

UNIVERSITY OF SOUTHAMPTON

PROVISION OF PLANT RESOURCES  
FOR BENEFICIAL ARTHROPODS IN ARABLE ECOSYSTEMS

ALAN MacLEOD

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ABSTRACT

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Plant resources were provided for epigeal beneficial polyphagous predators of cereal aphids, as a raised grassy bank 290m long, sown with grass species of contrasting structure, within a 7ha field. Densities of polyphagous predators overwintering in the grasses were estimated by sampling from grass plots during winters (1987/88 to 1993/94). Data are presented which illustrate how densities of taxa of polyphagous predators have fluctuated during the seven winters. Samples measuring densities of polyphagous predators over the last three winters of the study showed that the within-field grassy bank supported greater densities of beneficial predators than an adjacent permanent field boundary.

Floral resources in the form of the crucifer *Lobularia maritima*, provided along an arable field margin for hoverflies (Diptera: Syrphidae), in the summer, were selectively foraged upon and preferred to native arable weeds by a variety of hoverfly species with aphidophagous larvae. A white coloured variety, compared with a purple coloured variety of *L.maritima* was consistently visited and foraged upon more frequently, by *Episyrphus balteatus*, in laboratory and field experiments.

Observational studies showed that potential alternative crops were also foraged upon by beneficial Syrphidae. A field trial, using the potential alternative crop coriander, did not show any significant redistribution of Syrphidae between fields with and without border strips of coriander. Further observational studies on a hedgerow, with its floral diversity and available resources increased by sowing a mixture of alternative crops in a strip, between the hedge and crop, showed that *E.balteatus* remained at the enhanced strip for significantly longer periods than at the control strip. A simple model shows that the difference in numbers of *E.balteatus* caught in water-traps at either site cannot be fully explained simply by *E.balteatus* remaining at the florally diverse site for longer. To explain the differences in trap catches, *E.balteatus* must have immigrated to the florally diverse strip at a higher rate than to the control strip. Higher syrphid immigration rate to the florally diverse strip may have been due to the visual attractiveness of the diverse site.

Although Syrphidae are highly mobile, linear features on arable land influenced their distribution. A road and tall hedge were shown to be significant obstacles preventing the even distribution of at least one syrphid species. The potential and limitations of habitat enhancement techniques for biological control agents on farmland are discussed.

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**Dedicated to my mum**

**Joan MacLeod**

**10th September 1940 - 23rd January 1994**

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## CHAPTER ONE

### GENERAL INTRODUCTION: PREDATORY ARTHROPODS ON ARABLE LAND AND RESOURCES PROVIDED TO MANIPULATE THEIR DISTRIBUTION

This thesis is concerned with manipulating the abundance, distribution and behaviour of cereal aphid predators by providing resources in summer and winter. Chapter One gives a general introduction to crop pests, especially cereal aphids and their arthropod predators. It explains how cereal production is a major component of UK agriculture and describes the potential that arthropod predators and other biological agents have in the control of cereal aphid populations. Chapter Two examines the winter distribution of polyphagous predators of aphids (Coleoptera and Araneae) over a period of seven years, in a habitat created to represent a suitable overwintering site. Summer use of manipulated floral resources by Syrphidae in an arable landscape is investigated in the third chapter. Chapter Four studies the use of alternative crops as potential food resources by Syrphidae and examines whether such crops may be used to influence syrphid distribution on a field scale. Chapter Five investigates possible mechanisms by which differences in distribution of Syrphidae around resources may occur and Chapter Six investigates how linear features in the arable environment may influence movement and distribution of Syrphidae. The final chapter brings together the findings of each chapter and speculates on possible future research.

#### Crop pests and beneficial predatory arthropods

Throughout history, man has suffered crop losses that have been caused by insect pests. The Bible records the most egregious incident in the Old Testament, when a plague of locusts ate all the crops and other vegetation in Egypt (Exodus 10, v1-20). In response man has used cultural, chemical and biological techniques to limit crop pest damage (Burn, Coaker & Jepson, 1987). An insect can be described as a crop pest if the damage it causes to a crop sufficiently reduces the yield and/or quality by an amount unacceptable to the owner of the crop (Dent, 1990). Biological techniques of pest control have included the use of predatory arthropods to limit crop damage (Dent, 1990). Since such predators consume pests, they have been termed "beneficial". Beneficial predatory arthropods of arable land are those which feed

wholly or partly on arable crop pests during at least part of their life history.

DeBach (1964,1974) cites several historical examples including that of McCook (1882) who described the use of the predacious ant *Oecophylla smaragdina* F. by the ancient Chinese to reduce the number of caterpillars on orange trees; and Kirby & Spence (1815) who suggested that Coccinellidae could restrict aphid numbers on plants in glasshouses. Experiments in Europe were reported in the 1840's, where insect predators were collected and translocated to the field. In France, the carabid *Calosoma sycophanta* L. was used to control gypsy moth larvae on willows (Joly, 1842; cited by DeBach, 1974); and in Italy climbing and epigeal Carabidae as well as Staphylinidae were used against agricultural pests (Villa, 1845; cited by DeBach, 1974). These pioneers were attempting biological control, a term first coined by Smith (1919). Biological control can be described as limiting the abundance of a pest species by use of natural enemies.

#### Cereals - Major crops in the UK

Major crops in the UK which are susceptible to insect pest damage include cereals. Cereal crops are grown over a wide area in Britain; 14.9% of the total land area in the British Isles is involved in cereal production (Bunce & Heal, 1984). Between 1987 and 1992, the average area of agricultural land used to grow wheat in England and Wales was 1.89million ha. Average yields over this period were 6.62t ha<sup>-1</sup> giving a total average yield of 12.51million t per year (Figures calculated from Anon., 1992). Such large yields are a result of intensification of cereal production. Kolbe & Linke (1974) suggested that cereal intensification had resulted in aphids becoming more important as pests of cereals, although possible mechanisms were not proposed. Vickerman and Wratten (1979) suggested that there was little quantitative evidence to substantiate the view of Kolbe & Linke (1974).

#### Cereal aphids

The biology and pest status of cereal aphids has been reviewed by Vickerman and Wratten (1979), Carter, McLean, Watt & Dixon, (1980) and Dixon (1987). The importance of cereal pests and the damage they cause is briefly described below.

Aphids have been considered as cereal pests in the UK since the 1960's when major outbreaks occurred (Fletcher & Bardner, 1969). Three species of aphid can be found in large numbers in cereal crops in the UK (Holmes, 1984). Their

abundance varies from year to year (Rabbinge, Ankersmit & Pak, 1979; Carter *et al.*, 1980) and is variable between regions (George & Gair, 1979). Only two species, *Sitobion avenae* F. and *Metopolophium dirhodum* Walk. are commonly found on wheat in the summer (Fletcher & Bardner, 1969), the third species, *Rhopalosiphum padi* L. occurring most frequently on barley (Dean, 1973). Cereal aphids can be a major cause of loss in yield (Wratten, 1975) or of a reduction in grain quality (Lee Stevens, Stokes & Wratten, 1982). This primary damage is caused by consumption of plant sap. Secondary damage is caused by the deposition of honeydew; a residual solution of digested food, mainly sugars, stored in the dilated rectum before ejection to the exterior as a droplet (Cavalloro, 1982). Honeydew becomes the substrate for the growth of fungi and moulds, whose growth reduces the amount of light reaching the chloroplasts (Bardner & Fletcher, 1974). However, in general, it is likely that aphids do more damage to plants by transmitting viruses than by sap removal (Svenson, 1968). More plant viruses are transmitted by aphids than by any other faunal group (Svenson, 1968). Barley yellow dwarf virus (BYDV) is one of a number of viruses transmitted by aphids (Doodson, 1967). Plants severely infected with BYDV may be stunted and grain yields reduced. Early infestations of field crops can cause yield losses over 90%, but in most years these do not exceed 10% (Doodson & Saunders, 1970).

Despite the abundant literature describing damage caused by aphids, Owen (1977) suggests that aphids, depositing honeydew, some of which falls to the ground and encourages the growth of nitrogen-fixing *Azobacter* species, are of net benefit to plants. Available soil nitrogen is often a limiting factor in the growth of plants (Lee, Harmer & Ignaciuk, 1983) therefore the promotion of nitrogen-fixing bacteria will be advantageous to nitrogen limited plants. That aphids are beneficial to cereals is a view probably not held by most farmers; especially as nitrogen is added as a fertilizer and is therefore not usually limiting.

Aphids do not reach outbreak proportions every year, and insecticides do not always succeed in controlling their numbers (Way, Hardie & Galley, 1969). This has led to an increased awareness of the importance of native natural enemies in the control of aphid outbreaks (Basedow, Liedtke & Rzehak, 1990).

#### Natural enemies of cereal aphids

The natural enemies of cereal aphids can be classified as fungal pathogens



(Dean & Wilding, 1971), parasitoids (Powell, 1982; Vorley, 1986), polyphagous predators (Sunderland, Stacey & Edwards, 1981) and aphid-specific predators (see Minks & Harrewijn, 1988). The action of parasitoids and predators in cereals has been summarised by Wratten & Powell (1991).

### Pathogens

Dean and Wilding (1971) reported three species of *Entomophthora* (Entomophthoraceae) that killed large proportions of cereal aphids in Eastern England in 1970. In experiments carried out between 1975 and 1978, Entomophthoraceae infected aphids only in the moister seasons (Wilding, 1981). Experiments carried out by Dean & Wilding (1973) showed there were low numbers of aphids infected with *Entomophthora* in cereal fields until after heavy rainfall, when the proportion of infected aphids then increased. Trials with entomopathogenic fungi, introduced to cereal aphid populations, have been mainly unsuccessful to date (Latteur & Godefroid, 1982; Wilding, Mardell, Probyn, Wratten & Lomas, 1990) primarily because of the stringent abiotic requirements needed for transmission of spores between hosts (Pickering, Dutcher & Ekbohm, 1989) and low pathogenicity (Ankersmit, 1989). However *Entomophthora* already present in the field and the coincidence of favourable weather conditions can still make an important contribution to the suppression of aphid numbers (Bode, 1980). Chambers, Sunderland, Stacey & Wyatt, (1986) strongly suspected pathogenic fungi were responsible for halting cereal aphid population growth in the second year of a two-year study, together with the action of aphid-specific predators and parasitoids.

### Parasitoids

The most common species of primary parasitoids found in UK cereals are, *Aphidius ervi* Hal., *Aphidius picipes* (Nees), *Aphidius rhopalosiphi* De Stefani-Perez and *Praon volucre* Hal., (Carter *et al.*, 1980; Wratten & Powell, 1991). Reduction in aphid population growth rate has been attributed to parasitoid activity by Powell, Dewar, Wilding & Dean, (1983), Carter & Sotherton, (1983) Vorley & Wratten (1985) and Vorley (1986) among others. In all cases of successful "classical" biological control of aphids (where a non-native natural enemy is introduced into the aphids' habitat), the agents have been parasitoids (Carver, 1989)

As well as aphids, beneficial arthropods suffer from fungal, parasite and

parasitoid attack. Dean (1983) studied the parasites of syrphid and coccinellid aphid-specific predators and found parasitism rates were usually low (<25%). Jones (1972) suggested that increased aphid populations, in one year of a seven-year study, were partly due to reduced parasitoid action as a consequence of high hyper-parasitoid activity the previous year. The role of parasites and pathogens in the population dynamics of polyphagous predators, such as Carabidae, is unknown but is assumed to be small (Luff, 1987). To what extent beneficial arthropods, and their potential for the bio-control of cereal aphids are limited by pathogens, parasites and parasitoids is uncertain.

### Polyphagous predators

The diet of polyphagous predators found in arable crops consists of aphids, Collembola, small Diptera, earthworms, fungi, mites, and plants (Sunderland, 1975). Polyphagous predators received more attention as aphid predators after Potts & Vickerman (1974) published results from a 12-year study which implicated polyphagous arthropods in limiting cereal aphid population growth. Table 1.1 shows the various taxa of predatory polyphagous arthropods which include cereal aphids in their diets. Since such predators are polyphagous, they are not totally dependent on aphids and can maintain appreciable population levels in fields when aphid densities are still low (Dennis & Wratten, 1991). Seasonal changes in polyphagous predator diets have been studied by Mitchell (1963a) and Luff (1974). Dissecting individuals throughout the year and examining crop contents, Luff (1974) found that the diet of the adult carabid *Pterostichus madidus* F., early in the year was composed primarily of vegetation, and that as the season progressed, animal fragments became more common in the crop. The predators in Table 1.1 have rarely been shown to control aphids by themselves (Sunderland, 1988) but when polyphagous predator species diversity is high and individual species are numerous, they can reduce aphid abundance (Sunderland *et al.*, 1981; Ekbohm & Wikteliuss, 1985). The most important predators are those that consume aphids in sufficient quantity or with sufficient frequency to be significant in the population dynamics of aphids (Frazer, 1988).

Microscopic examination of gut contents of polyphagous predatory arthropods and the identification of aphid fragments confirmed that a number of Staphylinidae and Carabidae fed on aphids (Sunderland, 1975; Sunderland & Vickerman, 1980). Such a technique is unsuitable to identify the gut contents of the remaining species

of beneficial arthropod which are mainly liquid feeders (Sunderland *et al.*, 1987). Enzyme-linked immunosorbent assay (ELISA) however overcomes this difficulty (Chiverton, 1987; Sunderland *et al.*, 1987) and Sopp & Chiverton (1987) were able to identify species of Linyphiidae and Tetragnathidae, as well as other Carabidae and Staphylinidae which had not been shown to feed on aphids by dissection, which had fed upon both *S.avenae* and *R.padi*.

Manipulative experiments, in which field populations of polyphagous predator were artificially lowered or raised using exclusion barriers or cages, have shown that in plots where predators were excluded, aphid populations were two to six times greater than in unenclosed plots (Chiverton, 1986). De Clerq and Pietraszko (1982) found twice as many aphids in enclosed plots, protected from epigeal arthropods, than in open plots. Aphids are found mainly on the upper aerial parts of cereals. *Sitobion avenae* is found on the ear and upper leaves (Wratten, 1975), *M.dirhodum* is usually seen on the flag and lower leaves, while *R.padi* is found on lower leaves and stem of cereals (Vickerman & Wratten, 1979; Anon., 1984), but ground-zone predators can still contribute to a reduction of aphid numbers since 20% - 50% of the aphid shoot population falls to the ground each day (Sunderland, Fraser & Dixon, 1986) and at any one time 4% - 71% of the aphid population may be on the soil (Griffiths, Wratten & Vickerman, 1985). Aphids may become dislodged from their host plant by wind and rain, or deliberately drop to escape predators (Rotheray, 1989) and move to a new host plant. Winder (1990a;1990b) studied the rates at which aphids fell to the ground and subsequently climbed and returned to the crop canopy in plots surrounded by polythene barriers which excluded polyphagous predators. It was found that rates of aphid fall off were similar in all plots but the rate of return to the canopy was highest when predator density was lowest.

Discrete patches of aphids were artificially created in cereals using field cages by Bryan & Wratten (1984). The carabids *Agonum dorsale* Pont., *Amara plebeja* Gyll., *Bembidion lampros* Herbst. and *B.obtusum* Ser. aggregated, with two staphylinid species, *Philonthus cognatus* Steph. and *Tachyporus chrysomelinus* L., at patches of high aphid density while the carabids *Notiophilus biguttatus* F., *Loricera pilicornis* F. and *Nebria brevicollis* (F.) did not, but were found more evenly distributed in all patches. The mechanism by which predators located and stayed in experimental patches was not discovered but results showed that polyphagous predators had the ability to find localised prey patches and contribute to suppression of aphid

outbreaks. In field surveys, Sunderland & Vickerman (1980) found via suction sampling in cereal fields that *Amara plebeja*, *A. aneae* Deg. and *Tachyporus* spp. responded to aphid densities, consuming aphids only at the highest aphid densities. Sunderland (1975) studied gut contents of adult *Tachyporus hypnorum* F. and concluded that aphids were not an important part of their diet. However in laboratory feeding experiments with *T. hypnorum*, Dennis & Wratten (1991) found that aphids were the preferred food when given a choice of aphids, Collembola or Diptera. Nevertheless, *Tachyporus* larvae are probably more important predators of cereal aphids than are the adults because the larval stages are more closely synchronised with development of aphid populations (Kowalski, 1986).

Table 1.1 Beneficial polyphagous arthropods that have been recorded having consumed aphids in cereals and grasses. (Modified from Sunderland, 1988)

Taxa	Reference
Acari	Sunderland <i>et al.</i> (1987)
Araneae	
Linyphiidae	Fraser (1982); Sopp & Chiverton (1987); Sunderland <i>et al.</i> (1987)
Lycosidae	Sunderland <i>et al.</i> (1985); Sunderland <i>et al.</i> (1987)
others	Jones (1972)
Chilopoda	Sunderland <i>et al.</i> (1987)
Opiliones	Sunderland <i>et al.</i> (1987)
Coleoptera	
Cantharidae	Sunderland <i>et al.</i> (1987)
Carabidae	Sunderland & Vickerman (1980); Sunderland <i>et al.</i> (1987)
Staphylinidae	Sunderland <i>et al.</i> (1987); Sopp & Chiverton (1987)
Dermoptera	Vickerman & Sunderland (1975)
Diptera	
Chamaemyiidae	Tanasijtshuk <i>et al.</i> (1977)
Empididae	Sunderland <i>et al.</i> (1987)
Scathophagidae	Sunderland <i>et al.</i> (1987)
Heteroptera	
Miridae	Sunderland <i>et al.</i> (1987)
Nabidae	Sunderland <i>et al.</i> (1987)

Winder, Hirst, Carter, Wratten & Sopp, (1994) questioned the previously assumed significance of epigeal polyphagous predators, which scavenge dead aphids as well as predate upon live aphids, in aphid biocontrol, when it was shown that live aphid availability to ground predators was low. Sunderland & Vickerman (1980) suggested that successful aphid predation, at low aphid densities, may be related to the climbing ability of the predator. Climbing polyphagous predators such as *Tachyporus* spp. (Dennis, Wratten & Sotherton, 1990) and *Demetrias atricapillus* L. (Coombes, 1987) can make more significant contributions to aphid biocontrol than can epigeal predators, which are liable to have the smallest influence on aphid population growth (Winder *et al.*, 1994). Estimated aphid consumption rates in the field by all epigeal and climbing polyphagous predator species in the study by Winder *et al.* (1994) could be equalled by the aphid consumption rate of a single species of aphid-specific predator, in this case, larvae of *Episyrphus balteatus* Deg. (Diptera: Syrphidae) at field densities of  $0.1\text{m}^{-1}$ , assuming laboratory consumption rates are equal to field consumption rates (Winder *et al.*, 1994). Predatory activity by aphid-specific predators may therefore, in some years, swamp the effects of polyphagous predators (Winder *et al.*, 1994) in cereal aphid control. However Winder *et al.*, (1994) pointed out that such conclusions based on modelling depend heavily on accurate assessments of predator density, and to date, there have been limitations on achieving this.

#### Aphid-specific predators

Aphid-specific predators are found in the families Coccinellidae (Coleoptera), Chrysopidae (Neuroptera) and Syrphidae (Diptera), some of which are specialised aphid predators for at least part of their life cycle. *Coccinella septempunctata* L. is a common coccinellid species of cereals in Europe (Carter *et al.*, 1980; Chiverton, 1986). Basedow (1982) describes how *C.septempunctata* feeds on aphids at three times of the year; in the spring as adults in the field; in the summer as larvae in the field; and in the autumn on host plants as the adult coccinellids prepare for hibernation. Although larvae consume more aphids than the adults, the latter eat aphids earlier in the season and consequently have relatively more impact on developing aphid populations (Carter *et al.*, 1980). Unlike polyphagous predators, aphidophagous predators such as coccinellids require a threshold density of aphids in order to survive and reproduce (Hodek, 1970; Wratten 1973; McLean, Carter &

Watt, 1977).

Aphidophagous chrysopid larvae are highly mobile and can consume aphids at faster rates than can *C.septempunctata* (Carter *et al.*, 1980). Working in cereals, Chambers, Sunderland, Wyatt & Vickerman (1983) carried out manipulative experiments designed to exclude Chrysopidae, Coccinellidae and Syrphidae and allow the development of aphid patches - areas of the crop where aphid populations would not be inhibited by predators. Peak aphid populations outside the excluded patches, up to six times lower than inside, were attributed to the excluded predators. The most common chrysopid in cereals is *Chrysoperla carnea* Steph. (Dean, 1982) which overwinters as a diapausing adult enabling it to colonise crops early in the season when aphid populations start to grow (New, 1988). Dewar (1984) surveyed wheat fields in eastern England and credited low levels of aphids largely to the action of predators such as Chrysopidae, Coccinellidae and Syrphidae.

Unlike Coccinellidae and Chrysopidae, only the larvae of Syrphidae prey on aphids. Adult Syrphidae feed on pollen and nectar from flowers. Aphidophagous syrphid larvae were seen as potentially economically important in New Zealand early in the twentieth century by Miller (1918). In Europe, predation by syrphid larvae has the potential to limit aphid population growth (Chambers, Sunderland, Stacey & Wyatt, 1982; Chambers & Adams, 1986; Entwistle & Dixon, 1990; Tenhumberg & Poehling, 1993) and indeed has been the chief cause of (Chambers & Sunderland, 1982), or has contributed with other predators (Chambers *et al.*, 1983; Holmes 1984) to reduced aphid populations in cereals.

Syrphid larvae from a variety of genera are frequently found in cereals. These genera include *Episyrphus*, *Metasyrphus*, *Melanostoma* and *Platycheirus* (Chambers *et al.*, 1986) *Scaeva*, *Sphaerophoria* and *Syrphus* (Dean, 1974; Adams, 1984) all of which are obligate aphidophages except for *Melanostoma* and *Platycheirus* which are facultative aphid feeders (Gilbert, 1986).

Syrphid larvae develop from eggs at a duration inversely proportional to temperature (Ankersmit, Dijkman, Keuning, Mertens, Sins & Tacoma, 1986). The mean hatching time for *E.balteatus*, in a controlled environment at 10°C was 10.3 days, and at 20°C, 2.3 days. *Metasyrphus corollae* F. eggs hatched after 2.7 days at 21°C (Chambers, 1986).

