids caught on cylindrical and yellow sticky traps. P_D * <0.025 or >0.975; P_D ** <0.01 or >0.99; P_D * <0.001 or >0.999; ns = not significant at 5% and above level.**

Dolichopodidae	Aphids	X	P_D
Cylindrical traps date 1	Cylindrical traps date 1	-0.196	0.954 ns
Cylindrical traps date 2	Cylindrical traps date 2	0.114	0.183 ns
Cylindrical traps date 3	Cylindrical traps date 3	-0.064	0.706 ns
Cylindrical traps date 4	Cylindrical traps date 4	0.086	0.231 ns
Yellow traps date 3	Cylindrical traps date 3	-0.451	>0.999***
Yellow traps date 4	Cylindrical traps date 4	-0.198	0.947 ns

Date 3 Dolichopodidae yellow sticky trap distributions showed greater numbers primarily to the east and west, with no clustering around the pollen and nectar strip (Figure 4.11 A). Very few were caught in the southern traps. Since higher numbers of alate aphids were caught in the centre of the wheat field, when analysed via SADIE for association testing, a significant dissociation was observed (Figure 4.11 B).

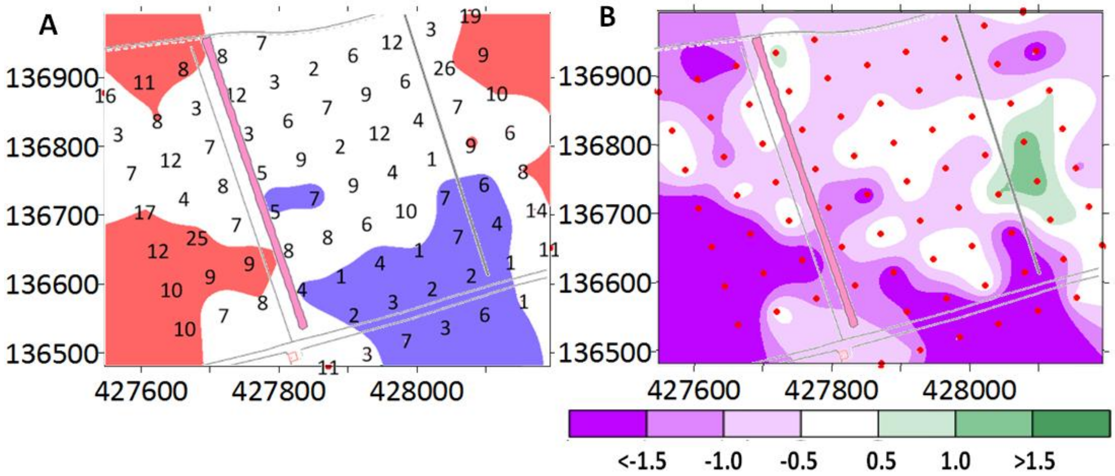


Figure 4.11 (A) SADIE red-blue plot map of cluster indices for Dolichopodidae on yellow sticky traps during date 3. Areas of high counts, patches, are indicated in red where $v_i > 1.5$ and low counts, gaps, indicated in blue where $v_j < -1.5$. The white areas indicate where aphid counts are effectively random. The numbers show the raw counts at each trapping station point. (B) Local association plot for Dolichopodidae trapped on yellow traps compared to alate aphids caught on cylindrical sticky traps during date 3. SADIE statistics are given in Table 4.10.

4.3.2.5. Other aphid predators

Relatively few other aphid predators were captured compared with the predatory flies and were comprised of Cantharidae and *Tachyporus* species (Table 4.2). These other groups of aphid predators did not show significant spatial pattern (e.g. *Tachyporus* spp.) or were not trapped in great enough numbers to determine their distribution (e.g. 2 and 3 individuals of Cantharidae caught on cylindrical traps during dates 1 and 2 respectively).

4.3.3. Rubidium marking main study

4.3.3.1. Floral rubidium levels

The pollen and nectar sown field margin was dominated by three main species: *Medicago lupulina, Trifolium hybridum* and *Lotus corniculatus* (Table 4.11).

Table 4.12 Floral resource densities for the six most common flowering plants found in the rubidium sprayed pollen and nectar strip.

Floral resource density (average flower heads/m^2)	**Species**
113.9	*Medicago lupulina* (Black medick)
89.5	*Trifolium hybridum* (Dutch clover)
21.7	*Lotus corniculatus* (Birds-foot trefoil)
6.5	*Trifolium repens* (Red clover)
0.4	*Cirsium vulgare* **(**Spear thistle)
0.6	*Papaver rhoeas* (Field poppy)

The clover sprayed with the rubidium solution in this study was successfully marked and the mark retained in the plant tissues beyond the initial four day invertebrate sampling period (Figure 4.11). The higher levels of rubidium present in the clover samples on the 13th July was due to the clover retaining some of the rubidium mark from having been sprayed previously with rubidium chloride on the 23rd June 2008. Invertebrates were not analysed for rubidium during trapping dates 1 and 2 due to the low numbers of individuals caught. Labour time and economic costs did not allow for hoverflies (or any other invertebrates) from dates 1 and 2 to also be tested.

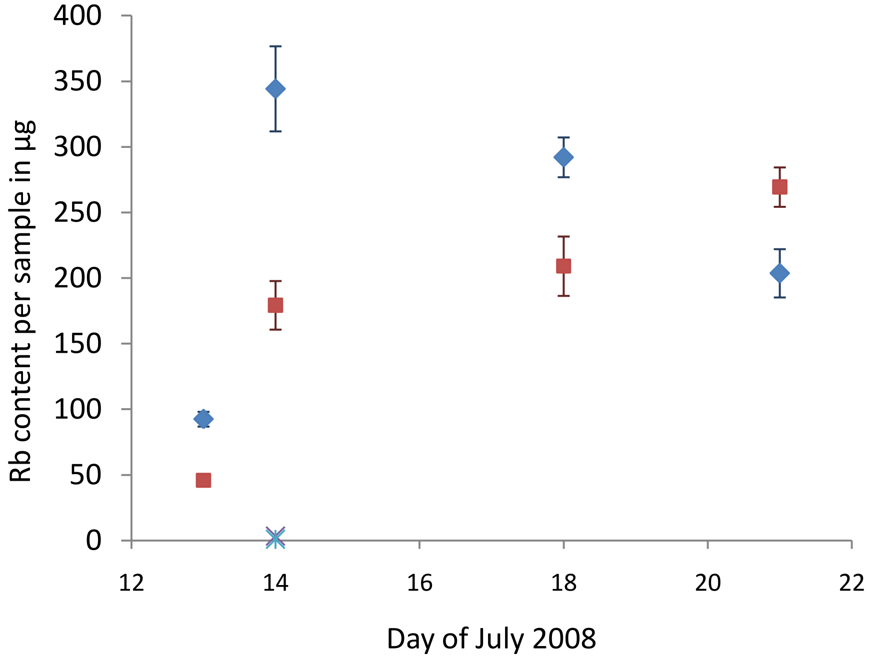


Figure 4.12 Rubidium content in µg per sample for *Trifolium hybridum* flower tissue (blue diamonds) and leaf tissue (red squares) for the mean per ten samples for the pre-spray date, 13th July, and immediately after spraying, 14th July and subsequent samples taken on the 18th and 21st July 2008 with error bars for the standard error of the mean. Control samples are also shown that were taken on the 14th July from a different area of the farm, showing flower tissue of the control clover (purple cross) and leaf tissue of control clover (blue cross).

The distribution of rubidium in the plant tissues was not at a universal concentration throughout all plant tissues but significantly varied in concentration between flowers and leaves (Figure 4.11). This variation was evident even in the very low background concentrations of rubidium measured in the control flower and leaf samples (t-tests carried out on $\log_{10}$ transformed data), ($t = 3.72$, $df = 10.36$, $P <0.01$). Immediately prior to the second spray, rubidium levels per sample of leaf tissue and in the flowers were significantly different ($t = 8.65$, $df = 17.27$, $P<0.001$) with greater rubidium concentrations present in the flower tissue. The day after spraying, the flowers of the clover contained significantly greater rubidium concentrations to that of the leaves ($t = 4.35$, $df = 16.36$, $P<0.001$). By the 18th July the quantity of rubidium in the flower tissues had dropped, but the concentrations in the leaves were still rising, although there was still significant difference in concentrations in the two tissue types ($t = 2.38$, $df = 10.86$, $P = 0.04$). By the 21st July there were higher concentrations in the leaves than the flowers (t = -2.97, df = 14.66, P = 0.01). Throughout the seven day monitoring period levels of rubidium in the floral components of the clover plants were many orders of magnitude greater than that of the control, and, as such, would be expected to enable hoverfly marking through feeding.

4.3.3.2. Episyrphus balteatus *rubidium levels and distribution*

Of the total 867 females tested for rubidium, 13 exceeded the threshold level and were considered marked (1.5%) and, on average, contained twenty-nine times the rubidium content than the average of unmarked individuals. The distribution of rubidium marked hoverflies was not statistically significantly associated with the distribution of the 867 female *E. balteatus* that were tested either when marked individuals were considered as absolute values (X = 0.147, P_D = 0.119) or as a proportion (X = 0.143, P_D = 0.129).

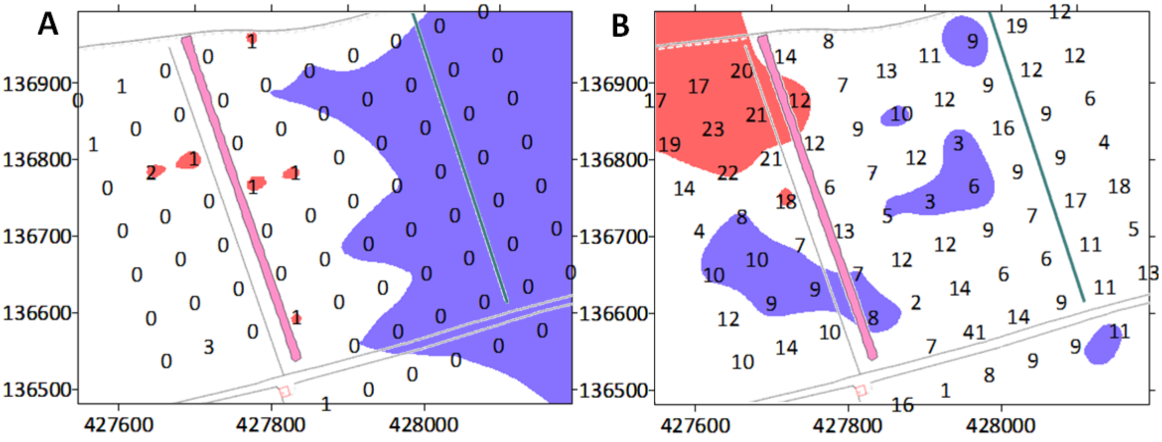


Figure 4.13 The distribution of rubidium marked *E. balteatus* (A) and female *E. balteatus* (B) that were tested for the presence of rubidium. The maps indicate areas of high counts, patches, in red where v_i > 1.5 and low counts, gaps, in blue where v_j < -1.5. The white areas indicate where *E. balteatus* counts are effectively random. The numbers show the raw counts at each trapping station point.

Of the 13 marked individuals, the furthest travelled reached approximately 150m from the floral strip, but one also managed to circumnavigate the large 3m high hedges that ran either side of the track (Figure 4.2) and was trapped at station D9.

4.4. **Discussion**

4.4.1. The effectiveness of rubidium chloride as a predator marker

The marking of both *E. balteatus* and *A. bipunctata* was successful in its implementation and demonstrated the effectiveness of rubidium marking outside the confines of a laboratory. The marking rate of 100% for hoverflies recaptured and the very high levels of rubidium found in each of the marked Syrphid individuals gave no doubt over the suitability of rubidium chloride as a marker in the subsequent large scale field trial. The hoverflies in the study would have obtained the rubidium mark through the floral nectar of the plants sprayed (Gu, 2001) although the nectar was not specifically tested in this study. The ability of *A. bipunctata* to be marked is also of considerable interest, demonstrating that the rubidium mark was potentially successfully transferred from the invertebrate herbivore prey to an invertebrate predator. It is not known whether the mark was obtained in *A. bipunctata* through feeding on prey that had taken up the mark or via feeding on pollen and nectar although *A. bipunctata* adults do demonstrate improved reproduction when fed on aphids (Jalali *et al.*, 2009) and would therefore potentially preferentially consume aphids over pollen. The lower levels of rubidium in terms of µg per gram that were found in *A. bipunctata* could also be related to a dilution effect if the rubidium marker was taken up via prey rather than direct feeding on the plant, although this study cannot clarify this point. The lack of a rubidium mark in one individual of *A. bipunctata* may be due to feeding on prey that had not yet obtained the mark through plant feeding or a time lapse of three days between rubidium chloride spray and invertebrate collection may be too short a time span when marking predators with rubidium. No prey for the Coccinellidae were specifically released into the enclosures during the pilot study so it is unknown what species the *A. bipunctata* may have predated on, if at all, to pick up the mark. This is, however, a demonstration that this technique is perfectly adequate to employ in the field, and is appropriate for both species. The very high levels of rubidium detected in the insects indicate that the mark was an internal one. The measures taken to prevent an external mark being detected, through spraying the rubidium chloride solution pre-release into the enclosures and washing the insects thoroughly prior to analysis would appear to have been effective in removing external rubidium compounds.

4.4.2. Large scale field study: predator distributions

4.4.2.1. Aphid distribution

Aphids counted within the crop and alate aphids caught above the crop displayed significantly similar spatial and temporal distribution patterns, although greater numbers of aphids were found on the cylindrical sticky traps than counted within the crop. This suggests that visual assessments of relatively small numbers of tillers hugely underestimate the numbers of aphids present within fields or alternatively there is high influx of alate aphids which fail to establish colonies. Very low aphid numbers were found on the tillers, possibly as a result of the huge numbers of *E. balteatus* found within the fields whose larvae would exert a large predation pressure on aphids available. Sticky traps also capture aphids from a wider area over a longer time frame than is covered through tiller counting and may therefore give a better indication of aphid distributions where numbers are very low.

The grid size of the traps (60m x 60m) was selected because this was considered appropriate for studying flying insects whereas previous studies concentrated on smaller grid sizes where the focus was on less mobile terrestrial invertebrates. For example, a 'large' grid size for the study of *S. avenae* was considered to be 30m in an early study using SADIE analyses by Winder *et al.* (1999). However, even with the 60m spacing used in this study there was highly significant clustering of aphids. The majority of aphids counted were of the species *S. avenae* which is supported in higher population numbers by wheat plants than barley plants (Acreman & Dixon, 1985). It is still noticeable, however, that the patch clusters of aphids tended to occur within the middle of the central winter wheat field, especially for alate aphids caught on cylindrical sticky traps. This is likely to be due to predation pressure by enemies on aphids at the edge of fields (Bowie *et al.*, 1999; Holland *et al.*, 1999; Collins *et al.*, 2002).

4.4.2.2. Empididae – an important but overlooked predator?

The difference in numbers and lack of association between Empididae caught on the cylindrical sticky traps compared with yellow traps is possibly due to the relative differences in the colour preferences of different Empididae species between those that are flower visiting and those that are not. In contrast, the passive cylindrical traps, lacking in colour, are likely to have collected individuals from the whole Empididae family within the "aerial soup" (Taylor, 1962). Presumably this is an adaptation in those species that obtain all their protein requirements from pollen (Cumming, 2006) to identify pollen rich floral resources in a similar way to other floral feeding insects (Kevan & Baker, 1983; Bowie *et al.*, 1999) and could aid in indentifying species of Empididae that may be manipulated by pollen and nectar resources on farmland. Empididae trapped on sticky traps were found in higher numbers next to where floral resources existed, for example adjacent to the floral strip, but were still found in numbers great enough mid-field to be associated with aphid distributions. The lack of higher numbers similar to those adjacent to the floral strip around the beetle bank suggests the higher numbers at the west and south edge of the winter wheat field are due to the presence of floral resources rather than a simple 'edge-effect' (e.g. Rand *et al*., 2006).

There were high levels of association, accounting for a four day lag, between Empididae trapped on yellow sticky traps and both aphids within the crop and above. Empididae are known invertebrate predators (Cumming, 2006) and have been observed readily killing aphids (author, 2007). This study is the first to identify such a strong link between Empididae and aphid distributions and the value of Empids as aphid predators seems to have been previously overlooked. The high mobility of Empids allows them to penetrate the centre of large fields easily, and the distribution maps created in this study show patch clusters of Empididae in the middle of the central field. A predator population response time of four days to their aphid prey is also a relatively short lag time, especially important when aphid populations have the potential to grow so fast (Dixon, 1977). This time lag is very favourable when compared to the two week lag detected for cereal aphids and carabid beetles (Winder *et al.*, 2001).

There was no obvious benefit of the floral strip to Empididae numbers, patch clusters of Empids did not exist around the floral strip, although numbers were especially high on the winter wheat side of the floral strip. Rubidium analyses of Empididae trapped could potentially reveal more about Empididae movement and utilisation of the floral resource, although more as a source of alternative prey than flower feeding.

4.4.2.3. Dolichopodidae

Dolichopodidae distributions did not match those of aphids, although date 3 did exhibit a significant dissociation. This may be due to the lack of identification of Dolichopodidae to genus or species level. Previously (Chapter 2, Section 2.4.3.3) it has been considered that other environmental factors, such as the presence of water bodies, can affect the distribution of Dolichopodidae individuals. Dolichopodidae are split into those that are predatory and those that feed on pollen and nectar through modified mouthparts (Brooks, 2005). Without the splitting of the group down to functional feeding groups the differing motivations of both types of Dolichopodidae are likely to affect the distributions seen in this study.

4.4.2.4. Distributions of other aerially dispersing aphid predators

The numbers of other aphids predators (Cantharidae in particular) were probably too low to enable any significant associations with the aphids to be detected. Although the central focus for this study was the floral strip located on the west side of the winter wheat field (Figure 4.2), the presence of other floral resources, due to the farm being in the Higher Level Scheme (section 1.5.1) could have influenced the distribution of aerially dispersing aphid predators in the area. The difference in Cantharidae species trapped by the two types of sticky traps could be either due to the attractivity of yellow to *R. fulva* or the difference in height that *R. fulva* and *C. lateralis* fly at, but is worth noting for future studies.

4.4.2.5. Episyrphus balteatus *distribution*

The division of *E. balteatus* individuals into female and male individuals was carried out to determine if there was a difference in their spatial and temporal distribution. Since female hoverflies rather than males make decisions on locating (Scholz & Poehling, 2000) and laying within suitably sized aphid colonies (Bargen *et al.*, 1998), there could be a difference in the movements of each of the sexes due to their different motivations. However, due to the highly associated spatial distributions of females and males, this concern does not seem to be fulfilled and supports studies where hoverfly distributions are determined and analysed but individuals not sexed.

The difference in association response to aphid patchiness may be due to the study capturing two different processes in *E. balteatus'* life history. The disassociation between alate aphids and *E. balteatus* during dates 1 and 2 could be due to the females of *E. balteatus* preferentially focussing on colonies where there are no or few winged aphids present (Kan, 1988; Scholz & Poehling, 2000) although the presence of *E. balteatus* larvae is not considered a deterrent (Chandler, 1968; Bargen *et al*., 1998).

During dates 3 and 4, however, associations were observed between aphid and *E. balteatus* patches. This may be as a result of the hatching of pupae of *E. balteatus* within the field and subsequently being trapped on the sticky traps at the same time aphid colonies were also producing winged morphs as the suitability of the wheat for aphid feeding declines (Karley *et al*., 2004).

4.4.3. Large scale field study: rubidium uptake and subsequent **Episyrphus balteatus** *distribution*

The larger scale study demonstrated that floral resources could be marked relatively easily and the mark be retained, in terms of *Trifolium repens* at least, for an extended period of time. The presence of a significant rubidium elevated levels post 10 days of the first spray demonstrates the persistence of rubidium in *T. repens*.

The difference in levels of rubidium in the plant tissues may be due to the differences the distribution of rubidium during flower growth with the plants producing pollen and nectar at the time of rubidium chloride spraying. The subsequent feeding on pollen and nectar by insects then may remove the higher concentrations of rubidium chloride in the floral tissues and hence lead to greater and more rapid declines of rubidium than in the leaf tissues. Rubidium salts diffuse rapidly throughout the tissues of plants (Levi, 1970) and Graham *et al.* (1978) found higher levels of rubidium in the fruiting bodies of cotton when sprayed with rubidium chloride although plants are known to deal with the presence of heavy metal concentrations within their tissues in a wide variety of ways depending on their species and subsequent genotype (Clemens, 2006).

There were very few *E. balteatus* individuals marked by rubidium. The marking technique is not called into question as those individuals that were marked contained, on average, nearly twice the rubidium threshold to be considered marked. There were huge numbers of hoverflies caught in the field, particularly during trapping dates 3 and 4, although the far greater numbers of *E. balteatus* caught on the cylindrical sticky traps could be attributed to the attractiveness of the yellow traps as the Syrphidae passed over them, which subsequently became stuck on the cylindrical traps. The high numbers of *E. balteatus* caught during dates 3 and 4 may be due to the hatching of *E. balteatus* pupae or the immigration of *E. balteatus* adults, both which are less likely to have visited the rubidium chloride sprayed pollen and nectar strip prior to being trapped. Of the 13 individuals that were marked, all were within a short distance (maximum distance travelled by a trapped *E. balteatus* was 160m) of the pollen and nectar strip, although the trapping stations did not penetrate far into the spring barley field. The very low percentage of female *E. balteatus* individuals trapped could be due to several reasons:

1. The immigration of large numbers of *E. balteatus* into the fields which became trapped prior to feeding on the rubidium chloride sprayed floral strip. *E. balteatus* are known to migrate in large numbers (Hondelmann *et al.*, 2005 and references therein) although this would not be expected until much later in the year.

2. The surrounding areas also have pollen and nectar strips (since the farm itself was in the Higher Level Scheme) which were also being utilised.

3. Female *E. balteatus* individuals remaining in the pollen and nectar strip and not venturing into the adjacent fields. Previous research has shown where field margins contain greater floral resources, *E. balteatus* are retained in greater numbers (MacLeod *et al.*, 1999).

4. *E. balteatus*, being highly mobile, disperse far further than the spatial scale of this study. This seems relatively unlikely due to the localisation of female *E. balteatus* trapped around the pollen and nectar strip, and the previous work by Marshall & West (2007) who found hoverflies (including *E. balteatus*) respond to farmland habitats at field rather than landscape scales.

5. The large numbers of *E. balteatus* trapped are as a result of a mass hatch of hoverfly larvae and are therefore trapped before feeding on the floral resources, this could lead to a 'dilution' effect, where discounting the newly hatched adults would increase the relative number of female *E. balteatus* marked.

6. Clover flowers are not utilised by *E. balteatus* despite being such a large component of pollen and nectar mixes. However, it is expected that *M. lupulina* flowers would similarly take up and pass on the rubidium mark in the same way as those of *T. pretense* (*E. balteatus* adults feed on *M. lupulina*, personal observation, 2008).

To improve the efficacy of this experiment, it would have been beneficial to spray rubidium chloride solution on the floral strip and bring the times of trapping forward to earlier in the season. An earlier rubidium chloride spray was conducted earlier on in the season (23rd June, 2008) but the low numbers of Syrphidae trapped did not make it feasible to analyse the data to obtain meaningful results. The study could not be repeated immediately afterwards with yellow traps to maximise the catch due to the high levels of rainfall experienced between 2nd July and 12th July 2008 (Met office data for Larkhill, located 13 miles from the field used in this study).

Rubidium chloride solution cannot be sprayed in periods of wet weather in case it is diluted by the wet ground and vegetation and subsequently not absorbed by the plants in high enough levels to provide a suitable level of marking.

4.4.4. Conclusions

There was a very large disparity in numbers of aphids counted within using the tiller method compared to the cylindrical traps although the distributions were highly associated suggesting cylindrical sticky traps could be used to monitor the distributions of aphids within cereal fields. Rubidium chloride is a useful tool to prove utilisation of plant resources by aphid predators within an open field system. Empididae, in particular, may have been overlooked in their usefulness as an aphid predator judging by their strong associations with aphids in the field and warrant further investigation, possibly through marking with rubidium chloride. The lack of numbers of marked female *E. balteatus* trapped within this study may be due to several reasons although the trapping of marked female *E. balteatus* does prove the effectiveness of the technique.

Chapter 5

General Discussion and Conclusions

5.1. **Introduction**

This study aimed to determine whether field margins have an effect on the spatial and temporal distributions of aerially dispersing aphid predators in UK winter wheat fields.

The main Hypotheses of each study chapter were as follows:

Chapter 2: The presence of a 6m florally enhanced field margin surround significantly enhances the numbers of aerially dispersing aphid predators trapped within winter wheat fields.

Chapter 3: Higher proportional areas of uncropped land (primarily composed of field margin habitat) surrounding winter wheat fields increase the number of aerially dispersing aphid predators within them and thereby levels of aphid control.

Chapter 4: Aerially dispersing aphid predators utilise field margin resources directly and subsequently move into adjacent winter wheat fields.