Eggs are laid by Syrphidae with a variety of ovipositional strategies. Different syrphid species use different-sized aphid colonies for optimal oviposition (Chandler,

1968a). *Platycheirus* and *Melanostoma* species may lay eggs in groups on plants which are uninfested with aphids. The larvae of these genera are cannibalistic and will eat unhatched eggs (Chandler 1968a;c). *Metasyrphus corollae* and *Syrphus ribesii* L. lay eggs very close to, even touching, aphids (Dixon, 1959; Chandler 1968,a;b). Aphids do not appear to react to the eggs (Chambers, 1988) although in Japan *Metasyrphus confrater* Wiedemann eggs laid on bamboo are attacked and removed by the bamboo aphid - *Pseudoregma bambucicola* Takahashi (Ohara, 1985).

Chandler (1968a) showed that increasing aphid densities on Brussels sprouts resulted in a reproductive numerical response (Solomon, 1949) by ovipositing *E. balteatus*. However Kumar, Kapoor & Mahal, (1988) studying *E. balteatus* and five other species of syrphid on brown mustard in India, showed that such a numerical response varied through the season. Early in the season, when aphid densities were at their lowest, eggs and larvae were found evenly distributed, but as aphid densities increased, eggs and larvae were assembled in an aggregated distribution corresponding to aphid patches.

As well as the density of an aphid colony being important as an ovipositional stimulant, the age structure of each colony is assessed by the females of a number of species prior to oviposition (Kan, 1988a,b). The efficiency with which larvae capture prey varies with the size of the larvae and age of intended target (Rotheray, 1987; Chambers, 1988). First-instar larvae of *Syrphus ribesii* caught adult *Myzus persicae* (F.) with a 56% success rate, while third-instar larvae caught adults with 98% success (Hagvar, 1974). Thus to ensure larvae have a good chance of feeding on nearby aphids, when they hatch, eggs are oviposited in young colonies of aphids (Kan, 1989; Hemptinne, Dixon, Doucet & Petersen, 1993). However, Chandler (1967) studied *Metasyrphus luniger* Meig. in cages and found that as females aged, a greater proportion of eggs were laid at greater distances from aphid colonies, and on uninfested plants. It was suggested that loss of precision when ovipositing in relation to aphid colonies, increased the efficacy of natural control, by allowing oviposition to occur at sites where the stimulus would otherwise be inadequate (Chandler, 1967).

#### Resources provided to manipulate the distribution of predatory beneficial arthropods

Techniques to manipulate beneficial predators can be divided into those that are applied inside the crop e.g. intercropping, undersowing, provision of artificial food

sources, and those that are applied to areas outside the crop e.g. improving the "attractiveness" of existing non-cropped habitat adjacent to the crop. In each case, the manipulative technique employed can be used in an attempt to increase the natural enemy:aphid ratio. Increasing the ratio of natural enemies to aphids is more important than increasing the absolute number of natural enemies (van Emden, 1988). Wratten & van Emden (1995) reviewed the reviews of habitat management which manipulated the activity of natural enemies in agriculture. Examples of manipulative techniques follow.

### Intercropping

Intercropping, also known as polyculture, strip cropping or mixed cropping (Gross, 1987) is the growing of two or more crops in close proximity, either in discrete patches or strips (Speight, 1983). A pest "searching for" a specific host plant has to locate the plant, but if it is obscured amongst other plants which do not provide the required stimulus, then the pests' searching efficiency and colonisation of new host plants should be reduced (Speight, 1983). This technique follows the "resource concentration hypothesis", first proposed by Root (1973) which states that herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands (monoculture). Also, the lack of diversity amongst abiotic and biotic factors in monocultures may reduce the effectiveness of general predators which could conceivably control pests, under more diverse conditions (Root, 1973). That predators and parasites are more effective in diverse systems than in simple ones is the axiom upon which Root (1973) also bases his "enemies hypothesis". Russell (1989) reviewed studies testing the enemies hypothesis and concluded that although predators and parasites kill herbivores at higher rates in polycultures than in monoculture the mechanisms by which this is achieved require more investigation e.g. researchers predicted that predators (Risch, Andow & Altieri, 1983) and parasites (Sheehan, 1986) should have reduced searching efficiency in diverse systems, however their greater abundance in polyculture could compensate (Andow, 1983). Letourneau & Altieri (1983) studied the flower thrip *Frankliniella occidentalis* Perg. and an anthocorid bug, *Orius tristicolor* White, which predated upon it. The study compared predation in sweetcorn, cowpea and zucchini, grown in monoculture and polyculture with each other. Thrip pest densities in monoculture were higher than in polyculture, where densities of the pest fell earlier in the season due to the earlier



colonisation and consequent predation of *O.tristicolor*. Earlier colonisation of polyculture plots was probably due to more suitable environmental conditions such as humidity and temperature provided in the diverse plots.

Risch *et al.* (1983) reviewed 150 papers which had investigated the effect of diversifying an agroecosystem on insect pest abundance. It was concluded that movement of pest and ability to locate new host plants was more important in differences in pest abundance between simple and diverse systems than the activity of predators. Kenny & Chapman (1988) investigated insect pest damage to cabbages grown conventionally and intercropped with dill. They found lower numbers of cabbage aphids on intercropped cabbages but differences were not ascribed to predation; it was postulated that the dill provided a physical barrier to aphid movement, which reduced searching efficiency of new host plants in accordance with the resource concentration hypothesis.

Financial considerations of intercropping include higher labour and management costs, reduced harvesting efficiency and a reduction in yields, on a per plant basis (Andow, 1983), which is perhaps why cereals are not widely intercropped in the UK.

### Undersowing

Undersowing is the sowing of a second crop with or after sowing a main crop. The second crop grows concurrently on the same land as the first crop and continues to grow after the primary crop has been harvested. A consequence of using such a technique is the creation of environments that increase survival and efficiency of natural enemies (Gross, 1987). Dempster & Coaker (1974) grew Brussels sprouts in plots with and without undersown clover. Weekly counts of *Pieris rapae* (L.) (cabbage caterpillar) eggs and larvae, during the summer, revealed no significant differences in eggs laid in either plot type, but there were lower numbers of larvae in undersown plots. The difference was ascribed to increased predation by the carabid *Harpalus rufipes* Deg. and the harvestman *Phalangium opilio* Linné, which were more abundant in the undersown plots. Significantly lower populations of the cabbage aphid, *Brevicoryne brassicae* L. and the cabbage root fly, *Erioischia brassicae* (Bouchet), were recorded in the undersown plots, but these could not be attributed to predation since there was less aphid immigration into undersown plots and the effect that the clover had on oviposition of *E.brassicae* was unknown.

Describing possible management systems, Bugg, Sarrantonio, Dutcher & Phatak, (1991) advocated the use of legumes as cover crops, more specifically understorey crops, in pecan orchards, where clover in the understorey is able to sustain Coccinellidae and other beneficial arthropods on alternative prey (Bugg, Dutcher & McNeil, 1991).

Vickerman (1978) sampled spring barley fields, spring barley fields undersown with grass and grass fields, with a suction sampler annually in June for three years. The diversity and density of arthropods were generally higher in the fields with crops which were undersown. The only taxon which was consistently less abundant in the undersown crops was Hemiptera. In two of the study years, Aphididae were 60% more abundant in barley fields which were not undersown than in barley fields which were undersown. It was suggested that the difference in aphid numbers between the two types of fields was due to increased predation of aphids in undersown crops by the more numerous polyphagous predators in fields which had been undersown.

Although not undersown, areas in a cereal field with high weed cover, specifically *Poa annua* L., had higher densities of predatory Carabidae and Staphylinidae. Bait provided in these areas suffered greater incidence of attack. It was suggested that weed cover provided shelter from climatic extremes which led to the differences in predator densities (Speight & Lawton, 1976).

Plots of a cereal field which were left unsprayed, when a mixture of broad-leaved herbicides were applied to the the rest of the field, contained significantly higher densities of weeds and polyphagous predators (Chiverton & Sotherton, 1991). When individual Carabidae were dissected, and gut contents identified, from the two types of plots, it was found that in the sprayed plots, which had a low diversity and abundance of prey, aphids formed an substantial proportion of the diet of Carabidae. However in unsprayed plots, which contained a more diverse and abundant source of prey, aphids formed a smaller proportion of the diet of polyphagous Carabidae (Chiverton & Sotherton, 1991). The presence of weeds in cereal crops have been shown to increase the number of polyphagous predators in the crops (Vickerman, 1974, 1978; Powell, Dean & Dewar, 1985; Chiverton & Sotherton, 1991)

Differences in syrphid densities, in plots of cereals that differed in floral diversity, were identified by Cowgill (1991) who investigated syrphid foraging on arable weeds. The cereal fields studied had not been undersown with weeds, but the herbaceous weed species had been artificially encouraged in regions of the cereal

field by selective use of herbicide, to create Conservation Headlands' (Rands & Sotherton, 1987).

### Conservation Headlands

The Conservation Headland is an area between the crop margin and the first "tramline" (tractor wheeling), the width of a boom of a mechanical sprayer, usually 6m. The area is selectively treated with pesticides to control grass weeds and *Galium aparine* L. but still allows most broad-leaved weeds and beneficial arthropods to survive (Boatman & Sotherton, 1988). Cowgill, Wratten & Sotherton (1993a) compared adult syrphid distribution in areas of Conservation Headlands and areas of headland that were conventionally managed i.e. pesticides were applied to the headlands at the same time and rate as the rest of the field. Counting weeds in transects of each type of headland, Cowgill *et al.* (1993a) recorded higher floral diversity in Conservation Headland plots. Syrphid species diversity, recorded by observing Syrphidae during standard walks, was also higher in the Conservation Headland plots than in conventional plots. Syrphid egg distribution in both types of headland was also investigated by Cowgill *et al.*, (1993a). Higher numbers of aphidophagous eggs per aphid were recorded from Conservation Headland plots than conventional plots. However there were higher numbers of aphids in the conservation plots so the egg distribution may have been a positive reproductive numerical response (Solomon, 1949), rather than due to any effect the flora may have had.

Conservation headlands not only benefit Syrphidae, but are of benefit to other, non-pest invertebrate species (Chiverton & Sotherton, 1991). Chiverton & Sotherton (1991) showed that crop headlands, which were left untreated with herbicide, supported significantly higher densities of non-target invertebrate species, which included beneficial species such as Carabidae and Staphylinidae.

### Improving habitat inside the field

Encouraging high plant diversity in and around crops can maintain alternative host plants for pests (Ellis, 1992) and can provide alternative prey and more suitable habitat for beneficial predators (Speight, 1983). The most highly ranked polyphagous predators (*Demetrias atricapillus*, *Agonum dorsale*) in a study by Sunderland & Vickerman (1980) were also those that predominantly overwinter in grassy hedge bottoms (Sotherton, 1984; 1985). Such important predators disperse from

overwintering sites slowly in the spring (Coombes & Sotherton, 1986). By creating suitable overwintering resource within a cereal field, such predators can disperse from within the field during the spring to provide an even predator cover more quickly at a critical stage of aphid population growth (Thomas, Wratten & Sotherton, 1991). Wild flowering herbs provided overwintering cover for polyphagous predators in 1.5m-wide strips within cereal fields in Switzerland (Nentwig, 1992; Heitzmann, Lys & Nentwig, 1992). Such a management technique takes land out of production and it was suggested that economic compensation be made as an incentive for Swiss farmers to adopt such a technique. Chiverton (1989) also took land out of production from within cereal fields in Sweden, creating grassy banks which were used as overwintering sites by beneficial polyphagous arthropods. Fuller, (1975; cited by Allen, 1979) also recognised the potential to provide cover for beneficial arthropods, but rather than recreate overwintering habitat, he provided simple rectangles of plastic, styrofoam and cardboard in cereal fields. He concluded that such apparatus was successful at providing cover to Carabidae, which aggregated beneath the rectangles, but no improvement in aphid predation was reported.

#### Supplementing within-field food resources

Other techniques that have potential to manipulate beneficial arthropod populations, including Syrphidae, include using artificial honeydew sprayed on crops (Ben Saad & Bishop, 1976). Spraying solutions of honey, molasses and yeast extract, to simulate honeydew in potato fields in Libya, Ben Saad & Bishop (1976) significantly increased the numbers of Syrphidae, Chrysopidae and Coccinellidae in sprayed plots. However syrphid oviposition was not promoted in the plots, probably due to the absence of aphids.

Powell *et al.*, (1983) combined undersowing with the provision of parasitised *Myzus festucae* Theobald in cereals. Winter wheat was undersown with *Lolium perenne* L.. *Myzus festucae* containing larvae of the parasitoid *Aphidius rhopalosiphi* (= *A. uzbekistanicus* Luzhetski) was released into plots on the undersown grass, where they overwintered. There was an increase in the number of polyphagous predators in the plots where *M.festucae* had been introduced, probably an aggregative numerical response, and a reduction in *S.avenae* populations, presumably by both parasitisation by *A.rhopalosiphi* and predation by polyphagous predators.

Holtz (1988) also investigated the provision of non-cereal aphids on grasses

as alternative food sources to enhance aphid-specific predators in Germany. The alternative prey however, was provided in grassy margin strips adjacent to cereal fields. More Coccinellidae and Syrphidae were recorded in the spring and autumn from such patches than from control patches without aphids.

#### Improving habitat outside the field

Leius (1967a;b) realised that the availability of adult food sources should be considered when manipulating populations of beneficial insects and suggested that plants which provided direct resources (pollen and nectar) or indirect resources (alternative host prey) should be deliberately cultivated to promote the activity of beneficial insects.

Knowing that adult Syrphidae feed on pollen and nectar from flowers to complete gametogenesis, and that some Syrphidae have aphidophagous larvae, the establishment of flowering plants near crops has been suggested as a means of potentially increasing the abundance of syrphid larvae (Chambers, 1988). However, experiments where additional floral resources have been provided have not always demonstrated a clear result in terms of better aphid control. Chandler (1968c) compared the number of eggs laid in plots of aphid-infested Brussels sprouts, approx. 13m<sup>2</sup> and 25m apart, with and without flowers of *Senecio jacobea* L., and found no significant differences between plot types. On a larger scale, using plots of 200m<sup>2</sup>, Sengonca & Frings (1988) investigated the incidence of syrphid adults and eggs in sugar beet plots with and without margin strips of *Phacelia tanacetifolia* Benth., a North American annual which is a good source of pollen for syrphids (Klinger, 1987). Sengonca & Frings (1988) reported higher numbers of adults in the plots with floral margins, but more eggs were found in the plots with no floral margins, where there were also higher aphid densities.

One of the earliest studies identifying increased syrphid predation on a crop associated with flowers sown adjacently, was by van Emden (1965a). Flowers were planted along parts of two edges of a Brussels sprout crop. More syrphid eggs were oviposited on the crop near the flowers than elsewhere, and *Brevicoryne brassicae*, suffered 65-70% predation mortality in the plots with flowers compared to less than 50% predation mortality at the sites without flowers. In a review of habitat manipulation to enhance effectiveness of aphidophagous Syrphidae in California, Bugg (1993) concluded that oviposition was probably influenced more by shelter than

by flowers, although his evidence was conflicting. Bugg (1993) also commented that because Syrphidae are strong fliers, and probably disperse widely, benefits from flowers adjacent to crops were difficult to demonstrate. Dempster & Coaker (1974) also suggested that pest control employing very mobile beneficial species could probably not be achieved simply by managing habitats around crops, although White, Wratten, Berry & Weigmann (1994) and Hickman & Wratten (in prep) disagree. White *et al.* (1994) grew *P.tanacetifolia* in strips 25m long on one side of each of four cabbage plots 790m<sup>2</sup> in a market garden. The plots with a *P.tanacetifolia* strip lay between contiguous plots of the same area but without *P.tanacetifolia* flowery strips. Over a 77 day period, there were consistently more Syrphidae caught in plots with a flowery strip, than in plots without such a strip. However, there was no significant differences found in oviposition by Syrphidae between plot types. Hickman & Wratten (in prep) used cereal fields between 3.6ha and 32.4ha as replicates in experiments to try and manipulate the local distribution of Syrphidae on a large scale using *P.tanacetifolia*. In the first summer of the experiment, there were significantly more Syrphidae caught by yellow traps in fields with a *P.tanacetifolia* border, but no such significant differences were found in the second summer.

Populations of Carabidae and Staphylinidae, individuals of which are much less mobile than Syphidae can however be manipulated by appropriate management of vegetation adjacent to crops (Altieri & Letourneau, 1982). Lagerlöf & Wallin (1993) compared beneficial arthropod species composition in two field margins with contrasting floral diversity. In plots of high floral diversity, polyphagous predators and Syrphidae were significantly more abundant. However predator differences were not attributed exclusively to floral differences; syrphid distribution was associated with flowers, but epigeal polyphagous predator differences were attributed to differences in the composition of the sod layer between sites. Mixed margin strips of *Sinapis alba* L. and *P.tanacetifolia* sown along the edge of a cereal field was investigated by Klinger (1987). Invertebrate sampling showed higher numbers of Carabidae and Syrphidae by the floral strips. There was also a reduction in infestation of *S.avenae* near the strips, compared with control sites, but not by a significant amount.

Molthan & Rupert (1988) and Molthan (1990) investigated field boundary strips, but instead of sowing plants, they studied naturally occurring wild flowers in boundary strips of three widths; less than 1m, 1.5-2m and 8m wide. Floral diversity of margins increased in relation to the increasing width of margins and an increase

in syrphid diversity and abundance was reported with increasing floral diversity. No measures of increased oviposition or predation were taken in these studies.

### Conclusions

Natural enemies depend on habitat complexity for sources of alternative hosts or prey, for pollen and nectar and for sites of shelter (Altieri & Letourneau, 1982). Diversification of agroecosystems, and/or manipulation of resources used by beneficial arthropods could result in increased opportunities for such natural enemies and consequently more effective biological control of pests such as cereal aphids.

### Aims of the study

The literature reporting promotion of beneficial predatory arthropods in areas where habitat has been manipulated to promote predatory activity is mostly descriptive and consideration of long term changes in artificial habitat is lacking. Similarly, literature reporting instances where resources have been provided for Syrphidae are often descriptive and the mechanism of distribution of Syrphidae around resources is not accounted for. This study investigated the use of resources provided both within and around arable fields by polyphagous and aphid-specific predators and addressed this shortfall in data.

The aims of the study were to examine temporal changes in an artificially created overwintering resource provided to manipulate the distribution of polyphagous predators within a cereal field. In addition it was hoped that new and potential floral resources utilised by Syrphidae in the summer could be identified and provided around field boundaries in field experiments to try to manipulate the distribution of Syrphidae on a field scale. Previously such experiments have drawn conflicting conclusions, in terms of distribution of Syrphidae about resources; consequently the mechanisms that influence the distribution of Syrphidae around such floral resources were to be investigated and factors such as landscape features which could influence distribution were also to be examined.

## CHAPTER TWO

### LONG-TERM CHANGES IN AN OVERWINTERING HABITAT CREATED TO INCREASE DENSITIES AND WITHIN-FIELD DISTRIBUTION OF POLYPHAGOUS ARTHROPODS ON ARABLE LAND

#### INTRODUCTION

In experimental investigations, the densities of polyphagous predators have been manipulated by creating suitable overwintering habitats within cereal fields (Chiverton, 1989; Riedel, 1989; Thomas *et al.*, 1991). Early results from the first three years' work on these habitats, which take the form of raised grassy banks, have been reported on a number of occasions by Thomas (1989), Thomas and Wratten (1990), Thomas (1991), Thomas *et al.* (1991) and Thomas, Mitchell & Wratten (1992). Success of the technique has been attributed to the stabilising effect that tussocky grasses have on temperature variation on the banks (Thomas *et al.*, 1992a). Working on a bank in Hampshire during the early winter period, when Carabidae are "selecting" overwintering sites (Wallin, 1985), Thomas *et al.* (1992a) recorded the lowest temperature fluctuations on the bank from tussocks of *Dactylis glomerata* L. (Cock's-foot) and *Holcus lanatus* L. (Yorkshire fog). Temperature variation was greatest at the surface of bare soil and in the air 0.3m above the bank (Thomas *et al.* 1992a). Temperature fluctuations in the matt-forming grasses, *Agrostis stolonifera* L. (creeping bent) and *Lolium perenne* (Rye-grass) were intermediate between the tussocky grasses and bare ground or open air. This agreed with earlier work by Luff (1965) working on *D.glomerata* and Bossenbroek, Kessler, Liem & Viljm, (1977) working on *H.lanatus*, who each reported lower temperature fluctuations in grass tussocks than temperature fluctuations recorded outside tussocks. Desender (1982) showed a positive correlation between a more stable temperature in the environment and the numbers of overwintering predators in that environment, with reduced insect mortality perhaps due to the less variable temperature.

The provision of overwintering habitat, in the form of a raised grassy bank, as advocated by Thomas *et al.* (1991) has received some media attention and is promoted by The Game Conservancy Trust and FWAGs (Farming and Wildlife Advisory Groups). The technique of providing grassy banks for overwintering habitat



has already been practised by a number of farmers and farm owners in the UK (N. Sotherton pers. comm.). Such grassy banks have been established in Dorset, Essex Hampshire, Leicestershire and Norfolk in England and in Fife in Scotland. However, this is without the fore-knowledge of the long-term ecological and agronomic implications of such a practice (Holland, Frampton, Wratten & Cilgi, 1994). There is a need to study such habitat manipulation in the longer term to determine whether conclusions drawn from data collected during the early years of such studies are maintained in later years. Long-term ecological studies of this type are uncommon. In a random sample of 749 ecological papers published in the journal "Ecology" between 1977 and 1987, the average (modal) study lasted for one year (Tilman, 1987). The great majority of studies (86%) were completed within three years. Only 1.7% of studies were field experiments lasting five or more years (Tilman, 1987). Woiwod (1991) classified any ecological study lasting five years or more as long-term. Despite allowing more careful interpretation of transient dynamics inherent in any short-term study, such long-term studies are uncommon (Aebischer, 1991). Hassell, Lato & May (1989) investigated density dependence in 63 published life table studies involving 58 insect species. As the number of generations studied increased, the likelihood of detecting density dependent processes increased, thus conclusions drawn from studies of a short duration can be completely different from conclusions drawn if the studies were carried out over a longer period (Aebischer, 1991).