Conclusions from the three Hypotheses considered and examined together clarify how field margins affect aerially dispersing aphid predators and the results could influence future management of field margins in order to maximise their potential for contributing to cereal aphid control in winter wheat fields.

In order to determine whether to accept or reject the Hypotheses, this study investigated the effects of field margins on aerially dispersing aphid predators at three levels.. Firstly at the single field scale, secondly at the landscape scale and finally determining direct utilisation of floral resources. Field margins in the context of this study were categorised as a perennial habitat strip, comprising of grass with or without a floral component between the boundary edges (such as hedges, fences etc.) and the crop edge (the outer edges of the cropped area in a field) in accordance with Greaves & Marshall (1987).

Field margins themselves were not designed to provide pest control, but were put into effect to protect wildlife habitat and improve landscape beauty and access

(Morris *et al.*, 2000). The effects of field margins on overall biodiversity have not been fully evaluated but studies that have considered the effects of field margins on invertebrate biodiversity deem them partially effective (Kleijn *et al.*, 2006) mainly when specific invertebrate families are the focus (Meek *et al.*, 2002; Carvell *et al.*, 2007). Generally, it is accepted that field margins boost numbers of some epigeal and aerial aphid predators (Denys & Tscharntke, 2002; Marshall & Moonen, 2002; Marshall *et al.*, 2006) through increasing numbers of common agricultural invertebrate species (Kleijn *et al.*, 2006). Although the study presented here did not measure invertebrates within field margins themselves, the potential effects of field margins could be far reaching (e.g. Tscharntke *et al.*, 2005) through the provisioning of a network of semi-natural habitat over the landscape that could be utilised by invertebrates foraging within crops.

This investigation needed to take into account the local and landscape scales at which invertebrates disperse. Despite greater numbers of studies now investigating the effects of non-crop and/or semi-natural habitat on aphid predators at landscape scales (Thies *et al.*, 2005; Schmidt & Tscharntke, 2005; Fiedler *et al.*, 2008; Haenke *et al.*, 2009) up to 4km radius (Haenke *et al.*, 2009), single field scale studies had not clarified how field margins might affect either specific aerially dispersing aphid predator species or groups, or the aerial predator guild as a whole (Schmidt *et al.*, 2003; Holland *et al.*, 2008b). The replicative single field scale study in Chapter 2 was necessary to establish a satisfactory link (if present) between the presence of field margin habitat and numbers of aerially dispersing aphid predators in both spatial and temporal terms. The impact of the proportional area of field margin habitat and the scale over which effects occurred was then investigated since it has been recognised previously that aerially dispersing aphid predators function at scales greater than the single field (Elliott *et al.*, 1999; Östman *et al.*, 2001; Elliott at al., 2002; Sarthou *et al.*, 2005; Freier *et al.*, 2007; Haenke et al,. 2009; Meyer *et al.*, 2009). Furthermore, the network of field margin habitats has been created over the UK landscape using agri-environment funding (Natural England, 2009) that may be enhancing biological control. Once these two scale components were addressed and conclusions established, the movements of predators in relation to aphid densities in the field were investigated in Chapter 4. This also involved a marking study to confirm the utilisation of field margin type habitat of the type pollen and nectar to establish direct utilisation.

There was also recognition that some groups of aerially dispersing aphid predators, such as Empididae, Dolichopodidae and Cantharidae, and their potential manipulation through habitat provisioning had been almost completely overlooked (Löbner & Hartwig, 1994; Schmidt *et al.*, 2003; Ulrich, 2005; Flückiger & Schmidt 2006; Grichanov, 2008; Harizanova, 2009; see also section 1.5.2, table 1.2); these groups were included and investigated within this study.

5.1.1. Summary of Results

Chapter 2 demonstrated that fields surrounded by 6m florally enhanced field margins could boost numbers of aerially dispersing aphid predators within winter wheat fields, especially early on in the season, when aphid population control is considered to be most effective (Edwards *et al.*, 1979; Chiverton, 1986). This study showed that groups and species of aphid predators previously trapped through epigeal methods can also be detected in flight/ballooning. Apart from Linyphiidae and *Tachyporus* spp., the other groups in Chapter 2 that were influenced by the presence of floristically enhanced field margins were Empididae, Dolichopodidae, Cantharidae and Syrphidae.

In the experimental design the addition of the cutting of two of the four margins, which was not expected, did add complexity to the statistical design and may have prevented the analysis of the field margin component in the model from generating more significant results because of the additional interactions. It did, however, present an opportunity to investigate the effect of cutting on aerially dispersing aphid predators; leading to the conclusion that field margin disturbance during the season can disrupt the movements of aerially dispersing predators. This may have the additional benefit of encouraging some predators into the adjacent crop, such as those belonging to the groups Linyphiidae, Dolichopodidae and Cantharidae, although the lack of the identification of Dolichopodidae to family or species led to the conclusion that the differences observed in numbers between cut and uncut margins were attributable to the presence of a water body rather than disturbance of the field margin due to cutting, however this point cannot be clarified. The removal of resources through cutting, however, could be considered to have a potentially negative effect in the medium term through depletion of floral resources.

Chapter 2 also demonstrates the necessity in choosing the correct method of invertebrate capture appropriate for the study and, uniquely, examines the suitability of both sticky traps and D-vac suction sampling for trapping aerially dispersing aphid predators belonging to various taxa with a variety of life history behaviours. Also, the combination of using sticky traps and D-vac suction sampling gave an indication at which point mainly epigeal species may fly, such as *Tachyporus* spp. The differing modes of locomotion temporally may affect the suitability of different trapping techniques depending on the time of the season for aerially dispersing aphid predators.

The four groups of aerially dispersing aphid predators studied in Chapter 3; Cantharidae, Empididae, *Tachyporus* spp. and Linyphiidae, were chosen on their responses to field margin presence at the single field scale in Chapter 2 and their expected differing responses based on their life histories. Neither Empididae or Linyphiidae exhibited a response to the proportional area of field margin habitat at any of the spatial scales studied, but Cantharidae and *Tachyporus* spp. did respond, although in both different ways and at different spatial scales. Aphid predation, measured using potted wheat and artificially introduced populations, was not affected by the proportional area of field margin habitat at any spatial scale. The lack of any effect may have been a consequence of the huge variation in each aphid pot population response within each field or the long period of rainfall between Julian days 14 and 22 may have masked subsequent population rises or falls owing to the proportional area of field margin habitat.

Chapter 4 allowed an in depth look at how flying aphid predators respond to aphid aggregations in a winter wheat field surrounded by different margin types that included a flower-rich strip. This allowed the additional trophic link between an aphid predator and floral resources to also be investigated and concluded that *Episyrphus balteatus* does use floral resources and move into adjacent winter wheat fields, although not at a distance greater than 120m in four days. Additionally, this aspect of the project discovered the close association between Empididae and aphid population patches and places the spotlight firmly on Empididae as a potentially very useful predator of cereal aphids that could be manipulated through the provisioning of floral resources.

The pilot study examining the suitability of rubidium chloride at marking *Episyrphus balteatus* and *Adalia bipunctata* was highly successful and hopefully will lead to more studies using this method to examine trophic links and resource utilisation in the agricultural ecosystem.

5.2. **The effect of at local and landscape scales by each predator taxa and resulting implications for aphid control**

Each of the aphid predator taxa responded differently to the field margins. Local scale responses to field margin presence did not necessarily lead to the detection of the effects of field margin densities at landscape scales. Of the four groups of aerially dispersing predators for which landscape effects were analysed in Chapter 3 (Cantharidae, Empididae, Linyphiidae and *Tachyporus* spp.) only two of these presented detectable effects of the proportional area of field margin habitat at the landscape scale. Each of the aerially dispersing aphid predator groups investigated and discussed previously is considered separately below, examining landscape scale responses, where present, to field margin densities for the four groups examined in Chapter 3 and taking into account the associations, where in evidence, with aphid aggregations in Chapter 4. Table 5.1 shows which groups of aerially dispersing aphid predators were investigated in each chapter.

Table 5.1 Aphid predator taxa investigated in each of the three chapters

Aphid predator group	Chapter 2	Chapter 3	Chapter 4
Cantharidae	✓	✓	✓
Carabidae	✓		
Coccinellidae	✓		
Dolichopodidae	✓		✓
Empididae	✓	✓	✓
Linyphiidae	✓	✓	
Neuroptera	✓		
Syrphidae	✓		✓
Tachyporus spp.	✓	✓	✓

5.2.1. Cantharidae

The group Cantharidae were mainly comprised of the species *Cantharis lateralis* in both studies carried out in Chapter 2 and Chapter 3. Since *C. lateralis* is a known aphid predator (Landis & van der Werf, 1997), manipulating numbers through habitat provisioning holds considerable potential. Chapter 2 indicated that the presence of a field margin boosted numbers of Cantharidae in adjacent winter wheat fields at a local scale; however, at a landscape scale there was a significant negative effect of the proportional area of field margin habitat on numbers of Cantharidae trapped. This does indicate some concerns regarding past research owing to the contradictory nature of results presented by Cantharidae in Chapter 2 and Chapter 3 which imply that the scale of the study influences the outcome. Considering Chapter 2 by itself would result in the conclusion that floristically enhanced field margins can benefit aphid control through the provisioning of aphid predating Cantharidae into adjacent winter wheat fields, however, Chapter 3 presents a different picture, showing that higher field margin densities result in lower numbers of Cantharidae present in the fields themselves, a result that is suppressed to an extent by the way sticky traps work by measuring activity-density. Cantharidae may exhibit increased levels of activity to locate resources that are fewer and farther between so are more likely to be trapped on the sticky traps, whereas the opposite is true; where there are larger numbers of resources, their activity is likely to be less (Chapter 3; Section 3.4.1.1). The difference in the response observed may be due to the availability of floral resources. In Chapter 2, floral resources were present in all field margins, whereas in Chapter 3, only a small portion of the field margins were had a floral component. The lack of floral resources present when correlating the proportional area of field margin habitat to numbers of Cantharidae may have affected the results. Repeating the study presented in Chapter 3 with field margins that are all floristically enhanced would clarify the difference in the response of Cantharidae based on field margin type.

Previous work that has focussed on landscape complexity as a factor affecting predators and parasitoids have not returned a negative correlation result, as far as is known, apart from one (Schmidt *et al.*, (2008) discussed further in Section 5.2.5); the majority have either found no or a positive correlation or a stalemate effect (where, although the beneficial enemy has increased in numbers caught, the number of aphid has followed suite) for at least one of the scales studied. Table 5.2 shows the categorisation of previous studies into these three divisions.

Table 5.2 results of past studies examining the correlations of landscape complexity an similar factors on aphid enemy species at different spatial scales (Table adapted and extended from Kremen & Chaplin, 2007). '+' :a positive correlation was found. '-' :a negative correlation was found; 'no' :no correlation and 'sm' :a stalemate response; 'Scale': the scale at which a relationship or relationships were found.

Study	Predictor variable	Enemy	+	-	no	sm	Scale (radius)
Purtauf *et al.*, (2005)	Percent cover of grassland	Carabidae	✓				1.5km
Clough *et al.*, (2005)	Percent cover of non-crop land	Spider diversity	✓				0.5km
Roschewitz *et al.*, (2005)	Percent cover of non-crop land	Parasitoids	✓			✓	1.0-2.0km
Thies *et al.*, (2005)	Percent cover of non-crop land	Parasitoids				✓	0.5-2.0km
Schmidt *et al.*, (2005)	Percent cover of non-crop land	Linyphiidae (by species)	✓		✓		1.0-3.0km
Schmidt *et al.*, (2008)	Percent cover of non-crop land	Spiders (by Species)	✓	✓			0.095-3.0km
Haenke *et al.*, (2009)	Percent cover of arable land	Syrphidae	✓				0.5-4.0km
Chapter 2	Proportional area of field margin habitat in m^2 per hectare	Cantharidae		✓			0.1-0.25km
Chapter 2	Proportional area of field margin habitat in m^2 per hectare	*Tachyporus* spp.	✓				0.5-1.0km
Chapter 2	Proportional area of field margin habitat in m^2 per hectare	Empididae			✓		0.05-1.0km
Chapter 2	Proportional area of field margin habitat in m^2 per hectare	Linyphiidae			✓		0.05-1.0km

5.2.2. Syrphidae

Although Syrphidae were not studied in Chapter 3 and were not trapped in high numbers, a parallel can be drawn between the conflicting results from studies examining the effect that floral resources have on *E. balteatus* and the results from Chapter 2 and Chapter 4. Cowgill *et al.* (1993a), Hickman & Wratten (1996), MacLeod (1999), Wratten *et al.* (2003b) and Kohler *et al.* (2008) found that *E. balteatus* were found close to field edges or floral resources, but were not found in large numbers within cropped fields, possibly due to a retention effect. This concurs with the results in Chapter 2; where floral resources were present there was a decreasing gradient in the number of Syrphidae between 20m and 80m into the field. This may also explain why so few rubidium marked *E. balteatus* were trapped in Chapter 4, but population patches of *E. balteatus* close to the floral resource were not observed as expected; reasons for this are discussed further in Chapter 4, Section 4.4.3.

5.2.3.* Tachyporus *spp.

Tachyporus spp. were found to exist at greater numbers in fields with floristically enhanced margin surrounds in Chapter 2 during mean trapping date 5th June which potentially places them in an ideal position, both spatially and temporally, to maximise predation on growing aphid populations.

Additionally, the ability of *Tachyporus* spp. to locate aphid aggregations (Bryan & Wratten, 1984) is most likely due to their flight capability and, furthermore, numbers of *Tachyporus* spp. can be manipulated by providing appropriate overwintering field margin habitat at a local scale (Dennis & Fry, 1992; Griffiths *et al.*, 2007). They were also affected by proportional area of field margin habitat in m^2 per hectare at the landscape scale with the greatest correlation effect occurring at the 750m radius scale. Previously the effect of field margins on species that overwinter within them have not been considered at landscape scales. The focus has either been on non-crop habitat as a whole or the influence of floral resources throughout the landscape. Chapter 3 confirms that increasing the density of overwintering sites for *Tachyporus* spp. in the form of field margins holds a very beneficial effect. However, since the strongest significant relationship was found at a 750m radius, this has profound implications for the maintenance of a network of field margins for aphid predators between neighbouring farms within the agricultural landscape. The mean farm size for the UK is 70 hectares, although this includes livestock farms and, hence, consists of 56% permanent pasture (data from 1993; Eastwood *et al.*, (2010)). The mean buffer size for the 750m radius in Chapter 3 was 279 hectares; considerably greater than a single farm area. Synergistic benefits can therefore potentially be attained through neighbouring farms developing a network of field margin habitats together.

5.2.4. Empididae

Empididae are an overlooked predator within the agricultural ecosystem, probably due to the large numbers of species that exist and their high levels of mobility as well as the focus on epigeal predators and the difficulty in identifying the huge number of species. Within this study overall they were highlighted as being an important aphid predator within winter wheat fields which responded positively to the presence of a florally enhanced field margin in Chapter 2, but also exhibited aggregations to aphid patches and field edges where floral resources existed in Chapter 4. Their presence in high numbers and the ability of some of the species found in agricultural fields and in this study (such as *Empis tessallata* trapped on sticky traps in Chapter 2) to be both predatory and flower-feeding (Burkhill, 1946; Chvála, 1994; Preston-Mafham, 1999) indicates potential to be manipulated through the provisioning of floral resources within agro-ecosystems. The lack of a response to the proportional area of field margin habitat in m^2 per hectare in Chapter 3 may be due to two reasons. Firstly, the lack of floral resources present surrounding the fields in the study and secondly, there are many species of Empididae that use a wide variety of habitats, such as trees and grasslands (Delettre *et al.*, 1992; 1997), that were present over the study areas in Chapter 3. Further identification and investigation of species that may be encouraged through habitat manipulation is required.

5.2.5. Linyphiidae

Linyphiidae were studied in Chapters 2 and 3, investigating the effect of field margins at the local and landscape scale. Linyphiidae were present in significantly higher numbers ballooning over fields with field margin surrounds, but this was not translated into those caught within the fields themselves despite evidence of previous studies to the contrary (Schmidt *et al.*, 2005; Schmidt *et al.*, 2008). The study in Chapter 3 did not show Linyphiidae to respond to proportional area of field margin habitat at the landscape scale for which there are two possible explanations:

1. Linyphiidae species respond to non-crop habitat both at different spatial scales and either negatively or positively depending on the species being studied (Schmidt *et al.*, 2008). Since Linyphiidae were not identified to species level, the response to proportional area of field margin habitat by different species may have been masked. Using the results from Schmidt *et al.* (2008) which enabled the grouping of Linyphiidae species into those that responded to landscape complexity either positively, negatively or no response and applying them to the Linyphiidae caught in this study may have identified which species (if any) responded to proportional area of field margin habitat and could be considered for similar future studies.

2. Linyphiidae use a variety of non-crop perennial habitats within which to overwinter (Schmidt *et al*., 2005), although field margins have been shown previously to be of particular use (Lemke & Poehling, 1997; 2002). The other habitats present within the study areas may have been also been used by Linyphiidae so overriding an effect of the margins. A greater number of replicates than used in this study would be needed to identify a correlation between total non-crop habitat or different habitat types and numbers of Linyphiidae. Additionally Linyphiidae disperse at different times temporally during the season, depending on their habitat, as shown by Thomas & Jepson (1999).

5.2.6. Dolichopodidae

Dolichopodidae were found in higher numbers closer to field edges in Chapter 2 but were not aggregated close to field margin edges in Chapter 4. Some of the distributions of Dolichopodidae between field types in Chapter 2 were attributed to the life history of some Dolichopodidae species that have been shown to increase in numbers in the presence of water bodies (Aquilina *et al.*, 2007). Dolichopodidae, unlike Empididae, are either predatory or feed on pollen and nectar (as far as is known), not both. This limits their potential manipulation through the use of floral resources but also may explain the lack of aggregations found at field edges in Chapter 4. Again, unfortunately, the lack of separation into genus and/or species may hide the distribution effects that may exist between those that are predatory and those that are not. Identification of this family of Diptera to species is time consuming owing to the difficult taxonomy and there was insufficient time available in this study.

5.3. **Do field margins have an effect on the spatial and temporal distributions of aerially dispersing aphid predators in UK winter wheat fields?**

Overall, the presence of field margins does have an effect on the spatial and temporal distributions of some aerially dispersing aphid predators, but the response of each predator group varies depending on numerous interlinking components of their life history. There are two main facets of aerially dispersing aphid predators that are evident from this study. Firstly, predators, such as *Tachyporus* spp., which primarily utilise field margins in the colder months in which to overwinter, do not require floral resources, respond to proportional area of field margin habitat positively at scales between 500m to 1000m, and possibly beyond, and are likely to exhibit long term distribution changes to the presence of field margins (Coombes & Sotherton, 1986; MacLeod *et al*., 2004). Secondly, those predators that use floral resources in field margins, respond to proportional area of field margin habitat at local scales (both positively and negatively possibly depending on the type of resources available) and are likely to exhibit short term distributional changes as a result of ephemeral floral resources for which they utilise field margins. Aerially dispersing aphid predators are therefore affected by:

1. Field margin type
2. The proportional area of field margin habitat
3. Scale

Although field margin type was not examined in this study overall, extrapolations can be made. The results from Chapter 2, showing a positive response of a range of aerially dispersing aphid predators is likely to be as result of a high proportion of floristically enhanced field margin habitat surrounding each field, which, as results from the field proportional area of field margin habitat data collected in Chapter 3, are not considered to be normal for the average winter wheat field. Therefore, the type of field margin, namely the presence of a floral component, is likely to affect the presence of predators that use floral resources and both within the margins themselves (Sutherland *et al*., 2001) and in adjacent fields (Harwood *et al*., 1994). If all the field margins that were mapped in Chapter 3 were florally enhanced, the anticipated results for the experiment would be expected to be different and it remains to be seen whether Cantharidae would still exhibit a negative response to proportional area of field margin habitat.

Field margins, in their current state in the UK, where only a very small percentage of them contain a floral component, cannot be said to enhance aphid control to their maximum capability. The positive response of *Tachyporus* spp. to proportional area of field margin habitat at larger landscape scales is notable but, as indicated by Tscharntke *et al*. (2007), it falls to a suite of predators to contribute to aphid control between years. The implementation of higher densities of floristically enhanced field margins throughout the UK and the result on aphid predators and subsequent aphid predation warrants further investigation if field margins are to be considered to be used to enhance aphid control.

5.4. **Limitations of this study**

The statistical power available in Chapter 3 study was limited due to the relatively low number of replicates (n = 12 to 10 depending on the scale used). Although previous studies have not used many more replicates (Steffen-Dewenter *et al.*, (2002); Kruess, (2003) and Thies *et al.*, (2003), all used 15 replicates), a higher number of replicates would allow for a greater number of analyses to be carried out. A more extensive study could have been conducted at the expense of within season sampling frequency but because of the relatively large temporal window over which predatory invertebrates may attack aphids and their within season variability, a frequent sampling programme was considered essential.. From Chapter 2 it is clear that field margins have both early-season and peak aphid season effects depending on the life history of the predator being concerned (discussed further in Chapter 3; Section 3.4.2). Through employing this 'catch-all' temporal pooling of data, some of the subtleties in the data may be lost, however, some important significant effects were detected.

The final study (Chapter 4) was disrupted by the weather which meant that trapping was delayed and consequently huge numbers of *E. balteatus* that were subsequently trapped; most likely due to either high levels of immigration or mass hatching of hoverfly pupae in the adjacent crops themselves. Additionally, a recent study by van Rijn & Wäckers (2010), found that *E. balteatus* do not obtain pollen and nectar from flowers belonging the family Fabaceae, such as clover. Therefore, although pollen and nectar were available from the other floral plants in the pollen and nectar strip, mainly *Medicago lupulina*, nearly half of the floral resources present at the time of the study were clover. This would have limited the uptake of the rubidium marker by *E. balteatus.*

5.5. **Overall conclusions and field margin management recommendations**

The scope of this study was broad since it examined a wide range of aphid predator taxa and their responses at local to landscape scales. It provides both a focussed and overarching view on how field margins may affect aerially dispersing predators in winter wheat fields.

Although field margins were not implemented in UK agri-environment schemes with the aim to provide pest control, rather, biodiversity, the 'insurance hypothesis', where a greater level of biodiversity present insures against loss of ecosystem functioning in fluctuating environments (Yachi & Loreau, 1999), would seem to applicable whereby increasing biodiversity network around arable fields increases the overall availability in terms of both numbers and species of predators involved in aphid control. Since each predator group responds to field margins in different ways, some even having a negative impact, there is likely to be redundancy in the system. Field margins cannot be expected to increase all aphid predators in adjacent fields and beyond and they may ‘draw’ beneficial invertebrates away from cropped fields in which control is required. What this study does show is that field margins may boost some aerially dispersing aphid predator numbers in adjacent winter wheat fields when proportional area of field margin habitat is considered at a landscape scale, but owing to the area over which this covers, neighbouring farms need to consider the implementation of a field margin network among themselves rather than at the single farm level.

5.6. **Further work**

The study of aphid predators at the landscape scale is in its infancy but has become more accessible in recent times due to the availability of technology such as Geographical Information Systems (GIS) programs and land and habitat use maps being available in digital form. This study highlights the need for ecology, especially when considering agricultural ecology, to be considered at scales larger than single field scale when the organisms themselves are able to travel at distances greater than this. The contradictory results presented by Cantharidae encourage larger scale studies to be implemented in order to gain knowledge of the wider influence that habitat manipulations can have. There is an overall need for studies to be carried out at landscape scales as pointed out by Clough *et al.*, (2007); Cronin & Reeve (2005) and Tscharntke *et al.*, (2005). The potential differences that florally enhanced field margins could have on the distributions of aerially dispersing aphid predators compared to solely grassy margins needs clarification. The investigation of the use of rubidium chloride in this study also marks it out as being useful in open systems at measuring the utilisation of habitat manipulations within the agro-ecological landscape by pest predators and warrants further investigations.

References

Acreman, T. M. & Dixon, A. F. G. (1985) Developmental patterns in wheat and resistance to cereal aphids. *Crop Protection*, **4**, 322-328.

Almohamad, R., Verheggen, F. J. & Haubruge, E. (2009) Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. *Biotechnology*, *Agronomy*, *Society and Environment*, **13**, 467-481.

Ankersmit, G.W., Dijkman, H., Keuning, N. J., Mertens, H., Sins, A. & Tacoma, H. M. (1986) *Episyrphus balteatus* as a predator of the aphid *Sitobion avenae* on winter wheat. *Entomologia Experimentalis et Applicata*, **42**, 271-277.

Aquilina, R., Williams, P., Nicolet, P., Stoate, C. & Bradbury, R. (2007) Effect of wetting-up ditches on emergent insect numbers. *Aspects of Applied Biology*, **81**, 261-262.

Asteraki, E.J., Hanks, C.B. & Clements, R.O. (1995) The influence of different types of grassland field margin on carabid beetle (Coleoptera, Carabidae) communities. *Agriculture*, *Ecosytems and Environment*, **54**, 195-202.

Atlihan, R., Kaydan, B. & Özgökçe, M. (2004) Feeding activity and life history characteristics of the generalist predator, *Chrysoperla carnea* (Neuroptera: Chrysopidae) at different prey densities. *Journal of Pest Science*, **77**, 17-21.