The Rothamsted Insect Survey is an example of a long-term, large scale, ecological study (Taylor, 1987). The survey was established in the early 1960's and is composed of a nationwide network of two types of trap. Light traps capture moths and 12.2m-tall suction traps are used to capture aerial populations of aphids. Data from the survey have been used to provide ecological information about a number of subjects including insect migration (Taylor, 1986). Another long term ecological monitoring study is that by The Game Conservancy Trust which has been monitoring invertebrate abundance in cereal fields in West Sussex since 1970. Invertebrates are sampled using a Dietrick vacuum sampler (Dietrick, 1961) annually in June, from farms in a 62km<sup>2</sup> area of West Sussex. Data from the study show that patterns of change for each of a wide variety of invertebrate taxa have been very similar between years; specifically there has been a steady decline in the mean number of staphylinids, spiders and harvestmen sampled annually (Aebischer, 1991). Neither The Game Conservancy Trust's study or the Rothamsted Insect Survey study are

manipulative; the data collected are of a monitoring nature.

One of the first studies which combined long-term monitoring with manipulative studies was the "Boxworth" project (Greig-Smith, Frampton & Hardy, 1992). The project was stimulated by the results of The Game Conservancy Trust's programme and was designed to investigate whether the sustained prophylactic use of pesticides caused harmful environmental effects (Greig-Smith, *et al.*, 1992; Çilgi, Wratten, Frampton & Holland, 1993). More specifically, it examined pesticide effects on invertebrates, small mammals and birds in cereal fields. The overall results of the Boxworth project showed that when conventional and integrated farming techniques were compared, there were more beneficial arthropods, small mammals and birds, in integrated plots, but this was in addition to more weeds and crop pests. Yields and economic gross margins were lower in integrated plots. The Boxworth project has been superseded by the SCARAB (Seeking Confirmation About Results At Boxworth) project, another long-term study of pesticide effects on farm "wildlife". This study is on a larger scale, is better replicated and covers more soil types than did the original Boxworth project. Across Europe, there are a number of similar long-term agro-ecological manipulative studies. They are primarily concerned with the management of experimental farming systems for integrated crop protection. Such studies have short histories and results from them will not be available until the mid-late 1990s', nevertheless, their background and preliminary results are reviewed by Holland *et al.* (1994)

A frequently used "indicator" group in these studies has been the Carabidae (Çilgi, 1994). Long-term investigations of the populations of this family include those by Luff (1982) who, in a nine-year study, recorded annual numbers of Carabidae caught by pitfall traps in a walled garden. There was very little between-year population fluctuation in the common species captured. This was attributed to the longevity, fecundity and rate of development of each species (Luff, 1982). Jones (1979), also used pitfall traps in a study of Carabidae in winter-wheat fields, between May and October for seven years. The numbers of different common species captured fluctuated greatly over the seven year study although total numbers of Carabidae caught each summer were very similar. This may indicate an equilibrium density that can be supported during the summer in the field (Jones, 1979). In the Netherlands, Den Boer (1977; 1981) has used pitfall traps to study population dynamics of Carabidae in a variety of habitats over 20 years. Using field-collected

data in computer simulation models, Den Boer (1981) showed that sub-populations that fluctuated unequally allowed the composite (meta) population to survive ten times better than a composite population whose sub-populations fluctuated synchronously. Schnitter (1994) compared carabid species diversity and species abundance over five years in a fallow field and a fallow meadow. Species diversity was greatest in the field, with maximum density occurring in year two in the field, and in year five in the meadow. Schnitter (1994) described the changing composition of the carabid communities in the field and meadow as a successional process, with some species e.g. *Bembidion quadrimaculatum* L., *Amara similata* Gyll. captured in greatest number in the first year then declining, while other species e.g. *Harpalus affinis* Schr. and *Amara littorea* Thoms. were recorded in greatest numbers during the middle years of the study, and species such as *Calathus fuscipes* Goez. and *Harpalus rubripes* Duft. being recorded in maximum abundance in the latter years of the study. Mader (1988) made a long-term study of Carabidae succession in a developing woodland, and reported both an increase in proportion and number of forest type carabid species, over five years, as vegetation cover increased.

Working on grassy banks as artificial overwintering habitats, Thomas *et al.* (1992b) described how over each of the first three winters that the grassy banks were studied, there was a decrease in the proportion of the sort of carabid species typically found in the open-field during winter months such as *Bembidion obtusum*, *Notiophilus biguttatus* and *Pterostichus* spp. (Sotherton, 1984; 1985). Thomas *et al.* (1992b), described such species as "open-field" type Carabidae. Over the same period, on the grassy banks, there was an increase in the proportion of carabid species which are almost exclusively found in field-boundaries during winter months, such as *Agonum dorsale*, *Bembidion lampros* and *Demetrias atricapillus* (Sotherton, 1984; 1985). Thomas *et al.* (1992b) termed these species as "boundary-type" Carabidae.

Together with changes in the invertebrate community over time, changes in the vegetational composition of the banks would be expected. Luff (1965) described three stages in the growth of *D. glomerata* tussocks; an immature stage from 0-3 years until tussocks reached a diameter of 10cm; a mature stage from 3-6 years when dead leaf litter gathered in the base of the tussock; and a third stage of decay when most of the tussock is dead but new growth occurs upwind of the tussock. The length of time a tussock will continue to produce new growth is unknown but is perhaps 12 years (Luff, 1965). Thomas (1991) did not study vegetation change during

his study of the grassy banks he established in Hampshire.

In an eight-year experiment studying *Arrhenatherum elatius* (L.) J.&C. Presl., *Festuca rubra* L. and *D.glomerata*, grown both in single species plots and as mixtures, Grubb (1982) noted that *A.elatius* was able to invade and take over ground occupied by other species while resisting invasion by others; *D.glomerata* was able to invade gaps and was superior to *A.elatius* in becoming established on bare ground; and *F.rubra* was able to prevent *D.glomerata* from invading because of its dense structure, down to soil level, although it was not able to prevent *A.elatius* from penetrating and establishing itself in the *F.rubra* plots. Thórhallsdóttir (1990) studied the mobility of five grasses (*Agrostis capillaris* L., *H.lanatus*, *L.perenne*, *Poa trivialis* L., *Cynosurus cristatus* L.) and *Trifolium repens* L., which were grown in contiguous single-species hexagons arranged in a mosaic. After 27 months, the hexagons were harvested and vegetation identified. *Holcus lanatus*, *C.cristatus* and *L.perenne* mostly remained in their original hexagons, but only 20% of the total *T.repens* biomass was harvested from its native hexagon plots. *Agrostis capillaris* and *P.trivialis* were distributed equally among native and non-native hexagons.

#### Aims of this chapter

The aims of the work described in this chapter are, i) to provide long-term data which describe temporal changes in patterns of abundance of predators in a raised grassy bank established by Thomas (1991), by continuing to measure the overwintering densities of polyphagous predators; ii) to introduce two new grass species to the bank to obtain information about overwintering opportunities for polyphagous predators in other grasses, iii) to describe any changes in the composition of the grasses on the bank, and iv) to compare the polyphagous predatory fauna in newly established banks in other parts of England with existing hedgerows nearby.

### **MATERIALS AND METHODS**

Three raised grassy banks have been described by Thomas (1991). This study investigated the bank which had been most intensively studied by Thomas (1991). The bank had been established during spring 1987. Polyphagous predator densities in the bank were recorded for three winters by Thomas from winter

1987/88 until winter 1989/90 and results have been reported by Thomas (1991). A description of how the bank was created is provided here for ease of reference.

#### Creation of the raised bank

The bank was sited in Field 21 (F21) on the Leckford Estates, a mixed arable farm of just over 1000ha on chalk, in northern Hampshire, UK (Grid ref SU 374 376). Two-way ploughing down the centre of F21, a 7.3ha field, during the spring cultivation period, resulted in the creation of a bank of earth 290m long, 1.5m wide and approximately 40cm higher than the rest of the field. The bank did not extend to any of the field boundaries but formed an "island" down the middle of the field and allowed access for farm vehicles to all parts of the field around the bank.

The bank was divided into six blocks of equal length. Each block was then sub-divided into eight treatments, each a plot 6m in length. Plots were marked with white painted wooden stakes. Appendix I is a tabulated representation of the original layout of the bank. The eight treatments comprised single species plots of *Agrostis stolonifera* sown at 8gm<sup>-2</sup>, *Dactylis glomerata* (3gm<sup>-2</sup>), *Holcus lanatus* (4gm<sup>-2</sup>), and *Lolium perenne* (3gm<sup>-2</sup>), a 25% mix by seed weight of each of the previous four grasses, a 33% mix by seed weight of *D.glomerata*, *H.lanatus* and *L.perenne* and a bare-ground treatment. An eighth treatment consisting of perennial herbs was also included but was used in a separate study and did not form part of the overwintering experiment.

Thomas completed his study in the summer of 1990. The experimental design of the bank was modified in the autumn of 1991 (see below).

#### Modification of the raised bank

Each of the plots on the bank which had originally been bare ground plots or herbaceous perennials, was sprayed with the broad spectrum herbicide, glyphosphate, at the recommended field rate (1440 g a.i.ha<sup>-1</sup>) on 19 September 1991 using a CP15 knapsack sprayer. Dead vegetation in the sprayed plots were cut on 3 October with a petrol-driven hand-held "trimmer", and cleared with a garden rake. Each plot was then cultivated, on the same date, with a 4HP rotovator and the soil raked evenly. The original bare ground plots were sown by hand with *Arrhenatherum elatius* and herbaceous plots sown with *Festuca rubra*, each at their commercial sowing rate of 3gm<sup>-2</sup> (Nix, 1993) on 6 October 1991.

### Choice of grasses

Thomas (1991) chose the first four grasses for use in the bank to provide two examples of each of two types of grass growth habit. *Agrostis stolonifera* and *L.perenne* both grow as a close turf, while *D.glomerata* and *H.lanatus* form tussocks. All four of these grasses are common on arable land. *Arrhenatherum elatius* and *F.rubra*, which were added to the bank in 1991, grow as tussocks, but *A.elatius* grows to 60-120cm, while *F.rubra* grows to 10-70cm (Clapham, Tutin & Warburg, 1962). *Festuca rubra* also has a creeping habit and in a grassy bank, would be expected to colonise any gaps quickly thus keeping out potential weed species. *Festuca* spp. are also resistant to many graminicides (Marshall & Nowakowski, 1992; Wratten & van Emden, 1995), which is an important consideration if herbicide applied to the crop drifted onto the grassy bank. The species were also chosen for the pragmatic reason that farmers would not consider the chosen grasses as invasive or aggressive weeds to the crop. Marshall (1989) and Davies & Carnegie (1994) studied the distribution patterns of flora from hedge bottoms into adjacent fields; *A.elatius*, *D.glomerata* and *H.lanatus* grew up to 1m into the field, *A.stolonifera* grew further, up to 1.5m into the field, but occurred at low densities (2.2 plants m<sup>-2</sup>).

### Collection of polyphagous predators

The methodology used by Thomas (1991) to estimate polyphagous predator densities during the winters 1988/89 and 1989/90 was followed in this study.

Turves 20cm x 20cm x 10cm deep were dug in each single-species grass plot and each turf placed in a strong polythene bag, 50cm x 100cm, containing a pencil-written paper label. Two turves were taken from each plot. The turves were taken to the laboratory and stored at 4°C until each was examined. Maintaining the samples at this temperature reduced the activity of invertebrates and inhibited predation (Mitchell, 1963b). Turves were individually broken up in a white plastic tray 45cm x 35cm x 8cm using size 8 knitting needles. Coleoptera and Araneae from the grass or soil of the turf were collected live from the tray using a pooter as the turf was being broken down. Contents of each turf were stored in 70% ethanol until organisms were identified.

#### Estimating the grass species composition in "single species" grass plots 1992/93

While collecting samples during the winter 1991/92, it was noted that *L.perenne* had become patchy in the plots where it had been sown as a single species. Plots originally sown with *L.perenne* had become dominated by *D.glomerata*. Since the first winter after establishment of the bank, no investigation had been carried out to determine whether the single-species plots had remained as single grass species plots. On 8 October, 1992, six 25cm x 25cm quadrats were randomly placed on each of the original single-species treatment plots and the new grass plots. The percentage ground cover was estimated by eye and the presence of any other grasses, not sown to that plot was noted.

#### Estimating ground cover by grasses 1993/4

Before being broken down with knitting needles, the vegetation from each 20cm x 20cm turf that was sampled from three of the blocks on the ridge (blocks A to C - Appendix I) during winter 1993/94 was cut a standard 2cm above the soil level. A 20cm x 20cm quadrat, divided by string into twenty-five 16cm<sup>2</sup> squares, was placed over each turf. The percentage ground cover was then estimated by eye.

#### Sampling of invertebrates from grassy banks in other parts of England 1994

Two relatively newly established grassy banks, outside Hampshire were sampled in January 1994, using a novel suction sampler (MacLeod *et al.*, 1994).

The first bank sampled was at Boarded Barns farm, Essex (Grid ref TL 559 049). The bank was established in May 1992. It was sown with a 3:4 mix of *D.glomerata* and *H.lanatus* at 3.5gm<sup>-2</sup>. It is 200m long and was used to divide one 7ha field into two fields of 3.5ha. One field (Well East) has become part of The Rotational Set-aside Scheme (Anon., 1990). The other field (Well West) was sown with winter wheat (cv. Mercia). On 20 January 1994, twenty individual samples were taken at 10m intervals along the middle of the bank. Twenty samples were also taken from the base of the hedge surrounding Well West. The hedge contained, *Quercus robur* L., *Alnus glutinosa* (L.) Gaerth. standards, *Crataegus monogyna* Jacq., *Rubus fruticosus* agg., *Hedera helix* L., *Galium aparine*, *H.lanatus*, *Festuca* spp. and *Lolium* spp. In a single sample, the suction sampler collected from an area of 0.01m<sup>2</sup> for 30s. Material collected by the sampler was then transferred to a plastic bag containing a pencil-written paper label and sealed before collecting the next sample.

On returning to the laboratory, the bags were stored at -20<sup>0</sup> C until the contents could be identified.

On January 21 1994 samples were taken from a bank at the Loddington Estate, Leicestershire (Grid ref SK 792 024). The bank was established in September 1992 and was sown with a 50:50 mix of *D.glomerata* and *H.lanatus*. It is 400m long and has been used to divide an 18.4ha field into two fields of 9.2ha. On one side of the bank, the field was sown to winter barley (cv. Paradise). On the other side the field forms part of a set-aside scheme (Anon., 1990). Twenty individual samples were taken from the middle of the bank at 10m intervals using the modified suction sampler as described before. Twenty individual samples were also taken at 10m intervals from the base of the hedge enclosing the field in which the bank was created. The base of the hedge was composed of *Alopecurus myosuroides* Huds., *Agropyron repens* (L.) Beauv., *Lamium purpureum* L., *Poa annua* and *Ranunculus repens* L..

## RESULTS

Data for the first three winters were collected by Thomas (1991) and are included here for completeness. However these data and the complete data set have been re-analysed.

### Densities of polyphagous predators - Carabidae

Carabidae were identified using keys by Lindroth (1974). Twenty-four species of Carabidae were identified from the bank from the fourth to the seventh winters. Thomas (1991) provides details of the densities of six genera and five species of Carabidae during the first three winters. Fig 2.1 shows the mean density of total Carabidae in each of the four original grass species sown on the bank together with the mean density from the adjacent hedge in winters five to seven. Mean densities of *Demetrias atricapillus*, the most abundant carabid each winter, are shown in Fig 2.2. Fig 2.1 shows how the mean density of total Carabidae has fluctuated in parallel with the fluctuation of *D.atricapillus* density over each winter in the grass species on the bank.

Table 2.1 shows the mean densities of Carabidae taxa in grass plots for each winter. Species which were rarely found were pooled with species where little is known about their overwintering biology and have been classed in Tables 2.1 and 2.2



as "other Carabidae".

Hartley's (1950)  $F_{\max}$  - test was used to check homoscedasticity (homogeneity of variances) of  $\log_{10}(X+1)$  transformed data before carrying out an analysis of variance (ANOVA) for each carabid taxon between grasses within years, with grass and block as factors (Table 2.1) and between winters within grasses, with winter and block as factors (Table 2.2). Appendices II and III show results of  $F_{\max}$  tests and ANOVA  $F$  ratios. Where no taxon was found in any plots of a particular single grass species, within a winter, the grass was excluded from the ANOVA and a density of 0.00 appears in tables. If a particular taxon did not occur in any of the grasses on the bank in a winter, the whole taxon appears in tables as dashes (-) for that winter.

The data in Tables 2.1 and 2.2 are the same but have been shown in two tables so that differences between grasses within winters, and between winters within grasses can be seen more clearly.

In the first winter of the study there were no significant differences in any of the mean carabid densities of each carabid taxon between grasses (Table 2.1). During subsequent winters there were significant differences in mean densities of both total Carabidae and specific carabid taxa between grasses. Tukey's (1949) test was used to determine which mean densities were significantly different and results are shown in Table 2.1 (between-grass differences) and Table 2.2 (between-winter differences). In the fifth (1991/92), sixth (1992/93) and seventh winters (1993/94) turf samples were taken from the base of the hedge around F21. Densities of carabid taxa in the hedge bottom are given in Tables 2.1 and 2.2 but were not included in the ANOVAs since the hedge was not part of the original experimental linear randomised block design. During the first winter, Thomas (1991) sampled only blocks A to D, and omitted E and F because of time constraints. Data from this winter was therefore not included in the ANOVAs for Table 2.2. For each of the original grass species, the highest mean total carabid density occurred during winter two (Table 2.2).

Carabidae are nearly all univoltine (Thiele, 1979) with two main annual seasons for breeding, spring and autumn. During all seven winters, Carabidae that breed in the spring dominated the carabid species present on the bank. The mean percentage of these spring-breeding species in the bank on any winter was  $93.6 \pm 4.2\%$ .

Fig. 2.1 Mean overwintering density ( $0.1\text{m}^{-2}$ ) of total Carabidae in four grasses from the bank and the existing hege of F21. See Tables 2.1 and 2.2 for range test results.

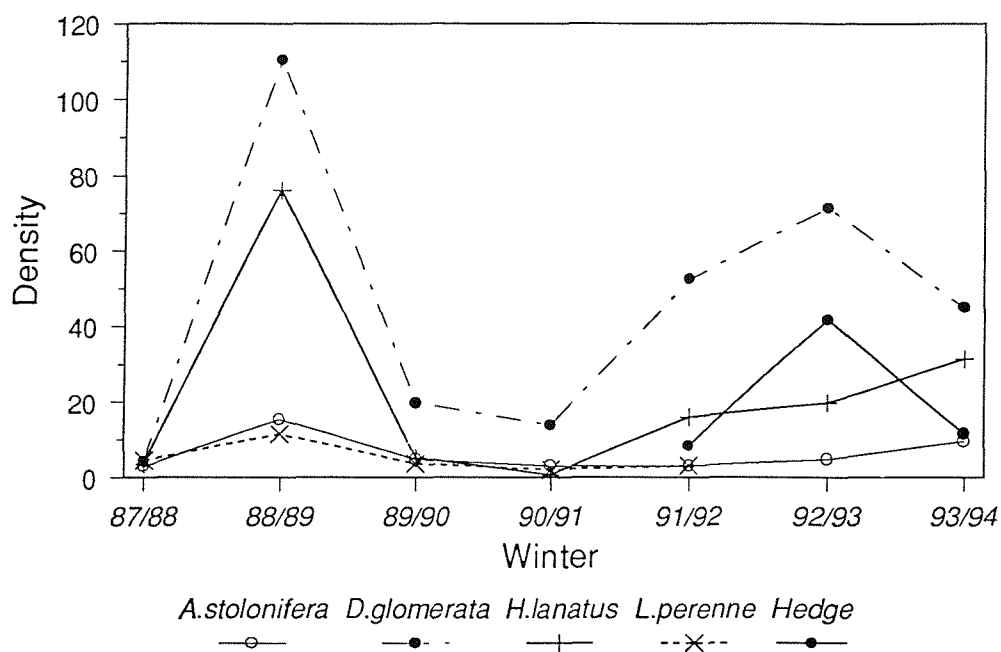


Fig. 2.2 Mean overwintering density ( $0.1\text{m}^{-2}$ ) of *Demetrias atricapillus* in four grasses from the bank and the existing hege of F21. See Tables 2.1 and 2.2 for range test results.

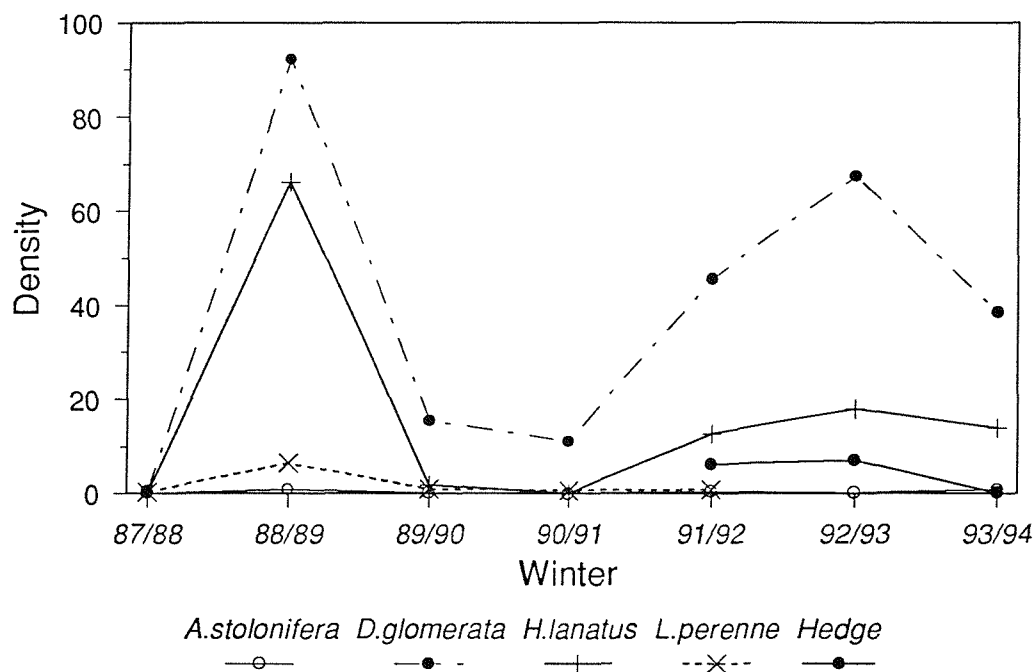


Table 2.1 Mean densities (0.1 m<sup>-2</sup>) of Carabidae in grass plots and adjacent field boundary during winters 1987/88 (1) to 1993/94 (7). Grasses sharing the same letter for each taxon, within a winter, do not significantly differ at P<0.05 (two way ANOVA on log<sub>10</sub> (X+1) transformed data - with grass and block as factors, followed by Tukey's (1949) test. Where no letters appear after a number, within a winter, data was excluded from the analysis - see text for explanation.

Winter/ grass	<i>Agonum dorsale</i>	<i>Amara spp.</i>	<i>Bembidion obtusum</i>	<i>Bembidion lampros</i>	<i>Demetrias atricapillus</i>	<i>Notiophilus biguttatus</i>	<i>Trechus spp.</i>	other Carabidae	TOTAL CARABIDAE
1 As	0.00	0.00	3.26 a	0.19 a	0.06 a	0.32 a	0.70 a	-	4.54 a
Lp	1.47a	0.13	3.78 a	0.19 a	0.51 a	0.51 a	0.38 a	-	6.98 a
Dg	0.00	0.00	8.33 a	0.31 a	1.04 a	0.42 a	0.52 a	-	10.63 a
HI	0.51a	0.00	3.71 a	0.13 a	0.13 a	0.70 a	0.26 a	-	5.44 a
2 As	-	0.63 a	6.88 ab	4.58 b	0.83 a	0.21	2.29 a	-	15.42 a
Lp	-	0.21 a	2.08 a	0.83 a	6.46 b	0.00	1.88 a	-	11.46 a
Dg	-	0.21 a	11.67 b	3.54 ab	92.29 c	0.00	2.71 a	-	110.42 b
HI	-	0.21 a	6.25 ab	1.88 ab	66.25 c	0.00	1.46 a	-	76.04 b
3 As	-	0.52 a	2.08 a	0.94 a	0.21 a	0.00	1.04 a	-	4.79 a
Lp	-	0.42 a	1.15 a	0.21 a	0.94 a	0.21 a	0.73 ab	-	3.65 ab
Dg	-	0.00 a	2.71 a	0.21 a	15.42 b	0.21 a	1.15 b	-	19.69 c
HI	-	0.31 a	2.29 a	0.10 a	1.77 a	0.21 a	0.52 ab	-	5.21 b
4 As	0.00	0.63	1.04 a	0.00	0.00	-	0.42 a	1.04 a	3.13 a
Lp	0.21	0.00	0.42 a	0.00	0.63 a	-	0.21 a	0.63 a	2.08 a
Dg	0.00	0.00	0.21 a	0.00	11.04 a	-	0.00 a	2.50 a	13.75 b
HI	0.00	0.00	0.21 a	0.21	0.00	-	0.00 a	0.21 a	0.63 a

continued overleaf

table 2.1 continued

Winter/ grass	<i>Agonum dorsale</i>	<i>Amara spp.</i>	<i>Bembidion obtusum</i>	<i>Bembidion lampros</i>	<i>Demetrias atricapillus</i>	<i>Notiophilus biguttatus</i>	<i>Trechus spp.</i>	other Carabidae	TOTAL CARABIDAE
5 As	0.00	1.25 a	0.63 a	0.42 a	0.42 a	-	-	0.42 a	3.13 a
Lp	1.25 a	0.21 a	0.00	0.42 a	0.83 a	-	-	0.42 a	3.13 a
Dg	3.54 a	0.21 a	0.00	0.42 a	45.63 c	-	-	2.71 b	52.50 b
HI	1.46 a	0.63 a	0.21 a	0.00	12.71 b	-	-	1.04 ab	16.04 a
Hedge	0.42	0.00	0.00	0.00	6.25	-	-	1.67	8.33
6 As	2.29 a	0.63 a	-	0.83 a	0.21 a	0.00	-	0.83 a	4.79 a
Dg	0.21 a	0.21 a	-	1.04 a	67.50 c	0.00	-	2.29 b	71.75 c
HI	0.21 a	0.42 a	-	0.21 a	17.92 b	0.00	-	1.04 ab	19.79 b
Ae	0.00	0.00	-	0.63 a	0.83 a	0.00	-	0.62 ab	2.08 a
Fr	0.63 a	0.00	-	0.83 a	1.88 a	0.21	-	0.00	3.54 ab
Hedge	27.92	1.25	0.42	2.92	7.08	0.00	-	2.08	41.67
7 As	1.04 a	0.21 a	1.04 a	0.83 a	0.83 a	-	2.71 a	2.92 b	9.58 a
Dg	0.00	0.00	0.21 a	0.21 a	38.54 c	-	2.29 a	3.75 b	45.00 b
HI	13.13 a	0.21 a	0.42 a	0.63 a	13.96 b	-	2.71 b	0.42 a	31.46 b
Ae	0.00	0.00	0.21 a	0.00 a	2.08 a	-	0.83 ab	0.83 a	3.96 a
Fr	0.00	0.42 a	0.42 a	0.63 a	1.88 a	-	0.63 ab	1.67 a	5.63 a
Hedge	3.54	0.21	0.00	3.96	0.21	1.46	0.21	2.08	11.67

**Key:** As = *Agrostis stolonifera*, Dg = *Dactylis glomerata*, HI = *Holcus lanatus*, Lp = *Lolium perenne*, Ae = *Arrhenatherum elatius*, Fr = *Festuca rubra*, Hedge = sample from base of hedge enclosing F21. - = no specimens found in any grasses on the bank.

Table 2.2 Mean densities (0.1 m<sup>2</sup>) of Carabidae in grass plots and adjacent field boundary during winters 1987/88 (1) to 1993/94 (7). Grasses sharing the same letter for each taxon, within each grass, do not significantly differ at P<0.05 (two way ANOVA on log<sub>10</sub> (X+1) transformed data - with winter and block as factors, followed by Tukey's (1949) test. Where no letters appear after a number, within a winter, data were excluded from analysis.

Winter/ grass	<i>Agonum dorsale</i>	<i>Amara spp.</i>	<i>Bembidion obtusum</i>	<i>Bembidion lampros</i>	<i>Demetrias atricapillus</i>	<i>Notiophilus biguttatus</i>	<i>Trechus spp.</i>	other Carabidae	TOTAL CARABIDAE
As 1	0.00	0.00	3.26	0.19	0.06	0.32	0.70	0.00	4.54
2	0.00	0.63 a	6.88 b	4.58 b	0.83 a	0.21	2.29 ab	0.00	15.42 c
3	0.00	0.52 a	2.08 a	0.94 a	0.21 a	0.00	1.04 a	0.00	4.79 ab
4	0.00	0.63 a	1.04 a	0.00	0.00	0.00	0.42 a	1.04 a	3.13 a
5	0.00	1.25 a	0.63 a	0.42 a	0.42 a	0.00	0.00	0.42 a	3.13 a
6	2.29 a	0.63 a	0.00	0.83 a	0.21 a	0.00	0.00	0.83 a	4.79 a
7	1.04 a	0.21 a	1.04 a	0.83 a	0.83 a	0.00	2.71 b	2.92 a	9.58 bc
Dg 1	0.00	0.00	8.33	0.31	1.04	0.42	0.52	0.00	10.63
2	0.00	0.21 a	11.67 b	3.54 b	92.29 c	0.00	2.71 a	0.00	110.42 c
3	0.00	0.00	2.71 a	0.21 a	15.42 a	0.21	1.15 a	0.00	19.69 a
4	0.00	0.00	0.21 a	0.00	11.04 ab	0.00	0.00	2.50 b	13.75 a
5	3.54 a	0.21 a	0.00	0.42 a	45.63 bc	0.00	0.00	2.71 b	52.50 abc
6	0.21 a	0.21 a	0.00	1.04 a	67.50 c	0.00	0.00	2.29 b	71.75 bc
7	0.00	0.00	0.21 a	0.21 a	38.54 bc	0.00	2.29 a	3.75 b	45.00 ab

table 2.2 continued

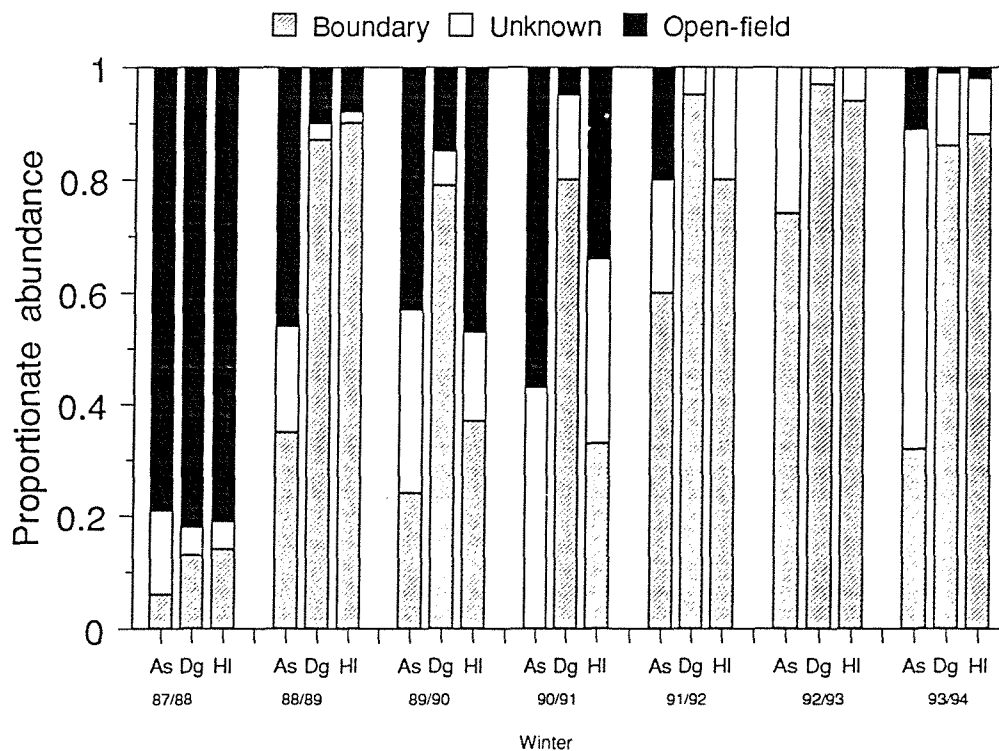
Winter/ grass	<i>Agonum dorsale</i>	<i>Amara spp.</i>	<i>Bembidion obtusum</i>	<i>Bembidion lampros</i>	<i>Demetrias atricapillus</i>	<i>Notiophilus biguttatus</i>	<i>Trechus spp.</i>	other Carabidae	TOTAL CARABIDAE
Lp 1	1.47	0.13	3.78	0.19	0.51	0.51	0.38 a	0.00	6.98
2	0.00	0.21 a	2.08 a	0.83 a	6.46 b	0.00	1.88 a	0.00	11.46 b
3	0.00	0.42 a	1.15 a	0.21 a	0.94 a	0.21	0.73 a	0.00	3.65 a
4	0.21 a	0.00	0.42 a	0.00	0.63 a	0.00	0.21 a	0.63 a	2.08 a
5	1.25 a	0.21 a	0.00	0.42 a	0.83 a	0.00	0.00	0.42 a	3.13 a
HI 1	0.51	0.00	3.71	0.13	0.13	0.70	0.26	0.00	5.44
2	0.00	0.21 a	6.25 b	1.88 b	66.25 c	0.00	1.46 ab	0.00	76.04 d
3	0.00	0.31 a	2.29 ab	0.10 a	1.77 a	0.21	0.52 a	0.00	5.21 b
4	0.00	0.00	0.21 a	0.21 a	0.00	0.00	0.00	0.21 a	0.63 a
5	1.46 a	0.63 a	0.21 a	0.00	12.71 b	0.00	0.00	1.04 a	16.04 bc
6	0.21 a	0.42 a	0.00	0.21 a	17.952 b	0.00	0.00	1.04 a	19.79 bc
7	13.13 a	0.21 a	0.42 a	0.63 ab	13.96 b	0.00	2.71 b	0.42 a	31.46 c
Ae 6	-	-	0.00	0.63	0.83 a	-	0.00	0.62 a	2.08 a
7	-	-	0.21	0.00	2.08 a	-	0.83	0.83 a	3.96 a
Fr 6	0.63	0.00	0.00	0.83 a	1.88 a	0.21	0.00	0.00	3.54 a
7	0.00	0.42	0.42	0.63 a	1.88 a	0.00	0.63	1.67	5.63 a
Hedge 5	0.42	0.00	0.00	0.00	6.25	0.00	0.00	1.67	8.33
6	27.92	1.25	0.42	2.92	7.08	0.00	0.00	2.08	41.67
7	3.54	0.21	0.00	3.96	0.21	1.46	0.21	2.08	11.67

**Key:** As = *Agrostis stolonifera*, Dg = *Dactylis glomerata*, HI = *Holcus lanatus*, Lp = *Lolium perenne*,  
Ae = *Arrhenatherum elatius*, Fr = *Festuca rubra*, Hedge = sample from base of hedge enclosing F21.

### Overwintering "boundary-type" and "open-field" Carabidae

Fig 2.3 shows the proportion of boundary-type Carabidae and open-field type Carabidae (*sensu* Thomas *et al.*, 1992b) found in the bank in each of three grass species which persisted as relatively pure stands over seven winters. Also included are the proportions of Carabidae whose overwintering strategies are unknown (Appendix IV).

Fig. 2.3: Proportion of "boundary", "unknown" and "open-field", -type Carabidae sampled in three grasses on the bank. Winters 1987/88 to 93/94



Key : As = *Agrostis stolonifera*, Dg = *Dactylis glomerata*, Hl = *Holcus lanatus*.

### Densities of polyphagous predators - Staphylinidae

Staphylinidae were identified following Joy (1932). Abundant members of the family which could be readily identified accurately such as *Tachyporus hypnorum* and *Stenus* spp. were identified to genus or species. Staphylinidae are a taxonomically difficult family of Coleoptera (P. Vickerman pers. comm.) and the contribution of individual species to aphid control in cereals is not well known (Sunderland *et al.*, 1985; Sopp & Chiverton, 1987; Dennis *et al.*, 1990; Dennis & Wratten, 1991). The remaining Staphylinidae were therefore identified to the level of subfamilies; Aleocharinae, Paederinae and Staphylininae. The mean density of total Staphylinidae is shown in Fig 2.4 for each of the original four grasses during winters one to seven and for the hedge around F21 for winters five to seven. Mean densities of *Tachyporus hypnorum*, the most abundant staphylinid during the study, are shown in Fig 2.5.

Table 2.3 shows mean densities of Staphylinidae taxa between grasses within winters and Table 2.4 show mean densities between winters within grasses. Paederinae were included in "other Staphylinidae" by Thomas (1991) which explains why the density of this taxon is zero in all grasses during the first three winters. The data for Staphylinidae densities were analysed using the same techniques as for carabid densities.  $F_{\max}$  results and ANOVA  $F$  ratios for Tables 2.3 and 2.4 are given in Appendices V and VI respectively. Significant differences in mean densities of both total Staphylinidae and specific taxa were found between grasses, within winters, during all winters except the fifth winter. The maximum mean densities of total Staphylinidae occurred in the sixth winter in all grasses sampled except *A.elatius* when maximum total Staphylinidae density occurred in the seventh winter.

Trends in total Carabidae and Staphylinidae densities over each of the seven winters have generally been similar, with densities higher in the second winter than in the first winter, then falling in the third and fourth winters, followed by rises in the fifth and sixth winters, falling again in the seventh winter (Figs 2.1 & 2.4).



Fig. 2.4 Mean overwintering density ( $0.1\text{m}^{-2}$ ) of total Staphylinidae in four grasses from the bank and the existing hedge of F21. See Tables 2.3 & 2.4 for range test results.

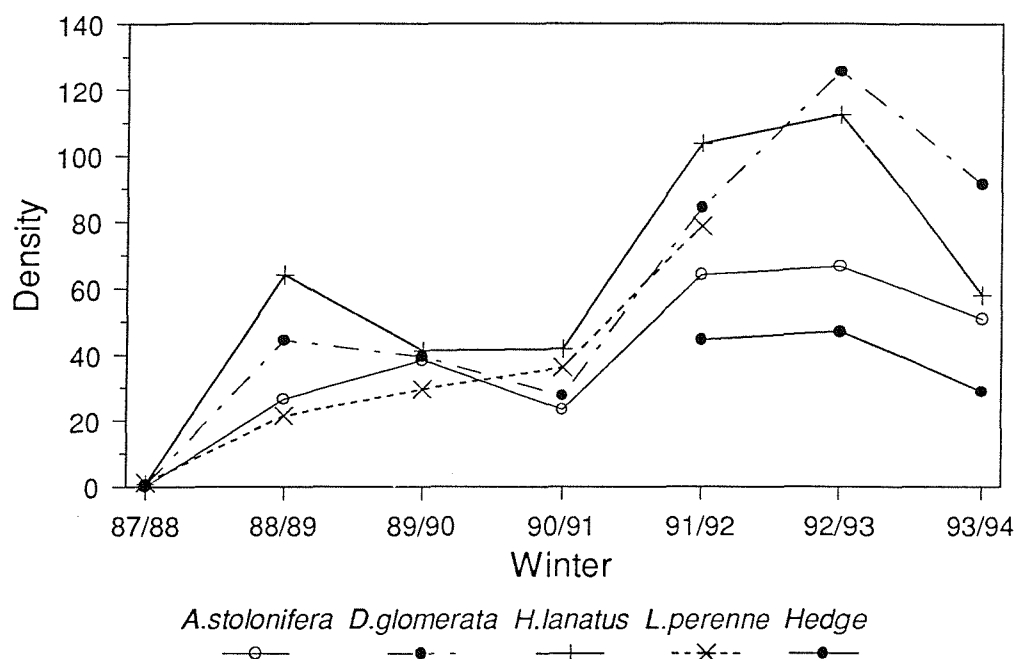


Fig. 2.5 Mean overwintering density ( $0.1\text{m}^{-2}$ ) of *Tachyporus hypnorum* in four grasses from the bank and the existing hedge of F21. See Tables 2.3 and 2.4 for range test results.

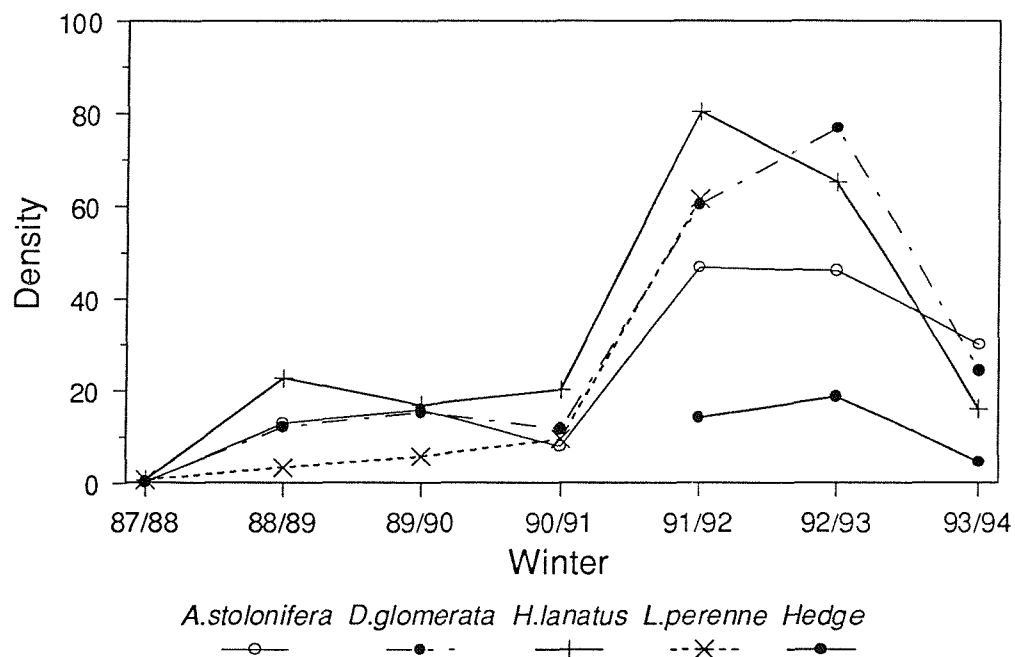


Table 2.3 Mean densities ( $0.1 \text{ m}^{-2}$ ) of Staphylinidae in grass plots and adjacent field boundary during winters 1987/88 (1) to 1993/94 (7). Treatments sharing the same letter for each taxon, within a winter, do not significantly differ at  $P < 0.05$  (two way ANOVA on  $\log_{10} X+1$  transformed data - with block and grass treatment as factors, followed by Tukey's (1949) test. Where no letter appears after a number, within a winter, data was excluded from analysis.