Aylor, D.E. & Irwin, M.E. (1999) Aerial dispersal of pests and pathogens: implications for integrated pest management. *Agricultural and Forest Meteorology*, **97**, 233-234.

Bargen, H., Saudhof, K. & Poehling, H. M. (1998) Prey finding by larvae and adult females of *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata*, **87**, 245-254.

Bell, J. R., Johnson, P. J., Hambler, C., Haughton, A. J., Smith, H., Feber, R. E., Tattersall, F. H., Hart, B. H., Manley, W. & Macdonald, D. W. (2002) Manipulating the abundance of *Lepthyphantes tenuis* (Araneae: Linyphiidae) by field margin management. *Agriculture Ecosystems & Environment*, **93**, 295-304.

Bergman, K. O., Askling, J., Ekberg, O., Ignell, H., Wahlman, H. & Milberg, P. (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography*, **27**, 619-628.

Berry, W. L., Stimmann, M. W. & Wolf, W. W. (1972) Marking of native phytophagous insects with rubidium: a proposed technique. *Annals of the Entomological Society of America*, **65**, 236-238.

Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1715-1727.

Bilde, T & Toft, S. (1997) Consumption by carabid beetles of three cereal aphid species relative to other prey types. *Entomophaga*, **42**, 21-32.

Boatman, N. D., Jones, N. E., Garthwaite, D. & Bishop, J. (2007) Evaluation of the operation of Environmental Stewardship. Final report to Defra, project MA01028 DEFRA.

Boatman, N. D. & Sotherton, N. W. (1988) The agronomic consequences and costs of managing field margins for game and wildlife conservation. *Aspects of Applied Biology*, **17**, 47-56.

Bommarco, R. & Fagan, W. F. (2002) Influence of crop edges on movement of generalist predators: a diffusion approach. *Agricultural and Forest Entomology*, **4**, 21-30.

Bommarco, R., Firle, S.O. & Ekbom, B. (2007) Outbreak suppression by predators depends on spatial distribution of prey. *Ecological Modelling*, **201**, 163-170.

Bowden, J., Sherlock, P. L. & Digby, P. G. N. (1985) Studies of elemental composition as a biological marker in insects. III. Comparison of apterous and alate cereal aphids, especially *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), from oats and wheat, and from oats infected with or free from barley yellow dwarf virus. *Bulletin of Entomological Research*, **75**, 477-488.

Bowie, M. H., Gurr, G. M., Hossain, Z., Baggen, L. R. & Frampton, C. M. (1999). Effects of distance from field edge on aphidophagous insects in a wheat crop and observations on trap design and placement. *International Journal of Pest Management*, **45**, 69-73.

Brooks, D. R., Perry, J. N., Clark, S. J., Heard, M. S., Firbank, L., Holdgate, R., Mason, N. S., Shortall, S. R., Skellern, M. P. & Woiwod, I. P. (2008) National-scale metacommunity dynamics of carabid beetles in UK farmland. *Journal of Animal Ecology*, **77**, 265-274.

Brooks, S. E. (2005) Characteristics and natural history of Dolichopodidae. North American Diperists Society. http://www.nadsdiptera.org/Doid/Dolichar/Dolichar.htm Accessed June 2007.

Bryan, K. M. & Wratten, S. D. (1984) The responses of polyphagous predators to prey spatial heterogeneity: aggregation by carabid and staphylinid beetles to their cereal prey. *Ecological Entomology*, **9**, 251-259.

Bugg, R. L. (1992) Habitat manipulation to enhance the effectiveness of aphidophagous hoverflies (Diptera: Syrphidae). http://www.sarep.ucdavis.edu/NEWSLTR/v5n2/sa-11.htm Accessed July 2007.

Burgio, G., Ferrari, R., Boriani, L., Pozzati, M. & van Lenteren, J. (2006) The role of ecological infrastructures on Coccinellidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems. *Bulletin of Insectology*, **59**, 59-67.

Burkhill, I. H. (1946) Flies of the family Empididae and other insect visitors to the flowers of *Tamus communis*. *Proceedings of the Linnean Society of London*, **157**, 99-102.

Cao, Y., Williams, D. D. & Larsen, D. P. (2002) Comparison of ecological communities: the problem of sample representativeness. *Ecological Monographs*, **72**, 41-56.

Carter, N., McLean, I. F. G., Dixon, A. F. G. & Watt, A. D. (1980) Cereal aphids - a case study and review. *Applied Biology*, **5**, 271-348.

Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29-41.

Chambers, R. J. & Adams, T. H. L. (1986) Quantification of the impact of hoverflies (Diptera, Syrphidae) on cereal aphids in winter-wheat - an analysis of field populations. *Journal of Applied Ecology*, **23**, 895-904.

Chambers,R.J., Sunderland,K.D., Wyatt,I.J. & Vickerman,G.P. (1983) The effects of predator exclusion and caging on cereal aphids in winter wheat. *Journal of Applied Ecology*, **20**, 209-224.

Chandler, A. E. F. (1968) Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). *Annals of Applied Biology*, **61**, 435-446.

Chapman, J. W., Reynolds, D. R. & Smith, A. D. (2004). Migratory and foraging movements in beneficial insects: a review of radar monitoring and tracking methods. *International Journal of Pest Management*, **50**, 225-232.

Chapman, J.W., Reynolds, D.R., Brooks, S.J., Smith, A.S. & Woiwod, I.P. (2006) Seasonal variation in the migration strategies of the green lacewing *Chrysoperla carnea* species complex. *Ecological Entomology*, **31**, 378-388.

Chapman, J.W., Reynolds, D.R., Smith, A.D., Smith, E.T. & Woiwod, I.P. (2004) An aerial netting study if insects migrating at high altitude over England. *Bulletin of Entomological Research*, **94**, 123-136.

Chiverton, P. A. (1986) Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Hom: Aphididae) in spring barley. *Annals of Applied Biology*, **109**, 49-60.

Chvála, M. (1994) The Empidoidea (Diptera) of Fennoscandia and Denmark. III. Genus Empis. *Fauna Entomologica Scandinavica*, **29**, 1-192.

Clemens, S. (2006) Toxic metal accumulation, responses to exposure and mechanisms of tolerance in plants. *Biochimie*, **88**, 1707-1719.

Clough, Y., Kruess, A. & Tscharntke, T. (2007) Local and landscape factors in differently managed arable fields affect the insect herbivore community of a non-crop plant species. *Journal of Applied Ecology*, **44**, 22-29.

Clough, Y., Kruess, A., Kleijn, D. & Tscharntke, T. (2005) Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *Journal of Biogeography*, **32**, 2007-2014.

Collins, K. L., Boatman, N. D., Wilcox, A., Holland, J. M. & Chaney, K. (2002) Influence of beetle banks on cereal aphid predation in winter wheat. *Agriculture*, *Ecosytems and Environment*, **93**, 337-350.

Colyer, C. N. & Hammond, C. O. (1968) *Flies of the British Isles.* Frederick Warne and Co. Ltd. London.

Coombes, D. S. & Sotherton, N. W. (1986) The dispersal and distribution of polyphagous predatory Coleoptera in cereals. *Annual of Applied Biology*, **108**, 461-474.

Cowan, R. & Gunby, P. (1996) Sprayed to death: path dependence, lock-in and pest control strategies. *The Economic Journal*, **106**, 521-542.

Cowgill, S. E., Wratten, S. D. & Sotherton, N. W. (1993a) The selective use of floral resources by the Hoverfly *Episyrphus balteatus* (Diptera, Syrphidae) on farmland. *Annuals of Applied Biology*, **122**, 223-231.

Cowgill, S. E., Wratten, S. D. & Sotherton, N. W. (1993b) The effect of weeds on the numbers of Hoverfly (Diptera, Syrphidae) adults and the distribution and composition of their eggs in winter-wheat. *Annals of Applied Biology*, **123**, 499-515.

Critchley, C. N. R., Fowbert, J. A., Sherwood, A. J. & Pywell, R. F. (2006) Vegetation development of sown grass margins in arable fields under a countrywide agri-environment scheme. *Biological Conservation*, **132**, 1-11.

Cronin, J. T. & Reeve, J. D. (2005) Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2225-2235.

Cumming, J. M. (2006) Characteristics and Natural History of "Empididae". http://www.nadsdiptera.org/Doid/Empidchar/Empidchar.htm Accessed May 2007.

De Cauwer, B., Reheul, D., De Laethauwer, S. & Milbau, A. (2006) The effect of light and botanical species richness on insect diversity. *Agronomy for Sustainable Development*, **26**, 35-43.

De Wolf, E. (2002) Barley Yellow Dwarf Virus. Field crop disease facts. Pennsylvania State University. Online. *Pennsylvania State University.Online.* http://extension.psu.edu/small-grains/documents/barley-yellow-dwarf.pdf Accessed October 2006.

Dean, G. J. W. (1982) Phenology of aphidophagous predators. *Annals of Applied Biology*, **108**, 219-231.

DEFRA. Environmental Stewardship: Entry Level Stewardship Handbook 1st Edition (2005) Department for Environment, Food and Rural Affairs.

Delettre, Y. R., Morvan, N., Tréhen, P. & Grootaert, P. (1997) Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea). *Biodiversity and Conservation*, **7**, 9-25.

Delettre, Y. R., Tréhen, P. & Grootaert, P. (1992) Space heterogeneity, space use and short-range dispersal in Diptera: A case study. *Landscape Ecology*, **6**, 175-181.

Dennis, P. & Fry, G. L. A. (1992) Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland. *Agriculture, Ecosytems and Environment*, **40**, 95-115.

Dennis, P., Thomas, M. B. & Sotherton, N. W. (1994). Structural features of field boundaries which inDaveris dtressed dsfluence the overwintering densities of beneficial arthropod predators. *Journal of Applied Ecology*, **31**, 361-370.

Denys, C. & Tscharntke, T. (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, **130**, 315-324.

Desneux, N., Decourtye, A. & Delpuech, J. (2007) The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology*, **52**, 81-106.

Dixon, A. F. G. (1977) Aphid ecology: life cycles, polymorphism, and population regulation. *Annual Review of Ecology and Systematics*, **8**, 329-353.

Dixon, A. F. G. (1987) Cereal aphids as an applied problem. *Agricultural Zoology Reviews*, **2**, 1-57.

Donald, P.F. & Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, **43**, 209-218.

Dover, J. W. (1994) Arable field margins: factors affecting butterfly distribution and abundance. *BCPC Monograph no 58, Field Margins: Integrating Agriculture and Conservation* (ed. By N. Boatman, N.) pp 109-116. British Crop Protection Council, Warwick.

Downes, J. A. & Smith, S. M. (1969) New or little known feeding habits in Empididae (Diptera). *The Canadian Entomologist*, **101**, 404-408.

Duelli, P. (1990) Population movements of Arthropods between natural and cultivated areas. *Biological Conservation*, **54**, 193-207.

Duffey, E. (1980) The efficiency of the Dietrick Vacuum Sampler (DVAC) for invertebrate population studies in different types of grassland. *Bulletin of Ecology*, **11**, 421-431.

Duffield, S. J, & Aebischer, N. J. (1994) The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter-wheat. *Journal of Applied Ecology*, **31**, 263-281.

Duffield, S. J., Bryson, R. J., Young, J .E. B., Sylvester-Bradley, R. & Scott, R. K. (1997) The influence of nitrogen fertiliser on the population development of the cereal aphids Sitobion avenae (F.) and Metopolophium dirhodum (Wlk.) on field grown winter wheat. *Annals of Applied Biology*, **130**, 13-26.

Dutilleul, P. (1993) Modifying the t-test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305-314.

Eastwood, R., Lipton, M. & Newell, A. (2010) Chapter 65: Farm Size. In: *Handbook of Agricultural Economics, Volume 4.* (ed. By Pingali, P. & Evenson, R.), pp. 3323-3397. Elsevier, Amsterdam.

Edwards, C. A., Sunderland, K. D. & George, K. S. (1979) Studies of polyphagous predators of cereal aphids. *Journal of Applied Ecology*, **16**, 811-823.

Ehler, L. E. (1998) Conservation biological control: past, present, and future. *Conservation Biological Control* (ed. by P. Barbosa), pp. 1-8. Academic, San Diego.

Ellingsen, I. J. (1969) Fecundity, aphid consumption and survival of the aphid predator *Adalia bipunctata* L. (Col., Coccinellidae). *Norsk Entomologisk Tidsskr*, **16**, 91-95.

Elliott, N. C., Kieckhefer, R. W. & Beck, D. A. (2002) Effect of aphids and the surrounding landscape on the abundance of Coccinellidae in cornfields. *Biological Control*, **24**, 214-220.