Winter/ grass	<i>Tachyporus hypnorum</i>	other <i>Tachyporus</i> spp.	<i>Stenus</i> spp.	Aleocharinae	Paederinae	Staphylininae	other Staphylinidae	TOTAL STAPHYLINIDAE
1 As	0.06 a	0.00	0.00	-	-	0.00	0.26 a	0.32 a
Lp	1.02 b	0.38 a	0.00	-	-	0.26 a	0.38 a	2.05 b
Dg	0.70 ab	0.00	0.10 a	-	-	0.10 a	0.30 a	1.20 ab
HI	0.96 b	0.06 a	0.06 a	-	-	0.00	0.45 a	1.54 b
2 As	12.92 b	3.13 a	0.00	10.42 b	-	-	-	26.46 ab
Lp	3.33 a	1.67 a	13.13 a	3.33 a	-	-	-	21.46 a
Dg	12.08 b	3.13 a	21.46 a	7.71 ab	-	-	-	44.38 bc
HI	22.71 b	4.58 a	24.79 a	12.08 b	-	-	-	64.17 c
3 As	15.83 b	12.08 a	1.77 a	-	-	0.42 a	8.23 a	38.33 a
Lp	5.73 a	14.17 a	1.77a	-	-	0.31 ab	7.50 a	29.48 ab
Dg	15.31 ab	9.90 a	3.75 a	-	-	0.73 b	9.58 a	39.27 b
HI	16.88 b	16.15 a	1.98 a	-	-	0.63 ab	5.73 a	41.35 b
4 As	7.92 a	6.04 a	0.00	4.38 a	0.42 a	4.58 a	-	23.33 a
Lp	9.58 ab	11.45 b	0.63 a	5.63 a	0.21 a	8.75 a	-	36.25 b
Dg	11.67 ab	3.96 a	0.42 a	6.46 a	0.00	5.21 a	-	27.71 ab
HI	20.21 b	10.21 ab	0.00	4.79 a	0.63 a	6.04 a	-	41.88 b

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table 2.3 continued

	Winter/ grass	<i>Tachyporus hypnorum</i>	other <i>Tachyporus</i> spp.	<i>Stenus</i> spp.	Aleocharinae	Paederinae	Staphylininae	other Staphylinidae	TOTAL Staphylinidae
5	As	46.88 a	6.88 a	1.04 a	8.33 a	-	1.04 a	-	64.17 a
	Lp	61.67 a	4.79 a	0.83 a	10.42 a	-	1.04 a	-	78.75 a
	Dg	60.42 a	9.58 a	2.71 a	10.63 a	-	1.04 a	-	84.38 a
	HI	80.42 a	10.83 a	1.25 a	9.38 a	-	1.88 a	-	103.75 a
	Hedge	14.17	12.50	0.83	13.75	1.67	1.67	-	44.58
6	As	46.25 a	6.25 c	2.50 a	2.92 a	6.67 a	2.08 b	-	66.67 a
	Dg	76.88 c	10.42 ab	5.00 b	17.71 c	12.50 b	2.92 ab	-	125.42 c
	HI	65.21 c	14.17 b	2.08 ab	13.96 bc	16.04 b	1.04 a	-	112.50 c
	Ae	15.42 b	7.71 ab	1.25 a	5.21 ab	12.29 ab	1.25 a	-	43.13 b
	Fr	22.29 b	4.17 a	0.21 a	6.88 abc	11.67 ab	1.25 a	-	46.46 b
	Hedge	18.75	2.92	0.00	11.67	0.83	12.91	-	47.08
7	As	30.00 ab	8.33 b	0.21 a	6.67 a	4.58 a	1.04 b	-	50.83 a
	Dg	24.38 b	16.25 ab	10.42 b	31.04 c	8.13 a	1.04 ab	-	91.25 c
	HI	16.04 ab	12.08 a	11.88 ab	14.17 b	3.13 a	0.83 ab	-	58.13 bc
	Ae	8.33 a	9.79 a	2.92 ab	12.92 b	7.50 a	0.42 a	-	41.88 b
	Fr	20.00 b	7.92 a	4.58 ab	8.96 b	7.71 a	1.04 ab	-	50.21 bc
	Hedge	4.58	1.88	0.83	16.46	2.29	2.71	-	28.75

**Key:** As = *Agrostis stolonifera*, Dg = *Dactylis glomerata*, HI = *Holcus lanatus*, Lp = *Lolium perenne*, Ae = *Arrhenatherum elatius*, Fr = *Festuca rubra*, Hedge = sample from base of hedge enclosing F21. - = No specimens found in any grasses on the bank in this winter.

Table 2.4 Mean densities (0.1m<sup>2</sup>) of Staphylinidae in grass plots and adjacent field boundary during winters 1987/88 (1) to 1993/94 (7). Winters sharing the same letter within a taxon, do not significantly differ at  $P < 0.05$  (two way ANOVA on  $\log_{10}(X+1)$  transformed data - winter and block as factors, followed by Tukey's (1949) test. Where no letter appears after a number, within a taxon, data was excluded from analysis.

Grass\ winter	<i>Tachyporus hypnorum</i>	other <i>Tachyporus</i> spp.	<i>Stenus</i> spp.	Aleocharinae	Paederinae	Staphylininae	other Staphylinidae	TOTAL STAPHYLINIDAE
As 1	0.06	0.00	0.00	0.00	0.00	0.00	0.26	0.32
2	12.92 ab	3.13 a	0.00	10.42 c	0.00	0.00	0.00	26.46 ab
3	15.83 bc	12.08 b	1.77 ab	0.00 a	0.00	0.42 a	8.23	38.33 bc
4	7.92 a	6.04 ab	0.00	4.38 bc	0.42 a	4.58 b	0.00	23.33 a
5	46.88 d	6.88 ab	1.04 ab	8.33 bc	0.00	1.04 a	0.00	64.17 bc
6	46.25 d	6.25 ab	2.50 b	2.92 ab	6.67 b	2.08 ab	0.00	66.67 c
7	30.00 cd	8.33 ab	0.21 a	6.67 bc	4.58 b	1.04 a	0.00	50.83 bc
Dg 1	0.70	0.00	0.10	0.00	0.00	0.10	0.30	1.20
2	12.08 a	3.13 a	21.46 ab	7.71 ab	0.00	0.00	0.00	44.38 ab
3	15.31 a	9.90 b	3.75 ab	0.00	0.00	0.73 a	9.58	39.27 a
4	11.67 a	3.96 ab	0.42 a	6.46 a	0.00	5.21 c	0.00	27.71 a
5	60.42 c	9.58 ab	2.71 ab	10.63 ab	0.00	1.04 ab	0.00	84.38 bc
6	76.88 bc	10.42 b	5.00 ab	17.71 bc	12.50 a	2.92 bc	0.00	125.42 c
7	24.38 ab	16.25 b	10.42 b	31.04 c	8.13 a	1.04 ab	0.00	91.25 bc

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table 2.4 continued

Grass\ winter	<i>Tachyporus hypnorum</i>	other <i>Tachyporus</i> spp.	<i>Stenus</i> spp.	Aleocharinae	Paederinae	Staphylininae	other Staphylinidae	TOTAL STAPHYLINIDAE
Lp 1	1.02	0.38	0.00	0.00	0.00	0.26	0.38	2.05
2	3.33 a	1.67 a	13.13 b	3.33 a	0.00	0.00	0.00	21.46 a
3	5.73 a	14.17 c	1.77 a	0.00	0.00	0.31 a	7.50	29.48 a
4	9.58 a	11.45 bc	0.63 a	5.63 a	0.21	8.75 b	0.00	36.25 ab
5	61.67 b	4.79 ab	0.83 a	10.42 a	0.00	1.04 a	0.00	78.75 b
HI 1	0.96	0.06	0.06	0.00	0.00	0.00	0.45	1.54
2	22.71 a	4.58 a	24.79 c	12.08 a	0.00	0.00	0.00	64.17 ab
3	16.88 a	16.15 b	1.98 ab	0.00	0.00	0.63 a	5.73	41.35 a
4	20.21 a	10.21 ab	0.00	4.79 a	0.63 a	6.04 b	0.00	41.88 a
5	80.42 b	10.83 b	1.25 a	9.38 a	0.00	1.88 ab	0.00	103.75 b
6	65.21 b	14.17 b	2.08 a	13.96 a	16.04 b	1.04 ab	0.00	112.50 b
7	16.04 a	12.08 ab	11.88 ac	14.17 a	3.13 a	0.83 a	0.00	58.13 a
Ae 6	15.42 b	7.71 a	1.25 a	5.21 a	12.29 a	1.25 a	-	43.13 a
7	8.33 a	9.79 a	2.92 a	12.92 a	7.50 a	0.42 a	-	41.88 a
Fr 6	22.29 a	4.17 a	0.21 a	6.88 a	11.67 a	1.25 a	-	46.46 a
7	20.00 a	7.92 b	4.58 b	8.96 a	7.71 a	1.04 a	-	50.21 a
Hedge 5	14.17	12.50	0.83	13.75	1.67	1.67	-	44.58
6	18.75	2.92	0.00	11.67	0.83	12.92	-	47.08
7	4.58	1.88	0.83	16.46	2.29	2.71	-	28.75

**Key:** As = *Agrostis stolonifera*, Dg = *Dactylis glomerata*, HI = *Holcus lanatus*, Lp = *Lolium perenne*, Ae = *Arrhenatherum elatius*, Fr = *Festuca rubra*, Hedge = sample from base of hedge enclosing F21. - = no specimens found in this grass in any winter.

### Polyphagous predator densities - Araneae

Araneae were identified to family following Jones-Walters (1989). The composition of the Araneae was dominated (>95%) by Linyphiidae and Lycosidae throughout the study period. Fig. 2.6 shows how mean winter spider density within each of four grass species has changed since winter 1987/88. Table 2.5 shows mean densities of groups of Araneae between grasses within winters; Table 2.6 shows mean densities of Araneae between winters, within grasses for winters one to seven. Statistical analysis followed that for the Carabidae and Staphylinidae. Appendices VII and VIII show  $F_{\max}$  results and ANOVA F ratios for Tables 2.5 and 2.6 respectively. Maximum density for each group of spiders in each grass occurred in different winters. Fig 2.7 shows the mean proportion of Linyphiidae, Lycosidae and other Araneae found each winter in the three grass species which persisted on the bank for the duration of the study.

Fig 2.6 Mean total density ( $0.1\text{m}^{-2}$ ) of spiders in four grasses from the bank and existing hedge of F21. See Tables 2.5 and 2.6 for range test results.

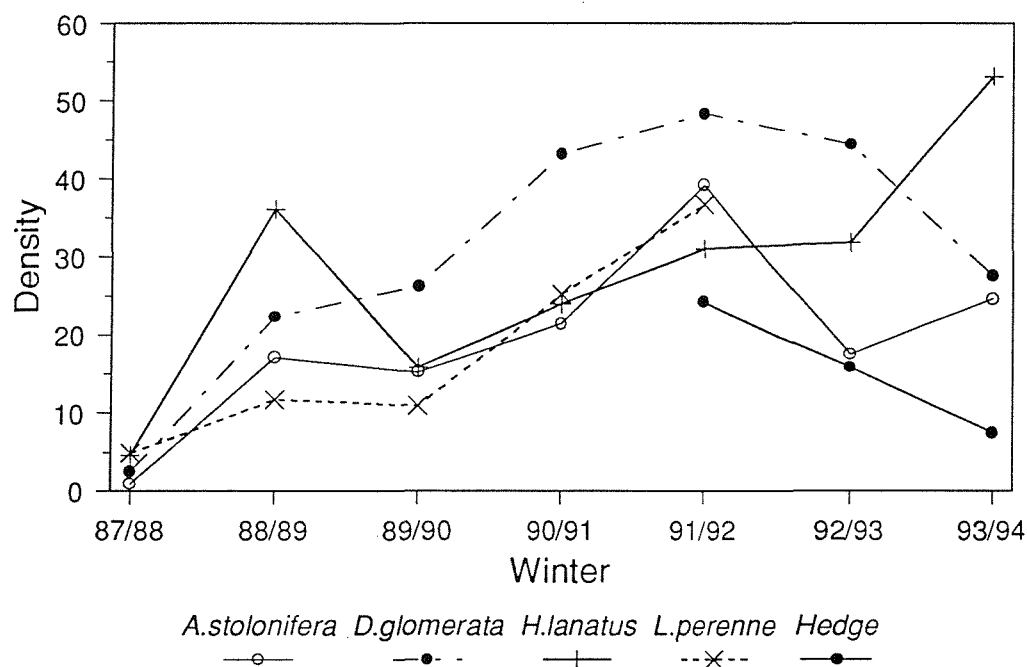


Table 2.5 Mean densities ( $0.1\text{m}^{-2}$ ) of spiders in grass plots and adjacent field boundary during winters 1987/88 (1) to 1993/94 (7) .Grass treatments sharing the same latter do not differ at  $P < 0.05$  (two -way ANOVA on  $\log_{10} X+1$  transformed data followed by Tukey's (1949) test.

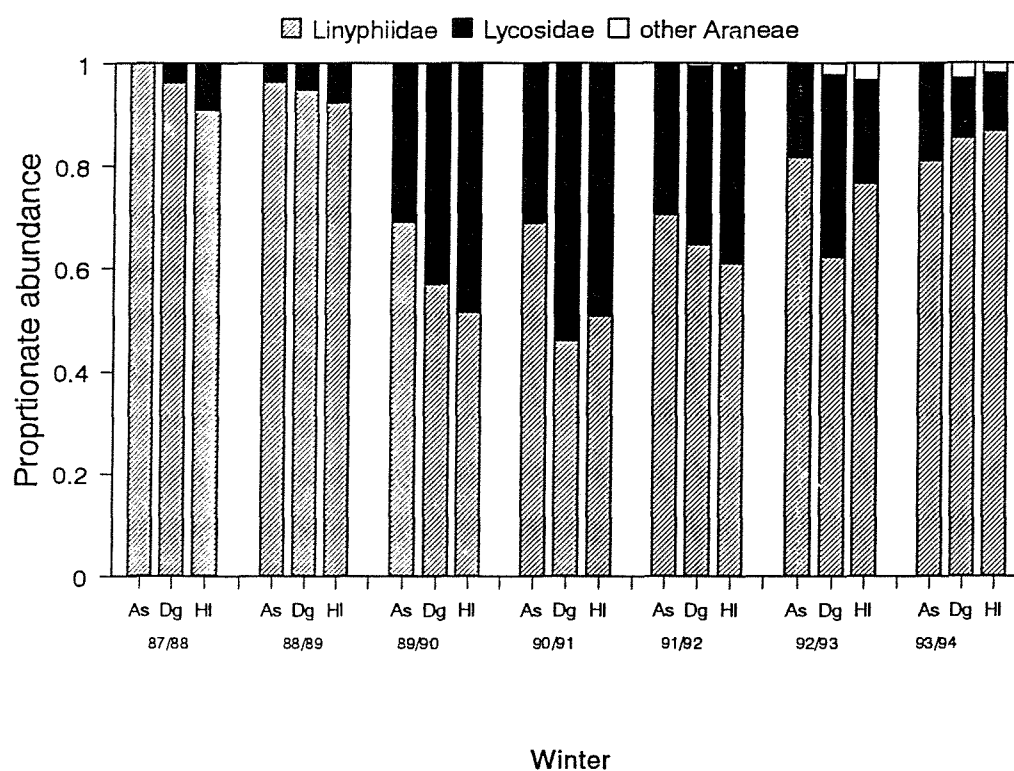
Winter/	grass	Linyphiidae	Lycosidae	other spiders
1	As	1.41 a	0.00 a	-
	Lp	7.30 c	0.19 ab	-
	Dg	5.73 b	0.42 ab	-
	HI	6.59 c	0.58 b	-
2	As	16.46 ab	0.63 a	-
	Lp	9.79 a	1.88 a	-
	Dg	21.04 bc	1.25 a	-
	HI	34.17 c	1.88 a	-
3	As	11.56 b	3.65 a	-
	Lp	6.98 a	3.96 a	-
	Dg	14.38 b	11.88 b	-
	HI	8.02 a	7.81 b	-
4	As	19.17 a	2.29 a	-
	Lp	19.79 a	5.42 ab	-
	Dg	20.21 a	22.92 b	-
	HI	14.79 a	9.17 c	-
5	As	21.92 a	11.25 a	0.21 a
	Lp	25.21 a	11.46 a	1.04 a
	Dg	27.50 a	20.83 a	0.42 a
	HI	20.63 a	10.42 a	0.21 a
	Hedge	20.00	4.17	2.08
6	As	14.58 c	2.92 b	0.21 a
	Dg	25.63 b	18.75 b	1.67 b
	HI	24.79 b	7.08 b	1.46 b
	Ae	9.58 a	1.45 a	0.00
	Fr	16.46 ab	0.63 a	0.42
	Hedge	15.83	0.00	0.00
7	As	20.42 b	4.17 b	0.21 a
	Dg	23.96 ab	0.58 a	0.42 a
	HI	46.04 b	7.08 a	1.25 b
	Ae	29.58 ab	2.92 a	0.21 a
	Fr	21.67 a	3.13 a	0.00 a
	Hedge	6.67	0.83	0.00

Table 2.6 Mean densities ( $0.1\text{m}^{-2}$ ) of spiders in grass plots and adjacent field boundary during winters 1987/88 (1) to 1993/94 (7). Grass treatments sharing the same letter do not significantly differ at  $P < 0.05$  (two-way ANOVA on  $\log_{10}(X+1)$  transformed data , followed by Tukey's (1949) test.

Grass / winter	Linyphiidae	Lycosidae	other spiders
As 1	1.41	0.00	0.00
2	16.46 ab	0.63 a	0.00
3	11.56 a	3.65 b	0.00
4	19.17 a	2.29 ab	2.08
5	21.92 b	11.25 c	0.21
6	14.58 ab	2.92 ab	0.21
7	20.42 ab	4.17 ab	0.21
Lp 1	7.30	0.19	0.00
2	9.79 a	1.88 a	0.00
3	6.98 a	3.96 a	0.00
4	19.79 b	5.42 ab	0.00
5	25.21 b	11.46 b	1.04
Dg 1	5.73	0.42	0.00
2	21.04 ab	1.25 a	0.00
3	14.38 a	11.88 b	0.00
4	20.21 ab	22.92 b	0.00
5	27.50 b	20.83 b	0.42 a
6	25.63 b	18.75 b	1.67 a
7	23.96 b	0.58 a	0.42 a
HI 1	6.59	0.58 a	0.00
2	34.17 cd	1.88 b	0.00
3	8.02 a	7.81 b	0.00
4	14.79 ab	9.17 b	0.00
5	20.63 bc	10.42 b	0.21 a
6	24.79 bcd	7.08 b	1.46 a
7	46.04 d	7.08 ab	1.25 a
Ae 6	9.58 a	1.45 a	0.00
7	29.58 b	2.92 a	0.21
Fr 6	16.46 a	0.63 a	0.42
7	21.67 a	3.13 b	0.42
Hedge 5	20.00	4.17	2.08
6	15.83	0.00	0.00
7	6.67	0.83	0.00



Figure 2.7: Mean proportion of Linyphiidae, Lycosidae and other Araneae found in each of three single species grasses on the bank. Winters 1987/88 to 1993/94.



Key: As = *Agrostis stolonifera*, Dg = *Dactylis glomerata*, Hl = *Holcus lanatus*

#### Estimating the grass species composition in "single species" grass plots 1992/93

Except for plots of *L.perenne*, each of the plots on the bank, sown with one of the four original grasses, remained relatively "pure", with little evidence of invasion by grasses from contiguous plots. *Agrostis stolonifera* plots remained dominated by *A.stolonifera* ( $85.1 \pm 11.0\%$  of the grass cover was *A.stolonifera*). *Dactylis glomerata* and *H.lanatus* plots remained pure ( $100.0 \pm 0.0\%$  and  $99.3 \pm 1.4\%$  respectively). These results contrast markedly with that of plots of *L.perenne*, where only  $1.3 \pm 0.03\%$  of grass cover in the plots consisted of *L.perenne*. All *L.perenne* plots had become dominated by *D.glomerata*. *Lolium perenne* plots had become so depleted of *L.perenne* that sampling was no longer possible after winter five (1991/92).

#### Ground cover and predator densities 1993/94

Densities of five groups of polyphagous predators (boundary carabids, open-field carabids, linyphiids, lycosids and staphylinids) in blocks A to C were plotted

against percentage grass ground cover of the turf from which the predators came. The resultant scatter diagrams showed no relationships between the densities of any predatory group and percentage ground cover (model II linear regression,  $r^2 < 0.1$  in all cases). The spread of the data was so wide, no other regression analysis was attempted.

#### Sampling from grassy banks in other parts of England

When two banks were sampled outside Hampshire, and mean densities of groups of polyphagous predators from these compared with densities of polyphagous predators from hedgerows around the fields containing the banks, there were few instances where significant differences occurred (Table 2.7).

Table 2.7: Mean densities ( $0.01\text{m}^2$ )  $\pm$  95% CL of polyphagous predators from grass banks and surrounding hedge bottoms at two sites in England. \* indicate significant difference between means at  $P < 0.05$  (Students'  $t$ -test).

Taxon	Essex			Leicestershire		
	Bank	Hedge	$t_{(38)}$	Bank	Hedge	$t_{(38)}$
<i>Demetrias atricapillus</i>	0.6 $\pm$ 0.5	1.5 $\pm$ 1.2	1.54 ns	4.1 $\pm$ 3.6	3.1 $\pm$ 2.6	0.50 ns
other Carabidae	0.1 $\pm$ 0.1	1.1 $\pm$ 0.8	2.7 *	1.0 $\pm$ 0.5	1.1 $\pm$ 0.8	0.21 ns
Total Carabidae	0.7 $\pm$ 0.6	2.6 $\pm$ 1.5	2.5 *	5.1 $\pm$ 3.6	4.2 $\pm$ 3.0	0.42 ns
Aleocharinae	1.1 $\pm$ 0.6	2.5 $\pm$ 1.4	1.92 ns	5.2 $\pm$ 3.2	2.7 $\pm$ 1.1	1.60 ns
<i>Stenus</i> spp.	4.0 $\pm$ 1.9	8.6 $\pm$ 4.0	2.16 *	2.7 $\pm$ 1.3	3.4 $\pm$ 1.5	0.75 ns
Total Staphylinidae	8.4 $\pm$ 2.7	14.6 $\pm$ 5.9	2.01 ns	9.3 $\pm$ 4.3	6.4 $\pm$ 2.4	1.22 ns
Linyphiidae	4.7 $\pm$ 1.3	4.4 $\pm$ 1.9	0.23 ns	5.3 $\pm$ 2.4	2.8 $\pm$ 1.5	1.90 ns
Lycosidae	1.8 $\pm$ 0.8	2.2 $\pm$ 1.0	0.65 ns	0.6 $\pm$ 0.5	0.7 $\pm$ 0.4	0.32 ns
Total Araneae	6.5 $\pm$ 1.8	6.6 $\pm$ 2.4	0.11 ns	5.9 $\pm$ 2.4	3.4 $\pm$ 1.7	1.75 ns

The bank in Essex had significantly fewer Carabidae and *Stenus* spp. than the surrounding hedge. All other polyphagous predator groups showed no significant differences between bank and hedge densities. In Leicestershire, there were no significant differences in mean densities of any of the polyphagous predatory groups from the bank or hedge (Table 2.7).

## DISCUSSION

The raised grassy bank in Hampshire, was shown to provide a suitable overwintering habitat for polyphagous predators when the first sampling took place nine months after the ridges' establishment (Thomas *et al.*, 1991). Since the first winter, densities of polyphagous predators have fluctuated and from the fifth winter have been sustained at levels comparable to, or greater than, the densities found in the surrounding field boundary. Two newly established banks, outside Hampshire, supported predator densities equivalent to, or greater than, the densities in the existing field boundaries after the first winter of establishment.

Carabidae which overwinter in field boundaries, and especially *D. atricapillus* have been found most frequently in the tussock forming *D. glomerata*.

The structure of tussocky grasses, which causes reduced temperature fluctuation, in the centre of the tussock, where many of the polyphagous predators are found (Luff, 1965; Bossenbroek *et al.*, 1977), is likely to be an important factor in determining the components of many arthropod communities in tussocky grasses. The less variable temperature in a tussock, compared to more open vegetation, is due to the height and density of the tussock. As the height of grass increases, the level at which radiation is absorbed increases; also as the density of a plant increases absorption of radiation increases. The absorbed radiation warms the plant and reduces temperature fluctuation in lower parts of the vegetation (Luff, 1965). Significant differences in mean density of Carabidae taxa did not occur until winter two. This was probably because the tussocky grasses in which the higher densities were later found, had not grown significantly differently in height or density by the first winter sampling period.

The change in overwintering community structure of Carabidae on the bank, from domination by open-field type in the first winter to boundary-type in later winters, has previously been described as succession (Thomas *et al.*, 1992b).

Whether or not the presence of open-field type Carabidae facilitate the introduction of boundary-type Carabidae onto the bank is questionable, although the changing vegetative nature of the bank, such as growth of tussocks, has provided an overwintering resource suitable for boundary-type Carabidae. The change in community structure could be a temporal rather than a successional process. The longer the bank remains in position, the greater is the probability that boundary-type Carabidae, "searching" for overwintering sites, will encounter the bank and use it as an overwintering resource.

Carabid succession has previously been reported by Hejkal (1985) and Mader (1988). Luff (1982) suggested that changes in the relative abundance of five different carabid species over a nine year period were attributable to habitat change.

Carabidae can be divided into spring breeders whose adults overwinter, and autumn breeders whose larvae overwinter (Luff, 1987). The majority of Carabidae sampled from the bank were spring breeders. More spring breeding carabids are found in winter crops, particularly cereals, than spring crops (Thiele, 1977) possibly due to destruction of larvae and pupae of autumn breeding carabids during the spring cultivation period associated with spring crops (Jones, 1979). The high proportion of spring breeding carabids in the bank can therefore be partially attributed to winter cereals being grown in F21 for the duration of the study, as well as the suitable overwintering habitat provided by the grasses on the bank.

High densities of *D. atricapillus* recorded in the second winter on the ridge encouraged workers to publicise the technique of creating overwintering habitat for polyphagous predators and led to media attention in both farming and national non-scientific press. The densities reported by the media have not been sustained or attained since the second winter. However, in the fifth and sixth winters, total carabid densities sampled from *D. glomerata* were not significantly different from the high densities recorded from *D. glomerata* in the second winter. This shows the need for longer term monitoring of such projects, which would allow for careful interpretation of fluctuating dynamics. While mean carabid densities have been generally higher in *D. glomerata*, staphylinid densities have been highest in *H. lanatus*.

The most abundant staphylinid throughout the study was *T. hypnorum*. In five of the seven winters the highest mean densities were recorded in tussocky grasses, usually *H. lanatus*, although not always by a significant amount. Working in Belgium, D'Hulster & Desender (1983) found more Staphylinidae species in shelter belts than

in cultivated fields during winter months. The distribution of Staphylinidae in "hibernation" sites, they concluded, were related to mean depth of the sod layer. The presence of suitable arthropod or fungal food may also be important in determining which sites are suitable for overwintering by Staphylinidae (Lipkow, 1966; Dennis, 1989).

The importance of providing suitable overwintering sites for Staphylinidae within a cereal field, in a system of integrated pest management is of uncertain value. While *T.hypnorum* is highly ranked as an aphid predator (Sunderland & Vickerman 1980) and does show an aggregative response to aphid density (Bryan & Wratten, 1984) it can fly and easily disperses into a crop in the spring (Coombes & Sotherton, 1986). *Stenus* species, which were also found in the grasses on the bank, however have not been recorded dispersing by flight (Horion, 1963). Their occurrence in relatively high numbers in the bank, in the field centre is possibly of benefit in a system to enhance potential biocontrol of aphids. However, *Stenus* spp. probably prey chiefly on Collembola (Weinreich, 1968) but have been recorded eating aphids (Sunderland *et al.* 1987). The bank nevertheless provided a site for overwintering Staphylinidae which have utilised the bank and become established down the middle of a field in winter months. Without the bank, high densities of Staphylinidae would probably not have been present in the middle of the field during winter months. From the bank, Staphylinidae can emigrate in the spring and prey on aphids in the middle of the field, early in the season (Thomas *et al.* , 1991).

Araneae formed a significant contribution to the total number of polyphagous predators overwintering in the grassy bank each winter. Robinson (1981), Greenstone (1984), Asselin and Baudry (1989) and Gibson, Hamblin & Brown (1992) all reported a strong link between the complexity of vegetational architecture and the spider community it supported. Web-building spiders were more commonly found in closely spaced vegetation, which provided suitable points of attachment for webs, while hunting spiders were more commonly found in more open vegetation (Robinson, 1981), which probably allowed easier movement. Bultman and Uetz (1982) however suggested that litter depth is more influential than vegetational structural complexity in determining spider community composition. Litter complexity ie. the spatial arrangement of litter, influences biotic and abiotic factors such as litter depth, prey abundance, temperature and humidity. Litter complexity significantly affects web-building species abundance, but not that of hunting spiders. (Bultman & Uetz, 1982).

The highest densities of Linyphiidae and Lycosidae on the bank each winter occurred in the tussock forming grasses, although they were not always significantly higher than in the other grasses. Such tussocky grasses would intuitively have greater architectural diversity as well as a deeper layer of dead leaf material than the matted grasses, so questions as to whether structural diversity or depth of leaf litter is the more influential in determining spider abundance remain unanswered by this study.

The winter ecology of spiders were studied by Schaefer (1977). Of the 233 species he studied, 84% overwintered in leaf litter or vegetation near the ground. In the same way that the protection from temperature fluctuations is afforded to Carabidae by grassy tussocks, Edgar and Loenen (1984) demonstrated that leaf litter is utilised by some Araneae for the same purpose. As the air temperature fell below zero around an artificial hill of leaf litter, specimens of the lycosid *Pardosa lugubris* Walck. moved deeper into the hill for greater insulation and protection from the drop in temperature.

Thomas (1992) found that Linyphiidae remain active during the winter in open fields. This would support the reason for high proportions of Linyphiidae on the bank during the first winter of the study when the bank still had many bare ground patches. Their continuing abundance would be due to the Linyphiidae being the most abundant family of spiders in cereals in Europe (Sunderland, 1987; 1991). Linyphiidae are characteristic of disturbed habitats being r- selected and primary colonisers (Asselin & Baudry, 1989). The larger Lycosidae are regarded as K- selected when considering the Araneae (Thomas, 1991). As with the change in carabid community structure, the trend towards a greater proportion of Lycosidae, and lower proportion of Linyphiidae, in each of the grasses on the bank over the first three winters of the study has been described as succession (Thomas *et al.*, 1992b). However as Fig 2.7 shows, since the fourth winter, Linyphiidae have formed a larger and growing proportion of the Araneae. This conflicts with the succession theory on the bank suggested by Thomas *et al.* (1992b) and with other reports on spider succession. Huhta (1971) and Nentwig (1988) reported changes in spider species composition with time. Nentwig (1988) used pitfall traps in strips of a meadow, over five years and showed an increasing proportion of Lycosidae with respect to Linyphidae. The fall in proportion of Lycosidae in the grasses on the bank in winters five to seven correspond to a fall in the proportion of Lycosidae in the field boundary around F21. It therefore appears that the drop in proportion of Lycosidae is not attributable to a

change in character of the bank, but possibly to an environmental factor, or number of factors acting on a much larger scale.

Sunderland *et al.* (1987) indicated the importance of Linyphiidae to cereal aphid biocontrol but it is still to be determined what potential Lycosidae have in the field. Mansour & Heimbach (1993) carried out laboratory experiments investigating the functional response of the lycosid *Pardosa agrestis* Westring and the linyphiids *Erigone atra* Westring and *Lepthyphantes tenuis* Blackwall to *R.padi*. Individual spiders were introduced into chambers of wheat infested with *R.padi* at different aphid densities. Significant reduction in aphid densities were recorded in all chambers with each species of spider compared to control chambers where no spiders were introduced. All spiders showed a type II functional response (inverse density dependence) to aphid density.

The ability of Linyphiidae to balloon and disperse very quickly over large areas (Duffey, 1956) means that sustaining high densities of such spiders in a grassy ridge within a relatively small field is of questionable benefit in a programme of integrated pest management. However the value of the bank will vary according to the densities of ballooning spiders immigrating into the field. The banks' value would be reduced if the densities of immigrant ballooning spiders was much higher than the densities of any spiders emigrating from the bank into the field in the spring. Conversely the value of the bank would be increased if the densities of spiders emigrating from the bank were much higher than densities of immigrating ballooning spiders.

The impact of polyphagous predators emigrating from a grassy bank in the spring, on populations of cereal aphids in the adjacent crop has recently been investigated by Mauremootoo, Joyce & Jepson (in prep). Polythene barriers were sunk into regions of a grassy bank. The barriers extended 5m into the adjacent cereal crop. Aphid densities and polyphagous predator densities in these plots were measured throughout the spring and summer and compared with plots of the same size which did not include an area of the bank. Significantly higher densities of polyphagous predators and lower aphid densities were found in plots which included a region of the bank.

There were no significant relationships found between percentage grass cover and densities of groups of polyphagous predators. The two dimensional measure of grass cover is consequently a weaker indicator of the possible density of any arthropod community than other measures such as vegetation height (Greenstone,

1984) or density (Luff, 1965) which takes into account the vertical dimension of vegetational structure.

The most significant change to the vegetational composition of the bank, during the study, was the elimination of *Lolium perenne* from plots where it had been sown as a single species. Charles (1964) reported that when grown in a sward, a variety of *L.perenne* (S22) could be completely out-competed within three years. In an experiment where *A.stolonifera*, *A.elatius*, *D.glomerata*, *F.rubra*, *H.lanatus*, and *P.trivialis* were grown in triangular plots around a hexagon of bare ground, Marshall (1990) reported that *P.trivialis* was almost completely eliminated by *A. elatius* and *D.glomerata* after three years. Plots of *D.glomerata*, *F.rubra* and *A.elatius* were largely uninvaded by other species. Species such as *A.elatius* and *D.glomerata* owe their success (in terms of greatest biomass produced) to rapid rate of resource capture, rapid growth rate and to the capacity to develop persistent tussocks, impenetrable by other species (Grime, 1987).

The nature of the vegetational composition of the grassy bank will continue to change through time. *Arrhenatherum elatius* would be expected to spread into contiguous plots, tussocks of *D.glomerata* would decay, with further growth upwind. *Festuca rubra* would persist as an understorey to *A.elatius* (Grime, 1987). If abandoned, the ridge (and surrounding field) would presumably succeed ultimately to the climax community found on chalk in southern England, that of a mixed deciduous woodland.

Grass banks have been established outside Hampshire in the UK and outside the UK in Denmark (Riedel, 1989), Finland (Helenius, 1995) and Sweden (Chiverton, 1989). Densities of polyphagous predators have established themselves in each bank at comparable densities to existing boundaries close to the banks. Whether the polyphagous predators are simply redistributing themselves in the arable environment or population densities are being increased on a farm scale is unknown. In the short term it is likely that redistribution is occurring. Schaefer (1977) reported a link between high densities of populations of overwintering spiders and low densities of spider populations the following spring. A possible connection was competition for overwintering space or food. In the long-term, there may be increases in the size of the metapopulation of spiders and other polyphagous predators resulting from an increase in suitable overwintering habitat with a resultant drop in competition. It is not known whether the lack of suitable overwintering habitat is a key-factor



(Morris, 1959; Varley & Gradwell, 1960) determining population density of any carabid or staphylinid species. It is possible that, for example, larval survival rate for spring-breeding Coleoptera, which are vulnerable to desiccation, is also an important factor (Jones, 1979).

In recent years there has been a net loss of hedgerows in England (Barr, Howard, Bunce, Gillespie & Hallam, 1991) associated with the enlargement of fields and intensification of farming (Davies & Dunford, 1962; Edwards, 1970, Greaves & Marshall, 1987). Many of the hedgerows and field boundary structures which remain, have become degraded due to modern farm practices such as ploughing very close to the field boundary or careless application of broad spectrum herbicides and fertilizers at the field margin. Such practices have resulted in degradation of field boundary flora (Boatman, 1989). In situations where such practices have occurred, benign perennials such as *D.glomerata* and *A.elatius* have been replaced by *Galium aparine* and *Bromus sterilis* L. which are pernicious annual weeds invasive of adjacent crops (Boatman, 1992). The provision of grassy banks within fields will help to counter the loss of suitable overwintering habitat at field edges or can ensure the provision of suitable overwintering habitat where the existing boundary is not lost, but has become degraded. It is interesting to note that recently established grassy banks on commercial farms have been used to divide large fields into two smaller areas which have separate cropping regimes and are therefore now considered as separate fields - thus opposing the trend of field enlargement.

As well as manipulating the overwintering habitat of beneficial arthropods, other resources can be introduced or manipulated on an arable farm to influence beneficial predators (see Chapter One). The remainder of this thesis explores other potential resources utilised by beneficial insects and how such resources could be employed to good effect. The studies move away from overwintering habits of beneficial Coleoptera to floral resource use by beneficial Syrphidae and mechanisms associated with the distribution of Syrphidae around summer flora. This enabled original research to be carried out on another important group of beneficial insects between winters when the grass bank was not being studied.

## CHAPTER THREE

### THE SELECTIVE USE OF ALYSSUM (*Lobularia maritima* (L.) Desv.

#### BRASSICACEAE) AND OTHER WILD FLOWERS

#### BY SYRPHIDAE ON ARABLE LAND

### INTRODUCTION

Adult Syrphidae use flowers as a food resource (Haslett, 1982). They feed on pollen and nectar; females require amino acids from pollen for the successful maturation of their reproductive system (Schneider, 1948). Males also probably require amino acids for the maturation of the accessory glands to their reproductive systems (Gilbert, 1986), although the importance of this is unclear as males of some species e.g. *Metasyrphus corollae* do have mature sperm on emergence from pupae (Gilbert, 1986). Nectar is used as an energy provider to both sexes and as the more active sex, males ingest significantly more nectar than females (Haslett, 1989b). Among insects that feed on pollen, foraging can be restricted to one or several closely-related plant species or genera (monolecty or oligolecty), or can be more diverse and foragers can feed on a variety of plants in more than one family (polylecty) (Cripps & Rust, 1989). By dissecting field-caught adult syrphid species, and identifying the pollen in the alimentary tract, Haslett (1989a) showed that Syrphidae could be grouped into those that are oligolectic e.g. *Cheilosia albitarsis* Meig. and *Rhingia campestris* Meig., and those that are polylectic e.g. *Episyrphus balteatus*. Haslett (1989a) suggested that more selective syrphid species use colour, or more specifically the reflectance spectra, of flowers to discriminate between flowers that are selected or not. Studying pollen and nectar feeding in a range of syrphid species, Gilbert (1981) showed a correlation between syrphid tongue length and the depth of corollae visited by syrphids to take nectar, with longer-tongued syrphids visiting flowers with deeper corollae.

Although not distinguishing between pollen and nectar feeding, Cowgill *et al.* (1993a) also showed that *E. balteatus*, the most commonly recorded syrphid on agricultural land in the UK (Dean 1982; Chambers *et al.* 1986), used floral resources selectively. Cowgill *et al.* (1993a) carried out observational studies and used an index of preference (Murdoch, 1969) to rank 27 species of arable weeds, with respect to

resource use, by *E.balteatus* on arable land.

Knowing that Syrphidae feed on flowers has led applied researchers to identify plants that could provide suitable floral resources to beneficial Syrphidae, and grow them within and/or around, arable crops that are liable to attack by aphids (Chaney, 1990; Harwood, Wratten & Nowakowski 1992; Hickman & Wratten, 1994), see also Chapter One) in attempts to influence biological control of aphids by Syrphidae.

Chaney (1990) grew 22 plant species in lettuce fields in California in an attempt to find the most suitable plants to act as "in-field insectaries." The insect populations on the plants were monitored weekly, using a variety of techniques. Insects were classified as beneficial or pest species. In three trials conducted, *Lobularia maritima* (L.) Desv. (commonly known as alyssum in the UK) had the highest number of beneficial insect species associated with it. It also had the highest ratio of beneficial species to pest species. However the insect species associated with the plants in the trials were not given in Chaney's (1990) paper.

#### Aims of this chapter

*Lobularia maritima* is native to the Mediterranean and has been introduced to the UK and is widely used as a garden ornamental plant (Clapham *et al.*, 1962). The aims of this chapter were to determine i) whether Syrphidae use *Lobularia maritima* as a food resource on agricultural land in the UK, ii) whether Syrphidae use *L.maritima* selectively, iii) to determine which of two coloured varieties of *L.maritima* are preferred by Syrphidae, and iv) to investigate whether *L.maritima* would grow successfully in an agricultural environment.

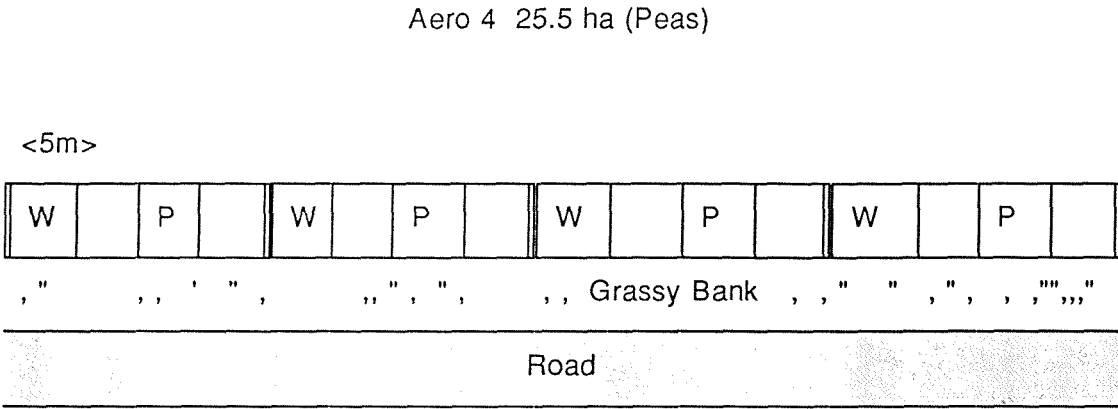
## **MATERIALS AND METHODS**

### Field observation experiment

The field experiment took place along the south-western boundary of "Aero 4", a 25.5ha field of peas (cv. Orb), on the Leckford Estates, Hampshire. A 1m-wide sterile strip was left around the field, between the crop and a grassy bank which defined the field boundary, next to a tarmac and concrete road. An 80m section within the sterile strip, along the middle of the south-western edge of Aero 4, was chosen and sub-divided into four 20m blocks which were further sub-divided into four contiguous plots, each of 5m. Each block consisted of a 5m strip of white *L.maritima*

(cv. Carpet of Snow), a 5m gap of sterile strip, a 5m strip of purple *L.maritima* (cv. Royal Carpet) and another 5m gap before the next block (Fig 3.1). Each 5m strip of *L.maritima* consisted of 30 plants, each with approximately 250 flowers. The plants had been purchased from a garden centre and were planted into Aero 4 on May 29, 1991. Once a week during July and August 1991, plots of *L.maritima* were watered and hand weeded to prevent their being overgrown by vigorous and competitive weeds.

Fig 3.1 Diagrammatic layout of 5m strips of white and purple *L.maritima* adjacent to a field of peas.



Key: W= white *L.maritima* (cv. Carpet of Snow) P= purple *L.maritima* (cv. Royal Carpet)

The bank adjacent to the strips of *L.maritima* was also divided into 16 plots. Each plot on the bank corresponded to a plot in the parallel *L.maritima* strips. The start and end of each plot on the bank was marked with a small pile of stones. Weeds on the bank were identified to species using Clapham *et al.* (1962). Syrphid foraging on *L.maritima* plots and flora in plots on the bank were recorded during observational studies. One week before observations started, a range of syrphid species was captured, using a butterfly net, from the study site. Syrphidae were killed in 70% alcohol and identified in the laboratory, following Stubbs and Falk (1983). Specimens were preserved in 70% alcohol in 1cm diameter glass specimen tubes. The specimens were taken to the field and used as references during observational studies while identification experience was acquired. Observations were carried out on each of the 5m plots during surveys in August 1991. Sixteen surveys were carried out during August 4, 8,

9, 14, 16 and 20. Surveys began in the mornings (06:30 BST) except when poor weather (strong wind or rain) would have prevented Syrphidae from foraging. Each 5m plot was observed for ten minutes in turn. Within each plot, approximately two minutes were spent observing each 1m of the 5m plot. To minimise disturbance to Syrphidae, surveys were conducted by moving very slowly along each plot with the observer standing such that no shadow, would be cast ahead of the observer, onto the plot. Syrphids seen foraging on *L.maritima* or bank plots were identified to genus and species if possible and sexed. Male syrphids have holoptic eyes i.e. compound eyes that extend dorsally and are contiguous along the mid-line; female syrphids have dichoptic eyes with each eye markedly separated medially. Results were recorded onto microcassette using a hand-held tape recorder. This proved much easier than recording sightings using a pencil and paper. However the cassette did have to be transcribed onto paper at a later stage. With the help of a co-worker, it was possible to observe both a *L.maritima* plot and the adjacent plot in the bank at the same time. The number of foraging Syrphidae in each site could then be compared at the same time and under exactly the same weather conditions. Time of day, temperature, relative humidity and wind speed affect the flight behaviour of a number of species found on arable land (Cowgill, 1991). Thus surveys of Syrphidae foraging in *L.maritima* plots and plots on the bank, were conducted concurrently. Observers did not exchange positions between bank and *L.maritima* plots, so there may have been some observer bias.

Floral abundance in each plot of *L.maritima* and equivalent plot on the bank was estimated by measuring the dimensions of a number of flower forms (single flower heads or inflorescences) then counting the number of such flower forms of each species in each plot. The flower forms were approximated to two dimensional shapes, e.g. circles, crosses as appropriate, and their surface area calculated.