Elliott, N. C., Kieckhefer, R. W., Lee, J. H. & French, B. W. (1999) Influence of within-field and landscape factors on aphid predator populations in wheat. *Landscape Ecology*, **14**, 239-252.

Eom, Y. S. (1994) Pesticide Residue Risk and Food Safety Valuation: A Random Utility Approach. *American Journal of Agricultural Economics*, **76**, 760-771.

Feber, R. E., Smith, H. & Macdonald, D. W. (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology* **33**, 1191-1205.

Fernandes, O. A., Wright, R. J., Baumgarten, K. H. & Mayo, Z. B. (1997) Use of rubidium to label *Lysiphlebus testaceipes* (Hymenoptera: Braconidae), a parasitoid of greenbugs (Homoptera: Aphididae), for dispersal studies. *Environmental Entomology*, **26**, 1167-1172.

Fernandez Garcia, A., Griffiths, G.J.K. & Thomas, C.F.G. (2000) Density, distribution and dispersal of the carabid beetle Nebria brevicollis in two adjacent cereal fields. *Annals of Applied Biology*, **137**, 89-97.

Flückiger, R. & Schmidt, M. H. (2006) Contribution of sown wildflower areas to cereal aphid control: from local to landscape scale. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants wprs Bulletin*, **29**, 41-44.

Fournier, E. & Loreau, M. (1999). Effects of newly planted hedges on ground-beetle diversity (Coleoptera, Carabidae) in an agricultural landscape. *Ecography*, **22**, 87-97.

Frampton, G. K., Ãilgi, T., Fry, G. L. A. & Wratten, S. D. (1995) Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. *Biological Conservation*, **71**, 347-355.

Frazer, B. D. & Raworth, D. A. (1974) Marking aphids with rubidium. *Canadian Journal of Zoology*, **52**, 1135-1136.

Freier, B., Triltsch, H., Möwes, M. & Moll, E. (2007) The potential of predators in natural control of aphids in wheat: Results of a ten-year field study in two German landscapes. *Biocontrol*, **52**, 775-788.

Graham, H. M., Wolfenbarger, D. A. & Nosky, J. B. (1978) Labeling plants and their insect fauna with rubidium. *Environmental Entomology*, **46**, 379-383.

Greaves, M. P. & Marshall, E. J. P. (1987) Field margins: definitions and statistics. In: *British Crop Protection Council Monograph No. 35: Field Margins* (ed. by J. M. Way & P. W. Grieg-Smith), pp. 3-11. Thornton Heath: British Crop Protection Council.

Greenleaf, S., Williams, N., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589-596.

Greenslade, P. J. M. (1964). Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, **33**, 301-310.

Greenslade, P. J. M. & Southwood, T. R. E. (1962) The relationship of flight and habitat in some Carabidae (Coleoptera). *The Entomologist*, **95**, 86-88.

Grichanov, I. (2008) Possibilities of application of predatory long-legged flies (Diptera, Dolichopodidae) for biological control of pests. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants*, *East Palaearctic Regional Section Bulletin*, **38**, 94-95.

Griffiths, G. J. K., Holland, J. M., Bailey, A. & Thomas, M. B. (2008). Efficacy and economics of shelter habitats for conservation biological control. *Biological Control*, **45**, 200-209.

Griffiths, G. J. K., Williams, E., Winder, L., Holland, J. M. & Thomas, C. F. G. (2000). The importance of field boundaries for whole-farm biodiversity conservation. *The BCPC Conference: Pests and diseases*, *Volume 1. Proceedings of an international conference held at the Brighton Hilton Metropole Hotel*, *Brighton*, *UK*, *13-16 November 2000*.

Griffiths, G. J. K., Winder, L., Bean, R., Moate, R., Neal, R., Williams, E., Holland, J. M. & Thomas, C. F. G. (2001) Laser marking the carabid *Pterostichus melanarius* for mark-release-recapture. *Ecological Entomology*, **26**, 662-663.

Griffiths, G. J. K., Winder, L., Holland, J. M., Thomas, C. F. G. & Williams, E. (2007) The representation and functional composition of carabid and staphylinid beetles in different field boundary types at a farm-scale. *Biological Conservation*, **135**, 145-152.

Gu, H., Wäckers, F., Steindl, P., Gunther, D. & Dorn, S. (2001) Different approaches to labeling parasitoids using strontium. *Entomologia Experimentalis et Applicata*, **99**, 173-181.

Guillebeau, L. P., All, J. N., Nutter, F. W. & Kuhne, C. (1993) Comparison of foliar and soil-drench applications of aqueous rubidium chloride solutions to plants for marking feeding aphids (Homoptera, Aphidae). *Journal of Entomological Science*, **28**, 370-375.

Gurr, G. M., Wratten, S. D. & Barbosa, P. (2000) Success in Conservation Biological Control of Arthropods. *Biological Control: Measures of Success*. (ed. by G.M. Gurr & S. D. Wratten) pp. 105-132. Kluwer Academic Publishers.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. & Thies, C. (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *Journal of Applied Ecology*, **46**, 1106-1114.

Hagler, J. R. & Jackson, C. G. (2001) Methods for marking insects: Current techniques and future prospects. *Annual Review of Entomology*, **46**, 511-543.

Halley, J. M., Thomas, C. F. G. & Jepson, P. C. (1996). A model for the spatial dynamics of linyphiid spiders in farmland. *Journal of Applied Ecology*, **33**, 471-492.

Hand, S. C. (1986) The capture efficiency of the Dietrick vacuum insect net for aphids on grasses and cereals. *Annals of Applied Biology*, **108**, 233-241.

Hand, S. C. (1989) The overwintering of cereal aphids on Gramineae in southern England, 1977-80. *Annals of Applied Biology*, **115**, 17-29.

Harizanova, V. (2009) *Rhagonycha fulva* Scop. (Cantharidae, Coleoptera) an effective predator of aphids (Aphididae, Hymenoptera [Homoptera]). *Vissh Selskostopanski Institut "Vasil Kolarov" Plovdiv Nauchni Trudove*, **40**, 129-132.

Harwood, J. D., Sunderland, K. D. & Symondson, W. O. C. (2001) Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology*, **38**, 88-99.

Harwood, J. D., Sunderland, K. D. & Symondson, W. O. C. (2003) Web-location by linyphiid spiders: prey-specific aggregation and foraging strategies. *Journal of Animal Ecology*, **72**, 745-756.

Harwood, R. W., Wratten, S. D., Nowakowski, M. & Marshall, E. J. P. (1994) Wild flower strips and winter/summer populations of beneficial invertebrates on farmland. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants*, *West Palaearctic Regional Section Bulletin*, **17**, 211-219.

Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L. & Bourke, A.F.G. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*, **3**, 638-641.

Hickman, J. M. & Wratten, S. D. (1996) Use of *Phelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *Journal of Economic Entomology*, **89**, 832-840.

Hickman, J. M., Wratten, S. D., Jepson, P. C. & Frampton, C. M. (2001) Effect of hunger on yellow water trap catches of hoverfly (Diptera:Syrphidae) adults. *Agricultural and Forest Entomology*, **3**, 35-40.

Hodek, I., Iperti, G. & Hodkova, M. (1993) Long-distance flights in Coccinellidae (Coleptera). European *Journal of Entomology*, **90**, 403-414.

Holland, J. M. and Luff, M. L. (2000). The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrated Pest Management Reviews*, **V5**, 109-129.

Holland, J. M., Oaten, H., Moreby, S., Southway, S. (2008b) The impact of agri-environment schemes on cereal aphid control. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants*, *West Palaearctic Regional Section Bulletin*, **34**, 33-36.

Holland, J. M., Oaten, H., Southway, S. & Moreby, S. (2008a) The effectiveness of field margin enhancement for cereal aphid control by different natural enemy guilds. *Biological Control*, **47**, 71-76.

Holland, J. M., Perry, J. N. and Winder, L. (1999) The within-field spatial and temporal distribution of arthropods in winter wheat. *Bulletin of Entomological Research*, **89**, 499-513.

Holland, J. M., Thomas, C. F. G., Birkett, T., Southway, S. & Oaten, H. (2005). Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. *Journal of Applied Ecology* **42**, 1140-1152.

Holland, J. M. (2002) *The Agroecology of Carabid Beetles.* p 356. Intercept, Andover.

Holland, J.M. (2006) The potential of agri-environment schemes to enhance biocontrol in arable crops. *Aspects of Applied Biology*, **81**, 127-134

Holland, J.M., Begbie, M., Birkett, T., Southway, S., Thomas, S.R., Alexander, C.J. & Thomas, C.F.G. (2004) The spatial dynamics and movement of *Pterostichus melanarius* and *P. madidus* (Carabidae) between and within arable fields in the UK. *International Journal of Ecology and Environmental Sciences*, **30**, 35-53.

Hondelmann, P., Borgemeister, C. & Poehling, H. M. (2005) Restriction fragment length polymorphisms of different DNA regions as genetic markers in the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae). *Bulletin of Entomological Research*, **95**, 349-359.

Irwin, M. E. (1999) Implications of movement in developing and deploying integrated pest management strategies. *Agricultural and Forest Meteorology*, **97**, 235-248.

Jalali, M., Tirry, L. & Clercq, P. (2009) Effects of food and temperature on development, fecundity and life-table parameters of *Adalia bipunctata* (Coleoptera: Coccinellidae). *Journal of Applied Entomology*, **133**, 615-625.

Jansen, J. P. (2000) A three-year field study on the short-term effects of insecticides used to control cereal aphids on plant-dwelling aphid predators in winter wheat. *Pest Management Science*, **56**, 533-539.

Jauker, F., Diekötter, T., Schwarzbach, F. & Wolters, V. (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, **24**, 547-555.

Jones, D. B., Giles, L. K., Chen, Y. & Shufran, K. A. (2004). Estimation of Hymenopteran parasitism in cereal aphids by using molecular markers. *Journal of Economic Entomology*, **98**, 217-221.

Jones, M. G. (1976) The arthropod fauna of a winter wheat field. *Journal of Applied Ecology*, **13**, 61-85.

Kan, E. (1988) Assessment of aphid colonies by hoverflies. I. Maple aphids and *Episyrphus balteatus* (de Geer) (Diptera: Syrphidae). *Journal of Ethology*, **6**, 39-48.

Karley, A. J., Parker, W. E., Pitchford, J. W. & Douglas, A. E. (2004) The mid-season crash in aphid populations: why and how does it occur? *Ecological Entomology*, **29**, 383-388.

Kevan, P. G. & Baker, H. G. (1983) Insects as flower visitors and pollinators. *Annual Review of Entomology*, **28**, 407-453.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947-969.

Kleijn, D., Baquero, R. A., Clough, Y., Diaz, M., De Esteban, Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruess, A., Marshall, E. J. P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T. M. & Yela, J. L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243-254.

Kleijn, D. & van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, **7**, 201-214.

Kohler, F., Verhulst, J., van Klink, R. & Kleijn, D. (2008) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *Journal of Applied Ecology*, **45**, 753-762.

Kollat-Palenga, I. & Basedow, T. (2000) Aphid feeding of predatory Staphylinidae on different strata (soil surface and wheat seedlings) in laboratory experiments. *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz-Journal of Plant Diseases and Protection*, **107**, 643-648.

Kruess, A. (2003) Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography*, **26**, 283-290.

Kuemmel, B. (2003) Theoretical investigation of the effects of field margin and hedges on crop yields. *Agriculture, Ecosystems & Environment*, **95**, 387-392.

Lagerlof, J. and Wallin, H. (1993) The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. *Agriculture, Ecosystems & Environment*, **43**, 141-154.

Landis, D. A. & van der Werf, W. (1997) Early-season predation impacts the extablishment of aphids and spread of beet yellows virus in sugar beet. *Entomophaga*, **42**, 499-516.

Landis, D. A., Wratten, S. D. & Gurr, G. M. (2003) Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology*, **45**, 175-201.

Lavandero, B., Wratten, S., Hagler, J. & Jervis, M. (2004) The need for effective marking and tracking techniques for monitoring the movements of insect predators and parasitoids. *International Journal of Pest Management*, **50**, 147-151.

Le Coeur, D., Baudry, J. & Burel, F. (1997) Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning*, **37**, 57-71.

Leather, S. R. (1993) Overwintering in six arable aphid pests: a review with particular relevance to pest management. *Journal of Applied Entomology*, **116**, 217-233.

Leather, S. R., Walters, K. F. A. & Dixon, A. F. G. (1989) Factors determining the pest status of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), in Europe: a study and review. *Bulletin of Entomological Research*, **79**, 345-360.

Lee, G., Stevens, D. J., Stokes, S. & Wratten, S. D. (1981) Duration of cereal aphid populations and the effects on wheat yield and breadmaking quality. *Annals of Applied Biology*, **98**, 169-178.