#### Laboratory choice experiment

Ten seeds of a purple variety of *L.maritima* (cv. Royal Carpet) were sown into each of four 3" diameter plastic flower pots containing Levington's F2 commercial compost. Ten seeds of a white variety of *L.maritima* (cv. Carpet of Snow) were also sown in the same way in four other 3" diameter pots. The seeds were grown in a glasshouse with a natural light period (August 1991). After germination, at the expanded cotyledons growth stage (Lutman & Tucker, 1987) individual plants were

"pricked out" and transplanted to individual 3" pots containing John Innes No. 2 compost. The plants were maintained in the glasshouse until flowering. The laboratory choice experiment was carried out in the insect culture rooms at Southampton University, on laboratory-reared specimens of *Episyrphus balteatus*. The *E. balteatus* culture contained both males and females and was maintained as a breeding population to supply syrphid eggs as part of another study. The syrphids were kept in a perspex culture box 55cm x 55cm x 90cm at  $20 \pm 2^{\circ}\text{C}$  with a 16:8h light:dark period. Syrphids were sustained on a 5% solution of honey in tap water soaked in cotton-wool, placed in 5cm diameter plastic Petri dishes, and an excess of *Populus deltoides* Bartr. (Eastern cottonwood) pollen, provided in other 5cm diameter Petri dishes. The water and honey solution and pollen were replaced twice a week. This method of culturing Syrphidae was adapted from Frazer (1972).

When *L. maritima* was in flower, two white flowering specimens and two purple flowering specimens, each with approximately the same number of open flower heads, were selected and introduced into the syrphid culture box. Peak feeding activity for *E. balteatus* is before 10:00 BST (Cowgill, 1991). At 07:20 BST on each of eight days of the study, the cotton-wool and pollen-containing Petri dishes were removed and replaced with the white and purple flowering *L. maritima*. After a ten-minute period, to allow the syrphids to settle after being disturbed, observations of syrphids visiting the plants were recorded. The hour between 07:30 and 08:30 was divided in six sequential ten-minute periods. For each ten-minute period, the number of males and number of females visiting each *L. maritima* plant to feed were recorded. At 08:30 observations were stopped and the *L. maritima* removed from the culture box and the soaked cotton-wool and pollen returned. When the *L. maritima* plants were removed, the number of flower heads on each plant were counted and the area of flowers calculated.

## RESULTS

### Field observation experiment

A total of 907 foraging visits by 11 genera and 16 species of Syrphidae were recorded foraging on either *L. maritima* flowers or flora on the bank plots. *Lobularia maritima* accounted for less than 8% of the total floral area in combined bank and *L. maritima* plots, but more than 36% of all recorded syrphid foraging visits were to

*L.maritima*. Although not recorded as separate activities, syrphids foraging on *L.maritima* were seen feeding on both pollen and nectar. When feeding upon nectar, a syrphid used the proboscis and probed into the centre of the inflorescence. When feeding upon pollen, the proboscis dabbed over the anthers. Of the nine genera foraging on *L.maritima*, eight were genera with aphidophagous larvae (Table 3.3) *Episyrphus balteatus* and *Metasyrphus* spp. were the most commonly seen Syrphidae, comprising 26.8% and 18.9% of all syrphids recorded from bank and *L.maritima* plots. Species in the same genus were pooled for statistical analysis. Pooling species into genera also allowed for prudent interpretation of data since errors distinguishing between species of a genus may have occurred during recording of observations.

Figures 3.2 to 3.21 show the mean number of observed visits to both varieties of *L.maritima* and flora on the adjacent bank per ten minute period during surveys and the number of expected visits, if foraging visits had been made in proportion to floral area, for two species and three other genera of Syrphidae. Table 3.2 gives a key to the flower species for the histograms in Figs 3.2 to 3.21.  $G_{adj}$ -tests (Sokal & Rohlf, 1981) were used to compare the observed distribution of forage visits with the expected distribution of visits, which were calculated according to the relative abundance (floral area) of floral species in the habitat. Over the period of the study, none of the most commonly recorded Syrphidae foraged from the flower resources available in proportion to their floral abundance in the environment (Table 3.1)

Table 3.1 G-test results for syrphid foraging on *L.maritima* and flora on the bank.

Syrphid	Sex	$G_{adj}$	DF	$P$
<i>Episyrphus balteatus</i>	Male	126.0	15	<0.01
	Female	70.4	15	<0.01
<i>Metasyrphus</i> spp.	Male	230.4	15	<0.01
	Female	53.9	15	<0.01
<i>Melanostoma</i> spp.	Male	168.3	15	<0.01
	Female	62.5	15	<0.01
<i>Sphaerophoria</i> spp.	Male	157.8	15	<0.01
	Female	85.6	15	<0.01
<i>Scaeva pyrastris</i>	Male	37.3	15	<0.01
	Female	33.5	15	<0.01

The test statistic,  $G_{adj}$ , does not indicate which floral resources were visited more or were visited less. It does demonstrate however that foraging, in both sexes of all syrphids tested, does not occur in relation to measured floral abundance. To determine which floral resources were selectively utilised, the data was analysed to measure  $\beta$  values (Manly, Miller & Cook, 1972) for each floral resource that was visited by five of the most abundant syrphid genera.

$$\beta = 1/(1+\alpha) \quad (1)$$

where  $\alpha = 1/\alpha'$  (2)

and  $\alpha' = \ln (N' / Ne') / \ln (N / Ne)$  (3)

$\ln$  = natural log (base e)

$N'$  = abundance of species 2

$Ne'$  = number of prey species 2 in diet

$N$  = abundance of species 1

$Ne$  = number of prey species 1 in diet

$\beta$  values have a scale of 0 to 1. In a system where there are two prey (two floral resources), a  $\beta$  value of 0.5 indicates no preference for either prey;  $\beta > 0.5$  indicates positive preference for prey type 1 (therefore negative preference for prey type 2);  $\beta < 0.5$  indicates negative preference for prey type 1 (therefore positive preference for prey type 2). It was possible to find an index for each specific floral resource, at a time when more than two resources were available, by pooling all except the specific resource being examined, into 'type 2' prey.

Beneath each histogram of observed and expected forage visits to flora in the study, in Figs 3.2 to 3.21, are histograms of the  $\beta$  values for each of the five most abundant genera with respect to floral resources foraged upon. Where no observed forage visits were recorded, there is no  $\beta$  value for that floral resource.



Table 3.2 : Key to the flower species in the histograms in Figures 3.2 to 3.21

Abbreviation in Figs	Flower species
Lm (w)	<i>Lobularia maritima</i> (cv. Carpet of Snow)
Lm (p)	<i>Lobularia maritima</i> (cv. Royal Carpet)
Am	<i>Achillea millefolium</i> L.
Av	<i>Artemesia vulgaris</i> L.
Ca	<i>Convolvulus arvensis</i> L.
Hh	<i>Hypericum hirsutum</i> L.
Hs	<i>Heracleum sphondylium</i> L.
La	<i>Lamium album</i> L.
Lp	<i>Lamium purpureum</i> L.
Pm	<i>Plantago major</i> L.
Ps	<i>Pastinaca sativa</i> L.
RI	<i>Reseda lutea</i> L.
Se	<i>Senecio erucifolius</i> L.
Tr	<i>Trifolium repens</i> L.
Vs	<i>Vicia sativa</i> L.

Fig 3.2 Mean number of observed and expected forage visits to flora by *Episyrphus balteatus* (male).

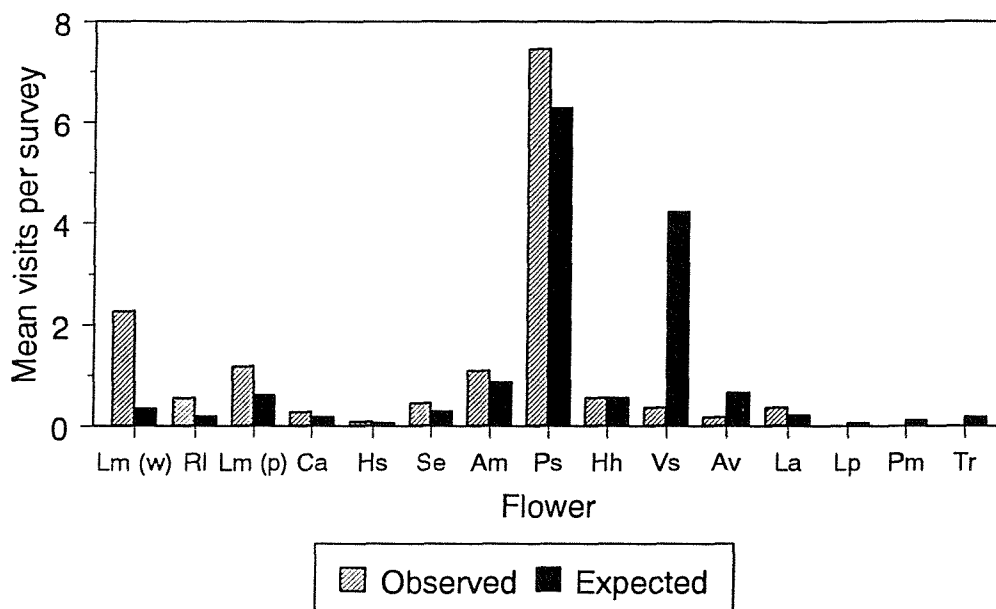


Fig 3.3 Male *E. balteatus*  $\beta$  values.

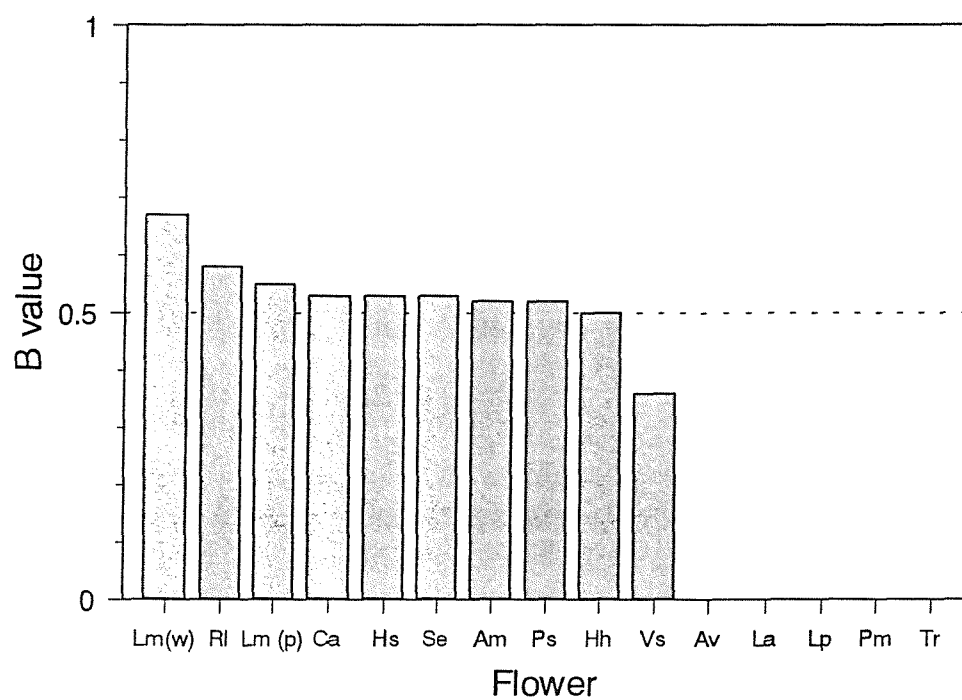


Fig 3.4 Mean number of observed and expected forage visits to flora by *Episyrphus balteatus* (female).

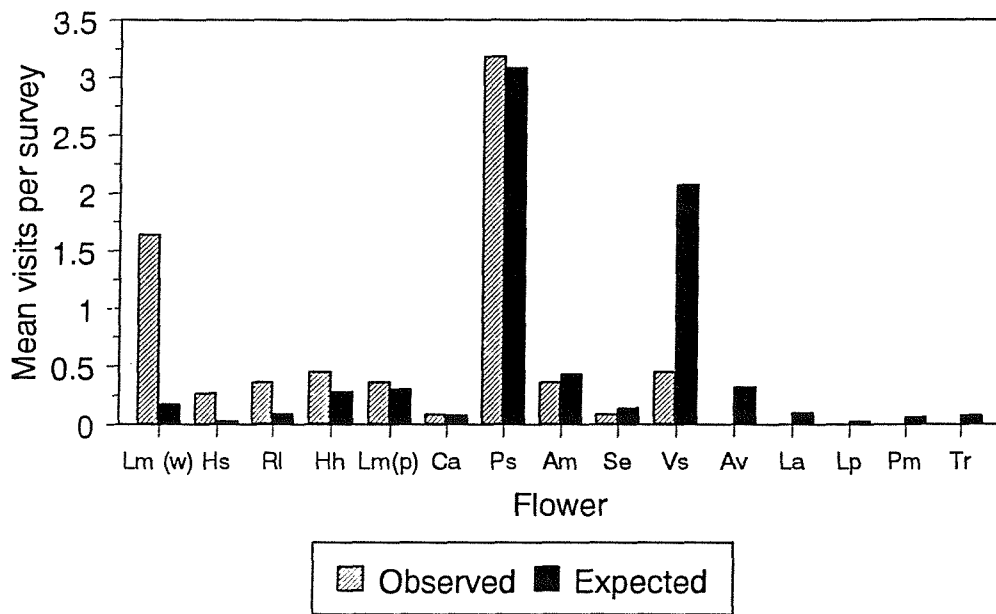


Fig 3.5 Female *E. balteatus*  $\beta$  values.

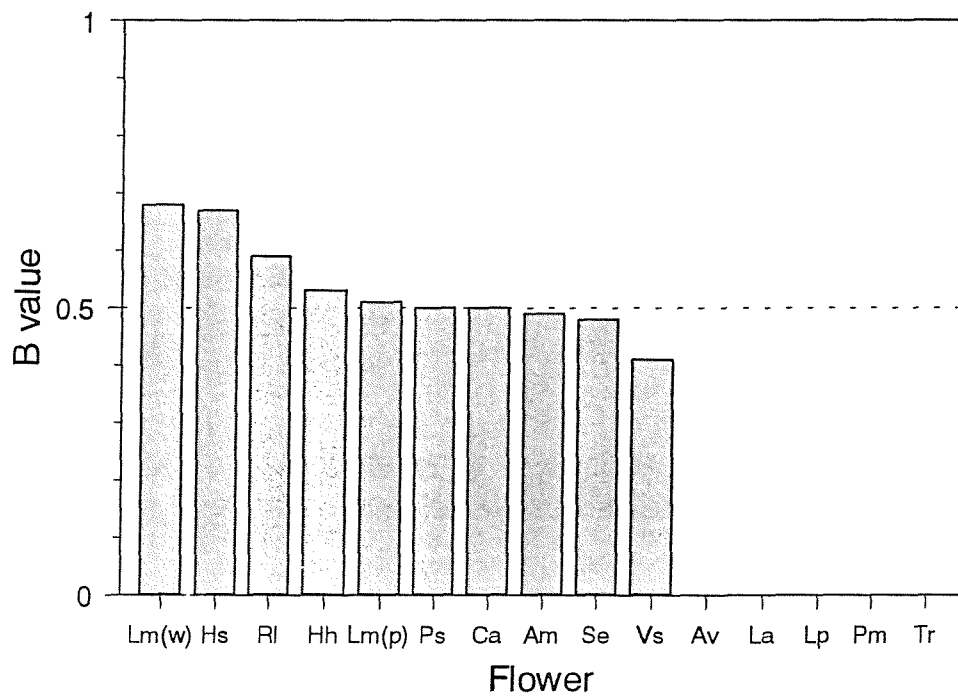


Fig 3.6 Mean number of observed and expected forage visits to flora by *Metasyrphus* spp.(male).

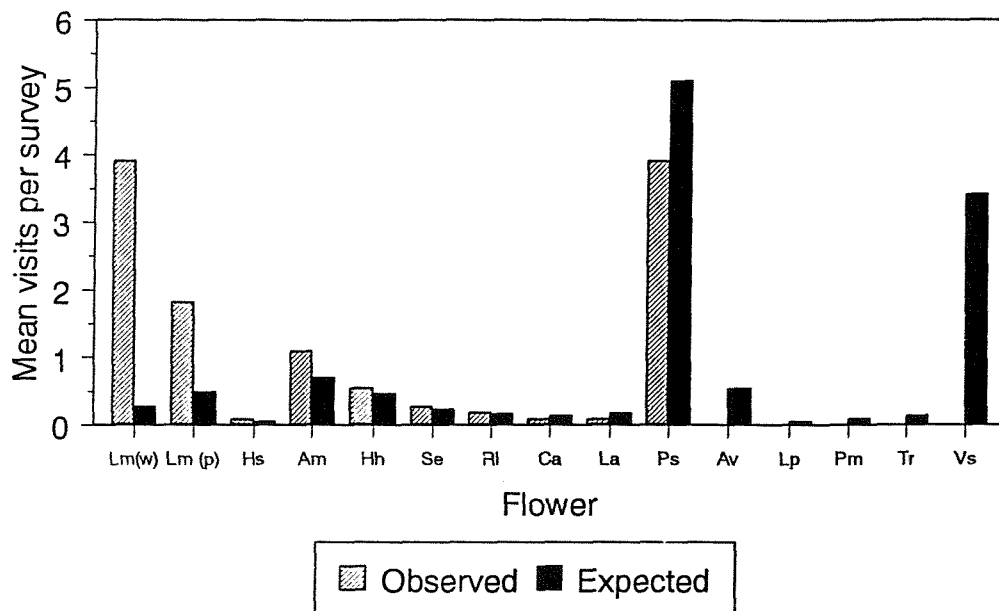


Fig 3.7 Male *Metasyrphus*  $\beta$  values.

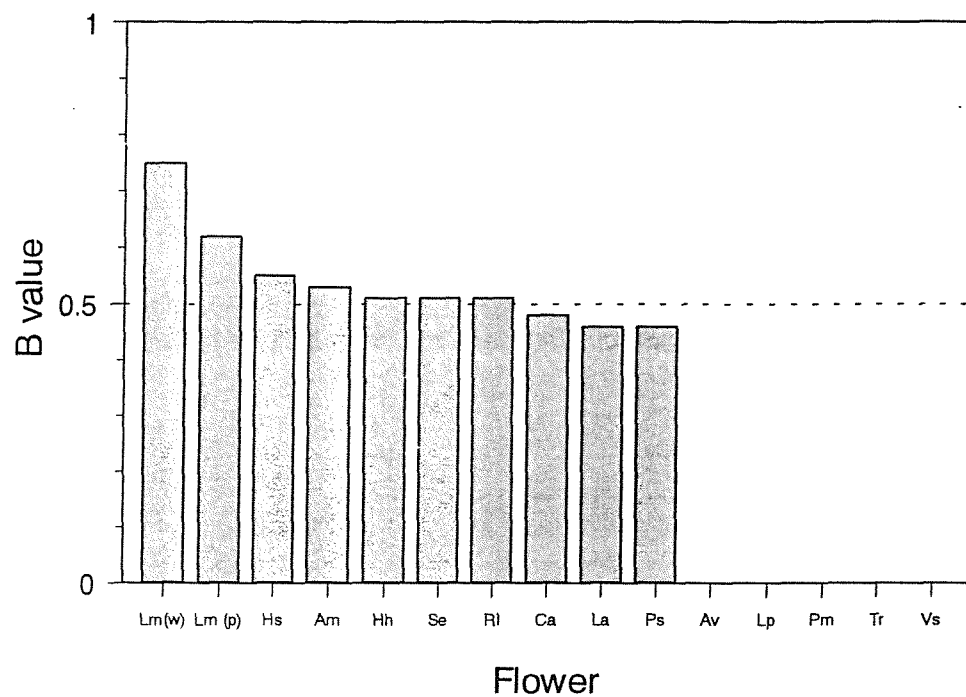


Fig 3.8 Mean number of observed and expected forage visits to flora by *Metasyrphus* spp. (female).

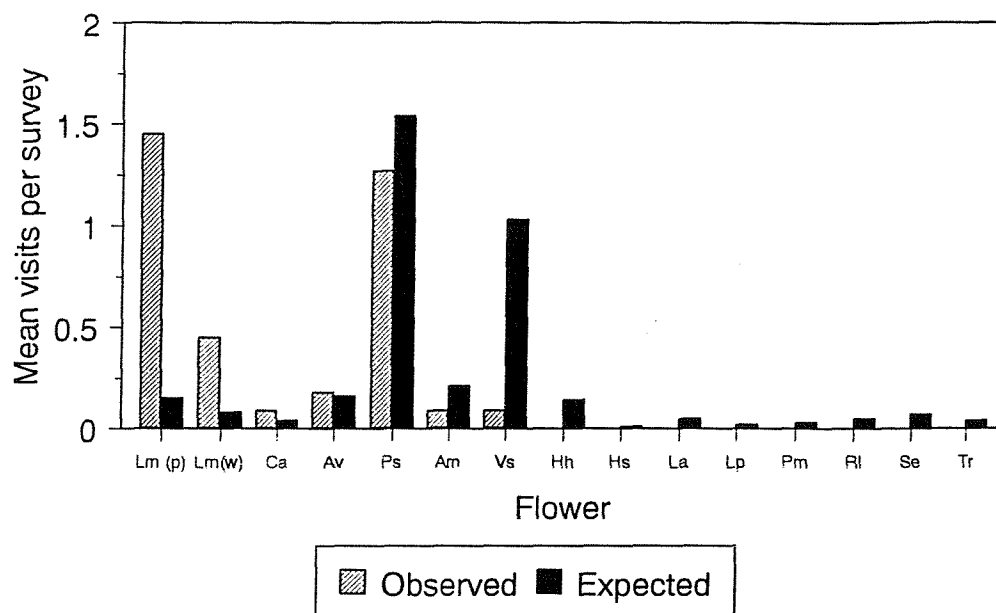


Fig 3.9 Female *Metasyrphus* spp.  $\beta$  values.