Lee, J. C. & Landis, D. A. (2002) Non-crop management for carabid beetles In: *The agroecology of carabid beetles.* (ed. by J. M. Holland) pp279-304 Intercept Ltd. Andover.

Ehler, L. E. (1998) Conservation biological control: past, present, and future. *Conservation Biological Control* (ed. by P. Barbosa), pp. 1-8. Academic, San Diego.

Lemke, A. & Poehling, H. M. (1997) Effects of sown weed strips in winter wheat on the abundance of cereal aphids and spiders. *Mitteilungen der Deutschen Gesellschaft fur Allgemeine und Agewandte Entomologie, Band 11, Heft 1-6, Dezember 1997 - Entomologists Conference*, **11**, 237-240.

Lemke, A. & Poehling, H. M. (2002) Sown weed strips in cereal fields: overwintering site and "source" habitat for *Oedothorax apicatus* (Blackwall) and *Erigone atra* (Blackwall) (Araneae: Erigonidae). *Agriculture, Ecosystems & Environment*, **90**, 67-80.

Levi, E. (1970) Penetration, retention and transport of foliar applied single salts of Na, K, Rb, and Cs. *Physiologia Plantarum*, **23**, 811-819.

Lewis, T. & Taylor, L.R. (1964) Diurnal periodicity of flight by insects. *Transactions of the Royal Society London*, **116**, 393-476.

Löbner, U. & Hartwig, O. (1994) Soldier beetles (Col., Cantharidae) and Nabid bugs (Het., Nabidae) - occurrence and importance as aphidophagous predators in winter wheat fields in the surroundings of Halle/Saale (Sachsen-Anhalt). *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants, West Palaearctic Regional Section Bulletin*, **17**, 179-187.

Long, R., Corbett, A., Lamb, C., Reberg-Horton, C., Chandler, J. & Stimmann, M. (1998) Beneficial insects move from flowering plants to nearby crops. *California Agriculture*, **52**, 23-26.

Longley, M. & Jepson, P.C. (1997) Cereal aphid and parasitoid survival in a logarithmically diluted deltamethrin spray transect in winter wheat: Field-based risk assessment. *Environmental Toxicology and Chemistry*, **16**, 1761-1767.

Longley, M., Jepson, P.C., Izquierdo, J. & Sotherton, N. (1997) Temporal and spatial changes in aphid and parasitoid populations following applications of deltamethrin in winter wheat. *Entomologia Experimentalis et Applicata*, **83**, 41-52.

Loreau, M., Mouquet, N. & Gonzalez, A. (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 12765-12770.

Lovei, G. L., Hickman, J. M., McDougall, D. & Wratten, S. D. (1993). Field penetration of beneficial insects from habitat islands: hoverfly dispersal from flowering crop strips. *Proceedings of the 46th New Zealand Plant Protection Conference*. 325-328.

MacLeod, A. (1999) Attraction and retention of *Episyrphus balteatus* (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. *Agriculture, Ecosystems & Environment*, **73**, 237-244.

MacLeod, A., Wratten, S. D., Sotherton, N. W. & Thomas, M. B. (2004) 'Beetle banks' as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. *Agricultural and Forest Entomology*, **6**, 147-154.

Madsen, M., Terkildsen, S. & Toft, S. (2004) Microcosm studies on control of aphids by generalist arthropod predators: Effects of alternative prey. *Biocontrol*, **49**, 483-504.

Markgraf, A. & Basedow, T. (2002) Flight activity of predatory Staphylinidae in agriculture in central Germany. *Journal of Applied Entomology- Zeitschrift fur Angewandte Entomologie*, **126**, 79-81.

Marshall, E. & West, T. (2007) Impacts of field margins, landscape and crop on the distributions of Syrphidae on an arable farm. *Aspects of Applied Biology*, **81**, 91-100.

Marshall, E. J. P. & Moonen, A. C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture*, *Ecosystems and Environment*, **89**, 5-21.

Marshall, E. J. P., West, T. M. & Kleijn, D. (2006) Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture Ecosystems & Environment*, **113**, 36-44.

Marshall, E. J. P. & Arnold, G.M. (1995) Factors affecting field weed and field margin flora on a farm in Essex, UK. *Landscape and Urban Planning*, **31**, 205-216.

Marshall, E. J. P. (1989) Distribution patterns of plants associated with arable field edges. *Journal of Applied Ecology*, **26**, 247-257.

Marshall, E. J. P. (2002) Introducing field margin ecology in Europe. *Agriculture*, *Ecosytems and Environment*, **89**, 1-4.

Marshall, E. J. P., West, T. M. & Kleijn, D. (2006) Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture Ecosystems & Environment*, **113**, 36-44.

Marshall, G. (2006) The effect of arable field margin structure and composition on Orthoptera assemblages. *Aspects of Applied Biology*, **81**, 231-238.

Mauremooto, J. R., Wratten, S. D., Worner, S. P. & Fry, G. L. A. (1995) Permeability of hedgerows to predatory carabid beetles. *Agriculture*, *Ecosystems & Environment*, **52**, 141-148.

Mayer, A. L. & Cameron, G. N. (2003). Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landscape and Urban Planning*, **65**, 201-217.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. (2002). The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, **106**, 259-271.

Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology*, **10**, 178-186.

Morris, J., Mills, J. & Crawford, I. M. (2000) Promoting farmer uptake of agri-environment schemes: the Countryside Stewardship Arable Options Scheme. *Land Use Policy*, **17**, 241-254.

Muratori, F., Perremans, D. & Hance, T. (2005) Rubidium marking of *Aphidius rhopalosiphi* (Hymenoptera: Braconidae) on *Sitobion avenae* (Hemiptera: Aphididae) reared on a diet supplemented with RbCl. *European Journal of Entomology*, **102**, 489-494.

Narisu, J. A. L. & Schell, S. P. (1999) A novel mark-recapture technique and its application to monitoring the direction and distance of local movements of rangeland grasshoppers (orthoptera: Acrididae) in the context of pest management. *Journal of Applied Ecology*, **36**, 604-617.

Nasreddine,L. & Parent-Massin,D. (2002) Food contamination by metals and pesticides in the European Union. Should we worry? *Toxicology Letters*, **127**, 29-41.

Noldus, L. J. P. (1989) Semiochemicals, foraging behaviour and quality of entomophagous insects for biological control. *Journal of Applied Entomology*, **108**, 425-451.

Oaten, H., Holland, J. M. & Smith, B. M. (2007) Attack from above: The effect of field margins on the movements of aerially dispersing aphid predators. *Aspects of Applied Biology*, **83**, 89-93.

Östman, Ö., Ekbom, B. & Bengtsson, J. (2001) Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology*, **2**, 365-371.

Östman, Ö., Ekbom, B. & Bengtsson, J. (2003) Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics*, **45**, 149-158.

Ovenden, G. N., Swash, A. R. H. & Smallshire, D. (1998) Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology*, **35**, 955-960.

Pedersen, M., Pedersen, L. T. & Abildgaard, K. (1990). Annual and diurnal activity of some *Tachyporus* species (Coleoptera: Staphylinidae) in two spring barley fields and a hedge. *Pedobiologia*, **34**, 367-375.

Perry, J. N. (1995) Spatial analysis by distance indices. *Journal of Animal Ecology*, **64**, 303-314.

Perry, J. N. (1996) Simulating spatial patterns of counts in agriculture and ecology. *Computers & Electronics in Agriculture*, **15**, 93-109.

Perry, J. N. (1998) Measures of spatial pattern for counts. *Ecology*, **79**, 1008-1017.

Petersen, M. K. (1999). The timing and dispersal of the predatory beetles *Bembidion lampros* and *Tachyporous hypnorum* from hibernating sites into arable fields. *Entomologia Experimentalis et Applicata*, **90**, 221-224.

Pfiffner, L. & Luka, H. (2000). Overwintering of arthropods in soils of arable fields and adjecent semi-natural habitat. *Agriculture*, *Ecosystems and Environment*, **78**, 215-222.

Pickett, C. H., Roltsch, W. & Corbett, A. (2004) The role of a rubidium marked natural enemy refuge in the establishment and movement of Bemisia parasitoids. *International Journal of Pest Management*, **50**, 183-191.

Polavarapu, S., Lonergan, G. C. & Seabrook, W. D. (1992) Labeling the blueberry leaftier, *Croesia curvalana* with foliar sprays of rubidium chloride. *Entomologia Experimentalis et Applicata*, **63**, 143-153.

Powell, W., A'Hara, R., Harling, R., Holland, J. M., Northing, P., Thomas, C. F. G. & Walters, K. F. A. (2004) Managing biodiversity in field margins to enhance intergrated pest control in arable crops, "3-D Farming" project. HGCA Project Report 356.

Prasad, R. P. & Snyder, W. E. (2006). Polyphagy complicates conservation biological control that targets generalist predators. *Journal of Applied Ecology*, **43**, 343-352.

Prasifka, J. R., Heinz, K. M. & Sansone, C. G. (2004) Timing, magnitude, rates, and putative causes of predator movement between cotton and grain sorghum fields. *Environmental Entomology*, **33**, 282-290.

Preston-Mafham, K. G. (1999) Courtship and mating in *Empis* (*Xanthempis*) *trigramma* Meig., *E. tessallata* F. and *E.* (*Polyblepharis*) *opaca* F. (Diptera: Empididae) and the possible implications of 'cheating' behaviour. *Journal of Zoology*, **247**, 239-246.

Purtauf, T., Thies, C., Ekschmitt, K., Wolters, V. & Dauber, J. (2005) Scaling properties of multivariate landscape structure. *Ecological Indicators*, **5**, 295-304.

Pywell, R. F., James, K. L., Herbert, I., Meek, W. R., Carvell, C., Bell, D., & Sparks, T. H. (2005) Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biological Conservation*, **123**, 79-90.

Qureshi, J. A., Buschman, L. L., Throne, J. E., Whaley, P. M. & Ramaswamy, S. B. (2004) Rubidium chloride and cesium chloride sprayed on maize plants and evaluated for marking *Diatraea grandiosella* (Lepidoptera : Crambidae) in mark-recapture dispersal studies. *Environmental Entomology*, **33**, 930-940.

Rabbinge, R., Drees, E. M., van der Graaf, M., Verberne, F. C. M. & Wesselo, A. (1981) Damage effects of cereal aphids in wheat. *European Journal of Plant Pathology*, **87**, 217-232.

Rand, T. A., Tylianakis, J. M. & Tscharntke, T. (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters*, **9**, 603-614.

Reynolds, A. M., Bohan, D. A. & Bell, J. R. (2007) Ballooning dispersal in arthropod taxa: conditions at take-off. *Biology Letters*, **3**, 237-240.

Roland, J. & Taylor, P. D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, **386**, 710-713.

Root, R. B. (1973) Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95-124.

Roschewitz, I., Hucker, M., Tscharntke, T. & Thies, C. (2005) The influence of landscape context and farming practices on parasitism of cereal aphids. *Agriculture Ecosystems & Environment*, **108**, 218-227.

Rossing, W. A. H., Daamen, R. A., Hendrix, E. M. T. (1994) Framework to support decisions on chemical pest-control under uncertainty, applied to aphids and brown rust in winter-wheat. *Crop Protection*, **13**, 25-34.

Roth, S. (2003) Spatial and temporal pattern of colonization of Nabidae (Heteroptera) in alfalfa (Medicago sativa). *Journal of Applied Entomology*, **127**, 221-227.

Rothery, F. A. (1994). Hoverfly foraging on hedgerow flowers. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants, West Palaearctic Regional Section Bulletin*, **17**, 148-155.

Salazar, M., Theoduloz, C., Vega, A., Poblete, F., Gonzalez, E., Badilla, R. & Meza-Basso, L. (2002) PCR-RFLP identification of endemic Chilean species of Rhagoletis (Diptera: Tephritidae) attacking Solanaceae. *Bulletin of Entomological Research*, **92**, 337-341.

Sarthou, J. P., Ouin, A., Arrignon, F., Barreau, G. & Bouyjou, B. (2005) Landscape parameters explain the distribution and abundance of Episyrphus balteatus (Diptera: Syrphidae). *European Journal of Entomology*, **102**, 539-545.

Scarratt, S. L., Wratten, S. D. & Shishehbor, P. (2008) Measuring parasitoid movement from floral resources in a vineyard. *Biological Control*, **46**, 107-113.

Schmidt, M. H. & Tscharntke, T. (2005a) Landscape context of sheetweb spider (Araneae : Linyphiidae) abundance in cereal fields. *Journal of Biogeography*, **32**, 467-473.

Schmidt, M. H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tscharntke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings Royal Society of London B*, **270**, 1905-1909.

Schmidt, M. H., Roschewitz, I., Thies, C. & Tscharntke, T. (2005b) Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology*, **42**, 281-287.

Schmidt, M. H., Thewes, U., Thies, C. & Tscharntke, T. (2004) Aphid suppression by natural enemies in mulched cereals. *Entomologia Experimentalis et Applicata*, **113**, 87-93.

Schmidt, M. H., Thies, C., Nentwig, W. & Tscharntke, T. (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, **35**, 157-166.

Schneider, F. (1969) Bionomics and physiology of aphidophagous Syrphidae. *Annual Review of Entomology*, **14**, 103-124.

Scholz, D. & Poehling, H. (2000) Oviposition site selection of *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata*, **94**, 148-158.

Schweiger, O., Maelfait, J. P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekotter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M. & Bugter, R. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology*, **42**, 1129-1139.

Sigsgaard, L. & Kollmann, J. (2007) Beneficial effects of hedgerow plants for insect predators in adjacent orchards - the value of pollen and nectar to *Anthocoris nemorum* (L.). *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants*, *West Palaearctic Regional Section Bulletin*, **30**, 9-30.

Sigsgaard, L. (2010) Habitat and prey preferences of the two predatory bugs *Anthocoris nemorum* (L.) and *A. nemoralis* (Fabricius) (Anthocoridae: Hemiptera-Heteroptera). *Biological Control*, **53**, 46-54.

Sih, A. (1984) The behavioral response race between predator and prey. *The American Naturalist*, **123**, 143-150.

Sopp, P. & Wratten, S. D. (1986) Rates of consumption of cereal aphids by some polyphagous predators in the laboratory. *Entomologia Experimentalis et Applicata*, **41**, 69-73.

Sotherton, N. W. (1984). The distribution and abundance of predatory arthropods overwintering on farmland. *Annual of Applied Biology*, **105**, 423-429.

Sotherton, N. W. (1985). The distribution and abundance of predatory Coleoptera overwintering in field boundaries. *Annals of Applied Biology*, **106**, 17-21.

Southwood, T. R. E. (1978) *Ecological Methods with particular reference to the study of insect populations* 2nd Edition. 524pp. Chapman and Hall, London and New York.

Sparks, D.L., Jaggard, K.W., Ramsden, S.J. & Scott, R.K. (1998) The effect of field margins on the yield of sugar beet and cereal crops. *Annals of Applied Biology*, **132**, 129-142.

Steffan-Dewenter, I. & Tscharntke, T. (1999). Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, **121**, 432-440.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421-1432.

Stelzl, M. & Devetak, D. (1999) Neuroptera in agricultural ecosystems. *Agriculture, Ecosystems & Environment*, **74**, 305-321.

Stimmann, M. W. (1974) Marking insects with rubidium: imported cabbageworm marked in the field. *Environmental Entomology*, **3**, 327-328.

Stoate, C. (1996) The changing face of lowland farming and wildlife. Part 2:1945-1995. *British Wildlife*, **7**, 162-172.

Stubbs, A. E. & Falk, S. J. (2002) *British hoverflies: an illustrated identification guide*. British Entomological and Natural History Society. 2nd Edition. 469pp.

Sunderland, K. D., Crook, N. E., Stacey, D. L. & Fuller, B. J. (1987) A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology*, **24**, 907-933.

Sutherland, J. P., Sullivan, M. S. & Poppy, G. M. (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata*, **93**, 157-164.

Sutherland, J. P., Sullivan, M. S. & Poppy, G. M. (2001) Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agricultural and Forest Entomology*, **3**, 57-64.

Tait, E. J. (1987) Planning an integrated pest management system. *Intergrated Pest Management* (ed. by A. J. Burn, T. H. Coaker & P. C. Jepson), pp. 189-208. Academic Press, London.

Tatchell, G. M. (1989) An estimate of the potential economic losses to some crops due to aphids in Britain. *Crop Protection*, **8**, 25-29.

Taylor, L. R. (1962) The efficiency of cylindrical sticky insect traps and suspended nets. *Annals of Applied Biology*, **50**, 681-685.

Taylor, L. R. (1963) Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology*, **32**, 99-117.

Taylor, L. R. (1974) Insect migration, flight periodicity and the boundary layer. *Journal of Animal Ecology*, **43**, 225-238.

Tenhumberg, B. & 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 & Environment*, **52**, 39-43.

Thies, C. & Tscharntke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, **285**, 893-895.

Thies, C., Roschewitz, I. & Tscharntke, T. (2005) The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 203-210.

Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *OIKOS*, **101**, 18-25.

Thomas, C. F. G. & Jepson, P. C. (1999) Differential aerial dispersal of linyphiid spiders from a grass and a cereal field. *Journal of Arachnology*, **27**, 294-300.

Thomas, C. F. G. & Marshall, E. J. P. (1999). Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture*, *Ecosystems & Environment*, **72**, 131-144.

Thomas, C. F. G. (1996). Modelling aerial dispersal of spiders. *Aspects of Applied Biology* **46**, 217-222.

Thomas, C. F. G., Hol, E. H. A. & Everts, J. W. (1990) Modelling the diffusion component of dispersal during recovery of a population of linyphiid spiders from exposure to an insecticide. *Functional Ecology*, **4**, 357-368.

Thomas, C. F. G., Brain, P. & Jepson, P. C. (2003) Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology*, **40**, 912-927.

Thomas, C. F. G., Parkinson, L., Griffiths, G. J. K., Fernandez Garcia, A. & Marshall, E. J. P. (2001) Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. *Journal of Applied Ecology*, **38**, 100-116.

Thomas, M. B., Wratten, S. D. & Sotherton, N. W. (1991). Creation of 'Island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *Journal of Applied Ecology*, **28**, 906-917.

Thomas, C. F. G., Brain, P. & Jepson, P. C. (2003) Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology*, **40**, 912-927.

Topping, C. J. & Sunderland, K. D. (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, **29**, 459-491.

Traugott, M. (2003) The prey spectrum of larval and adult Cantharis species in arable land: An electrophoretic approach. *Pedobiologia*, **47**, 161-169.

Tscharntke, T. & Brandl, R. (2003) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405-430.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., Tylianakis, J. M., van Nouhuys, S. & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294-309.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8**, 857-874.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002). Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*, **17**, 229-239.

Ulrich, H. (2005) Predation by adult Dolichopodidae (Diptera): A review of literature with an annotated prey-predator list. *Studia Dipterologica*, **11**, 369-403.

Van Driesche, R. G. & Bellows, T. S. (1996) *Biological Control*. Chapman Hall, New York.

van Huizen, T. H. P. (1990) "Gone with the Wind": Flight activity of carabid beetles in relation to wind direction and to the reproductive state of females in flight. *The Role of Ground Beetles in Ecological and Environmental Studies* (ed. by N.E. Stork), pp. 289-293. Intercept, Andover, UK.

van Langevelde, F. (2000) Scale of habitat connectivity and colonization in fragmented nuthatch populations. *Ecography*, **23**, 614-622.

van Rijn, P. C. J., Kooijman, J. & Wäckers, F. (2006) The impact of floral resources on sryphid performance and cabbage aphid biological control. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants wprs Bulletin*, **29**, 149-152.

van Steenwyk, R. A., Kaneshiro, K. Y., Hue, N. V. & Whittier, T. S. (1992) Rubidium as an internal physiological marker for Mediterranean fruit fly (Diptera: Tephritidae). *Journal of Economic Entomology*, **85**, 2357-2364.

Vereijken, P.H. (1979) Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat. *Agricultural Research Reports*, **888**, 58.

Vickerman, G. P. & Sunderland, K. D. (1975) Arthropods in Cereal Crops - Nocturnal Activity, Vertical Distribution and Aphid Predation. *Journal of Applied Ecology*, **12**, 755-766.

Vickerman, G. P., Dowie, W. & Playle, K. E. (1987) The potential of *Tachyporus* spp. (Coleoptera: Staphylinidae) as predators of cereal aphids. In 'Integrated Crop Protection in Cereals'. (Eds R Cavalloro and KD Sunderland) pp. 69-80. (C.E.C.: Rome)

Vickery, J. A., Carter, N. & Fuller, R.J. (2002) Promoting farmer uptake of agri-environment schemes: the Countryside Stewardship Arable Options Scheme. *Agriculture*, *Ecosystems & Environment*, **89**, 41-52.

Villenave, J., Deutsch, B., Lode, T. & Rat-Morris, E. (2006) Pollen preference of the Chrysoperla species (Neuroptera : Chrysopidae) occurring in the crop environment in western France. *European Journal of Entomology*, **103**, 771-777.

Vockeroth, J. R, & Thompson, F.C. (1987) Syrphidae. *Manual of Nearctic Diptera*, *Volume 2*. (ed. by J. F. McAlpine) pp. 713-743 Research Branch, Agriculture Canada, Monograph No. 28.

Vugts, H. F. & Wingerden, W. K. R. E. (1976) Meteorological aspects of aeronautic behaviour of spiders. *OIKOS*, **27**, 433-444.

Wäckers, F., van Rijn, P. C. J., Winkler, K. & Olson, D. (2006) Flower power? Potential benefits and pitfalls of using flowering vegetation for conservation biological control. *International Organisation for Biological and Intergrated Control of Noxious Animals and Plants*, *West Palaearctic Regional Section Bulletin*, **29**, 161-164.

Wallin, H. (1985). Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. *Pedobiologia* **28**, 19-34.

Watt, A.D. & Dixon, A.F.G. (1981) The role of cereal growth-stages and crowding in the induction of alatae in *Sitobion avenae* and its consequences for population-Growth. *Ecological Entomology*, **6**, 441-447.

Westhoff, V. & van der Maarel, E. (1973) The Braun-Blanquet approach. *Handbook of Vegetation Science Part V: Ordination and classification of Communities* (ed. R.H. Whittaker) pp. 617-726. Junk, The Hague.

Weyman, G. S. & Jepson, P. C. (1994). The effect of food supply on the colonisation of barley by aerially dispersing spiders (Araneae). *Oecologia*, **100**, 386-390.

Whittingham, M.J. (2007) Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, **44**, 1-6.

Winder, L. (1990) Predation of the cereal aphid Sitobion avenae by polyphagous predators on the ground. *Ecological Entomology*, **15**, 105-110.

Winder, L., Alexander, C. J., Holland, J. M., Symondson, W. O. C., Perry, J. N. & Woolley, C. (2005) Predatory activity and spatial pattern: the response of generalist carabids to their aphid prey. *Journal of Animal Ecology*, **74**, 443-455.

Winder, L., Alexander, C. J., Holland, J. M., Woolley, C. & Perry, J. N. (2001) Modeling the dynamic spatio-temporal response of predators to transient prey patches in the field. *Ecology Letters*, **4**, 568-576.

Winder, L., Woolley, C., Holland, J. M., Perry, J. N. & Alexander, C. J. (1999) The field scale distribution of insects in winter wheat. *Proceedings of the 2000 Brighton Conference - Pests and Diseases*, **2**, 573-578.

Winder. L,, Woolley, C., Holland, J. M., Perry, J. N. & Alexander, C. J. (2000) The field scale distribution of insects in winter wheat. *BCPC Conference: Pests & Diseases 2000*, **1-3**, 573-578.

Wratten, S. D., Bowie, M. H., Hickman, J. M., Evans, A. M., Sedcole, J. R. & Tylianakis, J. M. (2003b) Field boundaries as barriers to movement of hover flies (Diptera : Syrphidae) in cultivated land. *Oecologia*, **134**, 605-611.

Wratten, S. D., Lavandero, B., Tylianakis, J. M., Vattala, D., Cilgi, T. & Sedcole, J. R. (2003a) Effects of flowers on parasitoid longevity and fecundity. *New Zealand Plant Protection*, **56**, 245.

Wratten, S. D., White, A. J., Bowie, M. H., Berry, N. A. & Weigmann, U. R. S. U. (1995) Phenology and ecology of Hoverflies (Diptera: Syrphidae) in New Zealand. *Environmental Entomology*, **24**, 595-600.

Wratten, S. D. (1975) The nature and the effects of the aphids *Sitobion avenae* and *Metopolophium dirhodum* on the growth of wheat. *Annals of Applied Biology*, **79**, 27-34.

Wratten, S. D. (1978) Effects of feeding position on the aphids *Sitobion avenae* and *Metopolophium dirhodum* on wheat yield and quality. *Annals of Applied Biology*, **90**, 11-20.

Wratten, S. D., Watt, A. D., Carter, N. & Entwistle, J. C. (1990) Economic consequences of pesticide use for grain aphid control on winter wheat in 1984 in England. *Crop Protection*, **9**, 73-78.

Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The Insurance Hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 1463-1468.

Zadoks, J. C., Chang, T. T., Konzak, C. F. (1974) A decimal code for the growth stages of cereals. *Weed Research*, **14**, 415-421.