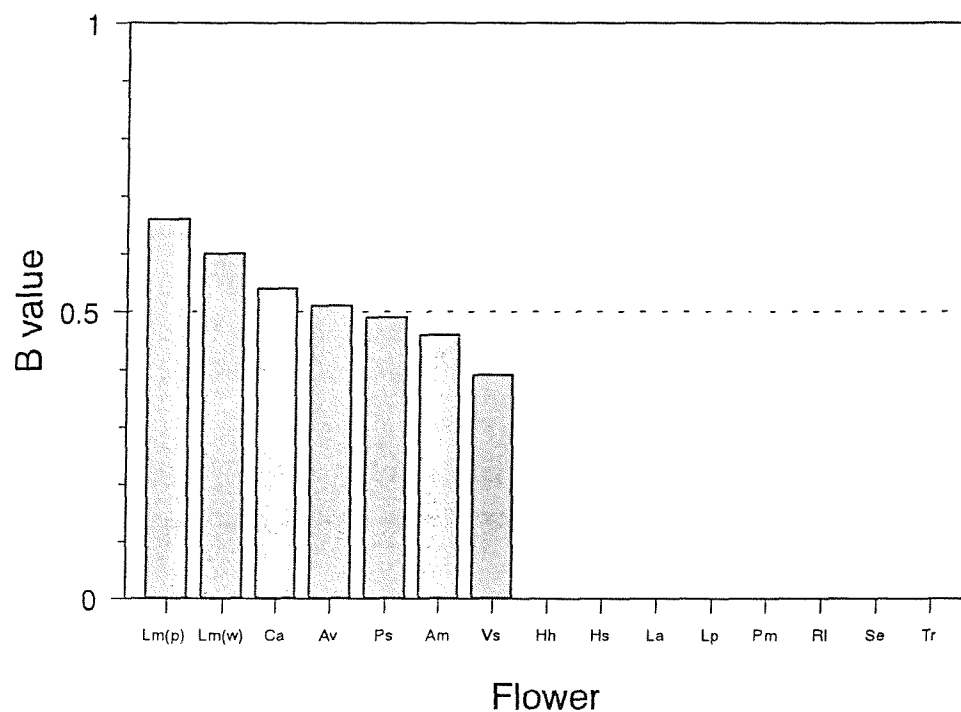


Fig 3.10 Mean number of observed and expected forage visits to flora by *Scaeva pyrastris* (Male).

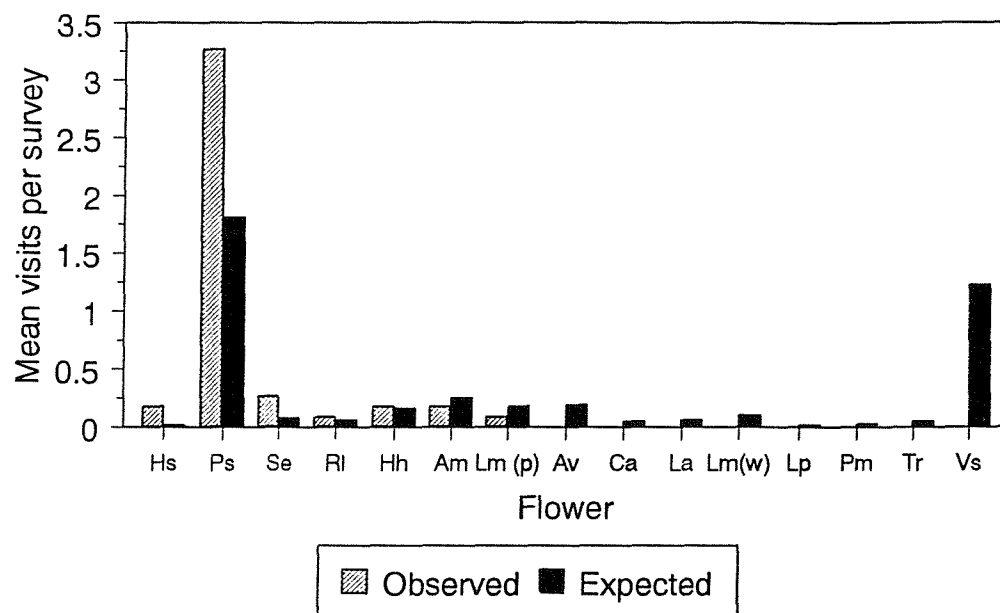


Fig 3.11 Male *Scaeva pyrastris*  $\beta$  values.

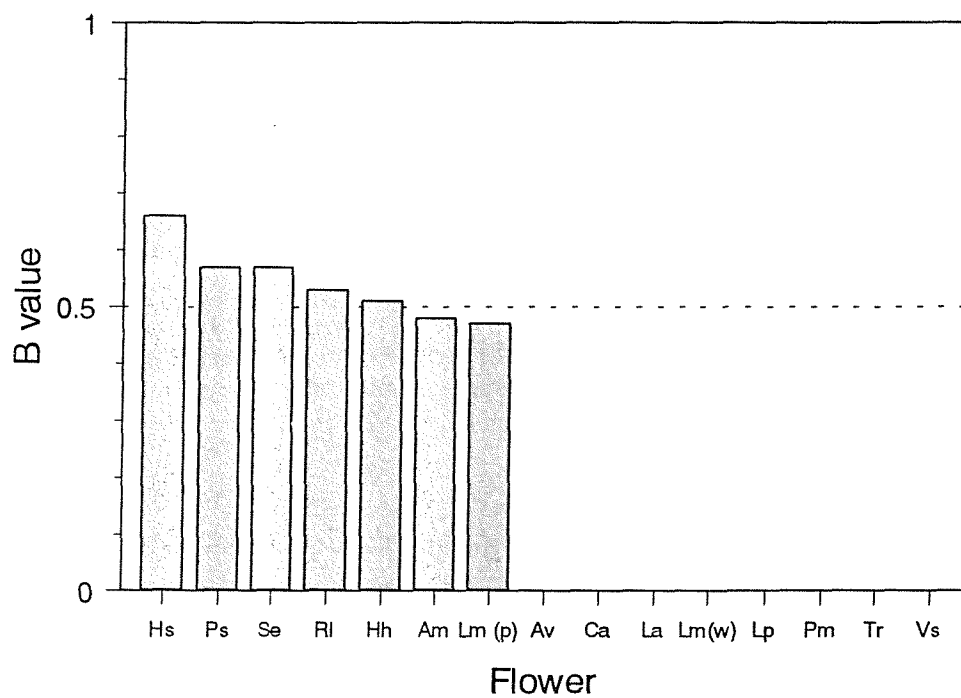


Fig 3.12 Mean number of observed and expected forage visits to flora by *Scaeva pyrastris* (female).

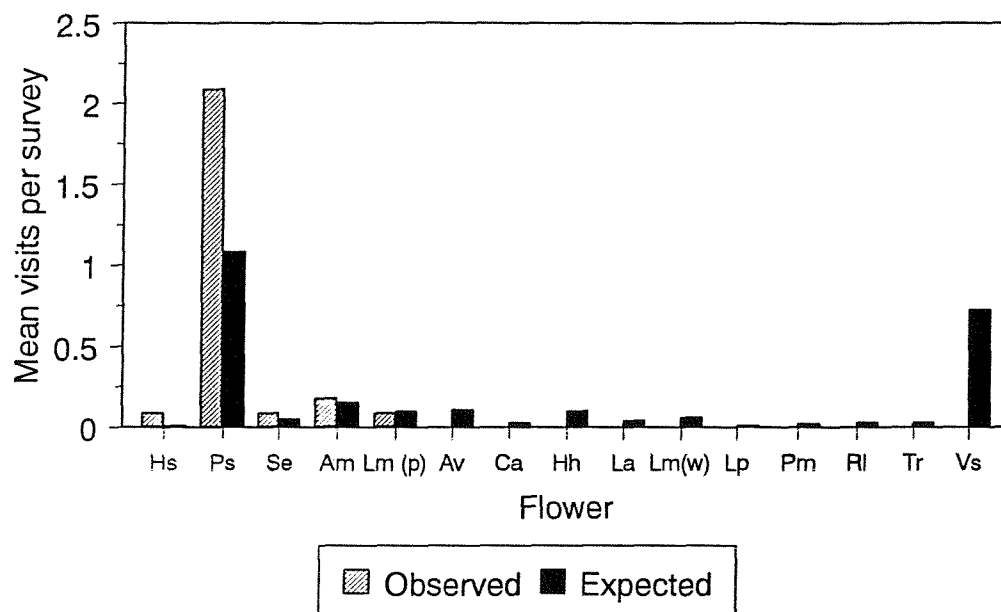


Fig 3.13 Female *Scaeva pyrastris*  $\beta$  values.

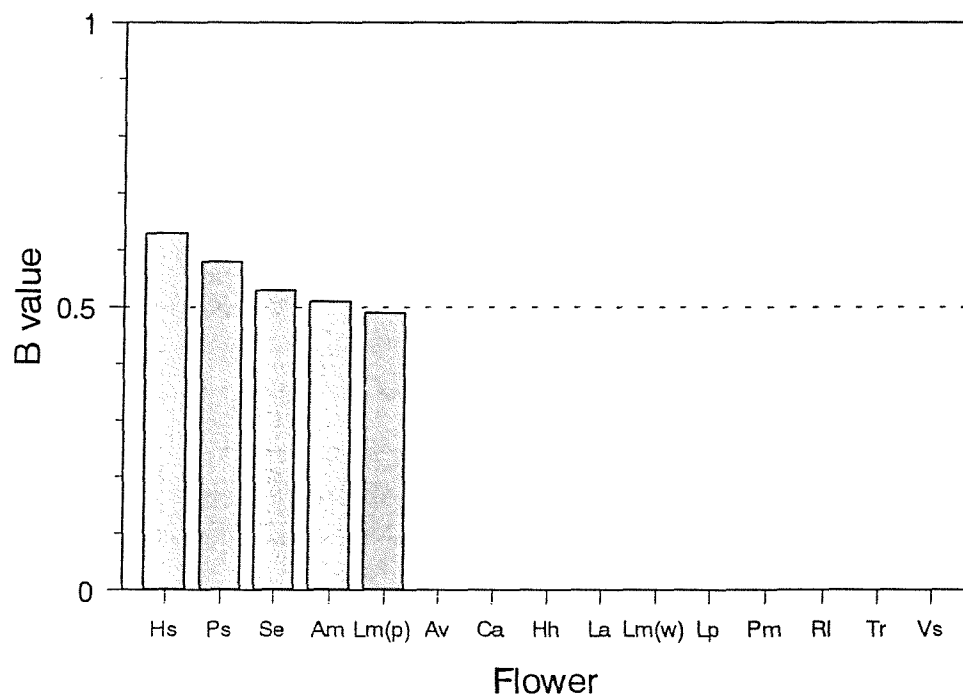


Fig 3.14 Mean number of observed and expected forage visits to flora by *Melanostoma* spp. (male)

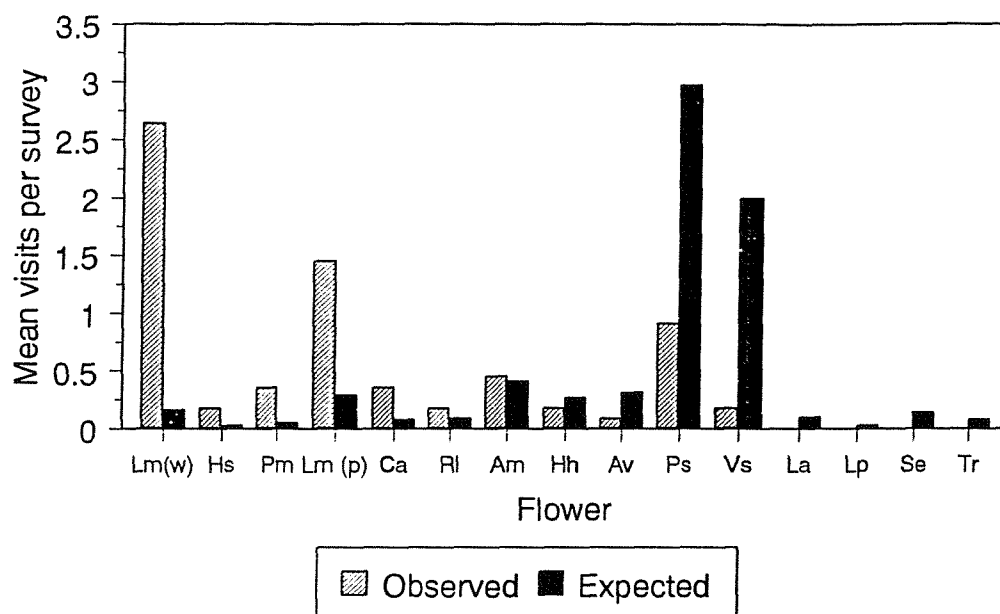


Fig 3.15 Male *Melanostoma* spp.  $\beta$  values.

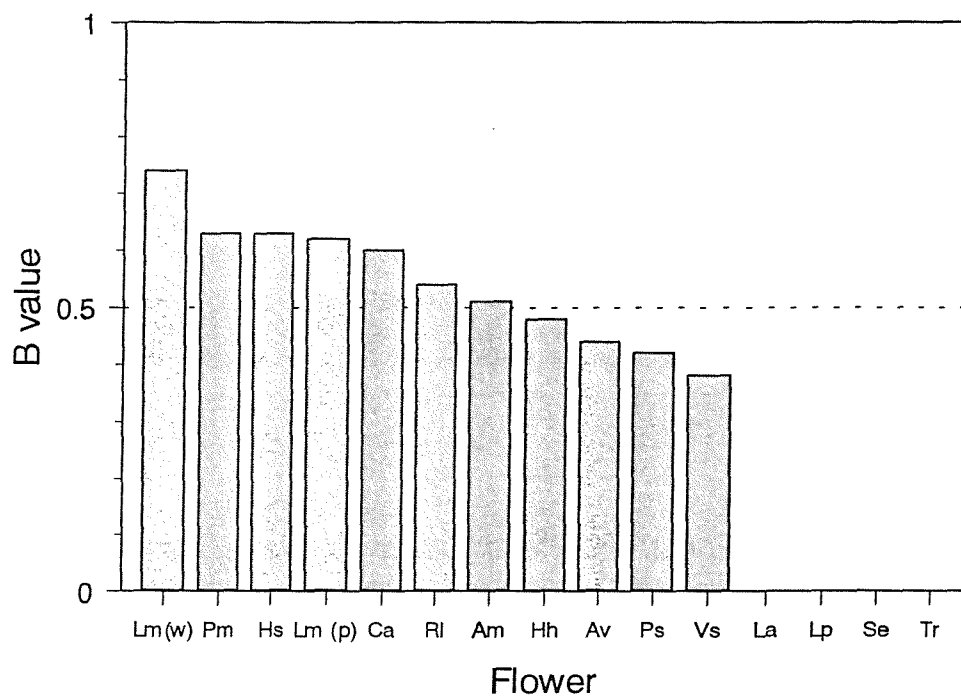




Fig 3.16 Mean number of observed and expected forage visits to flora by *Melanostoma* spp. (female).

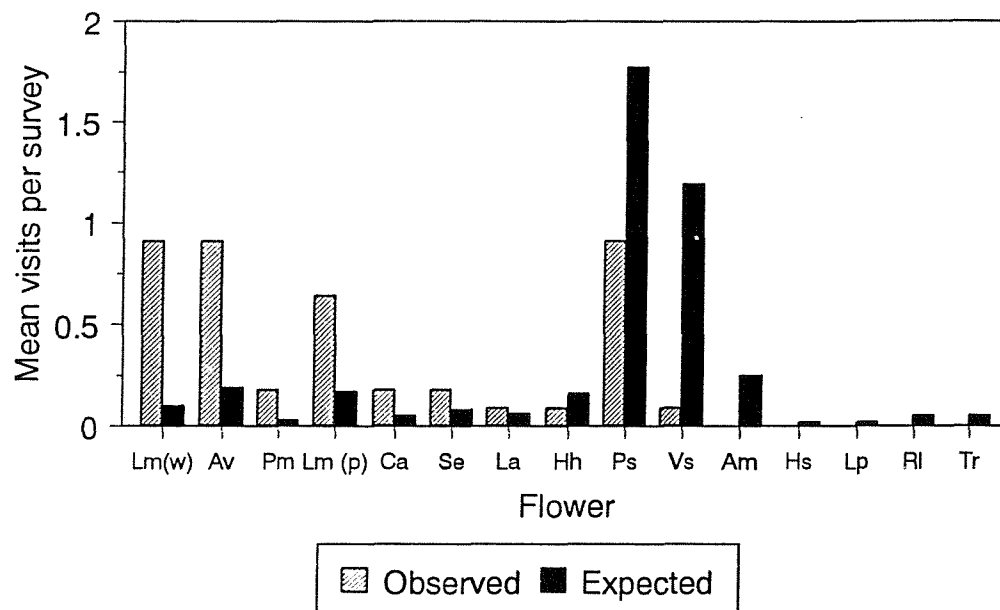


Fig 3.17 Female *Melanostoma*  $\beta$  values.

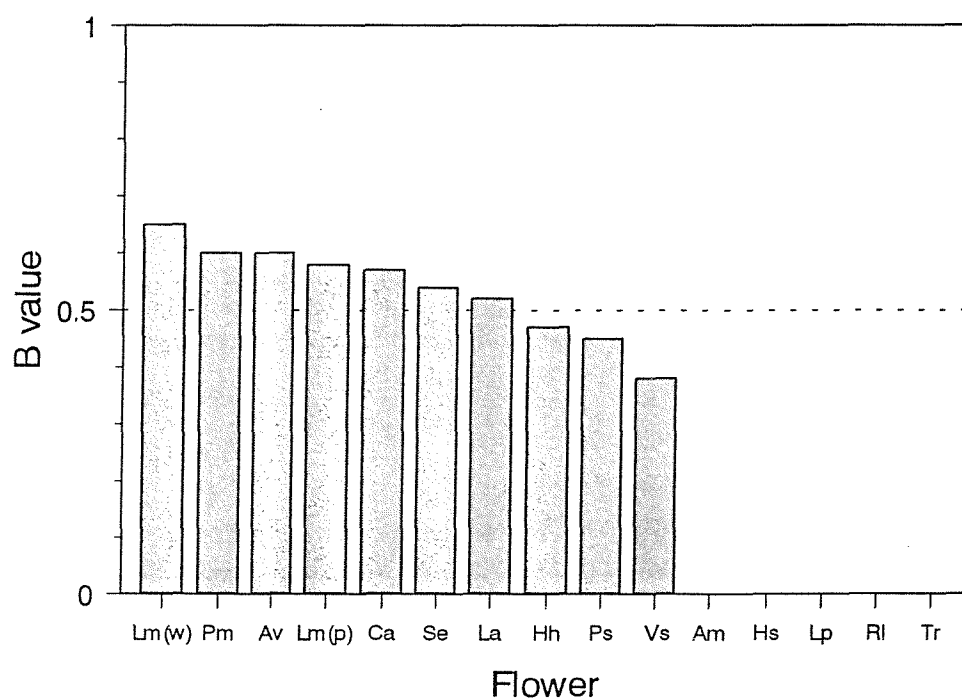


Fig 3.18 Mean number of observed and expected forage visits to flora by *Sphaerophoria* spp. (male).

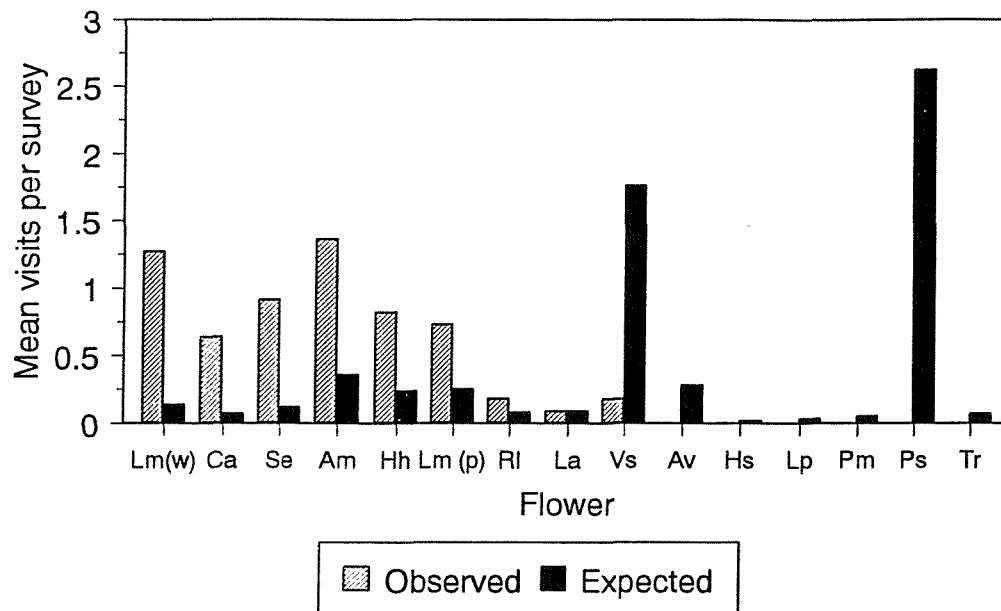


Fig 3.19 Male *Sphaerophoria*  $\beta$  values.

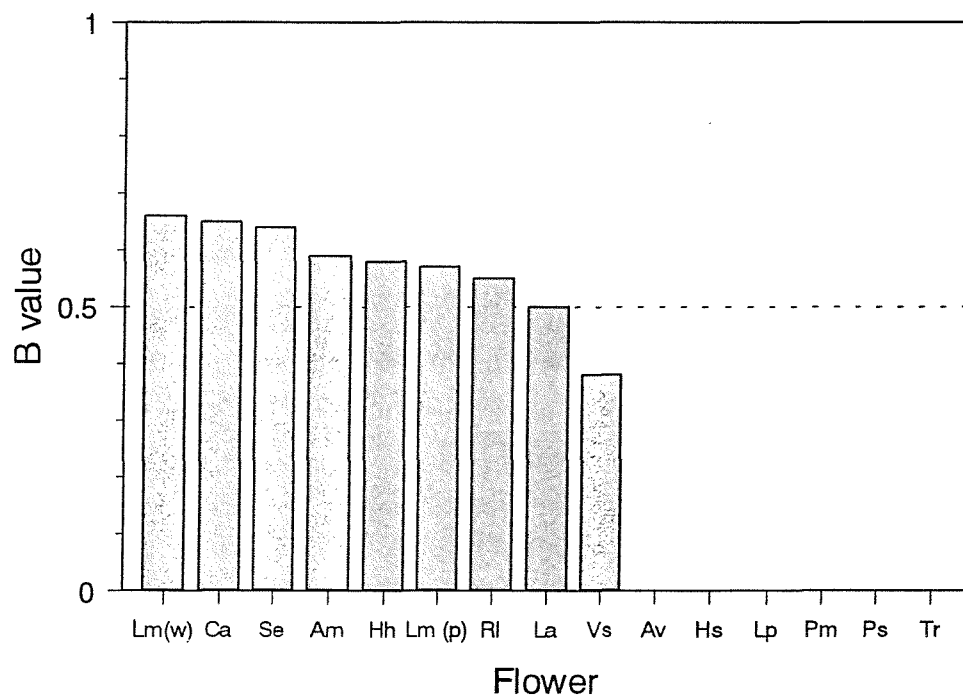


Fig 3.20 Mean number of observed and expected forage visits to flora by *Sphaerophoria* spp. (female).

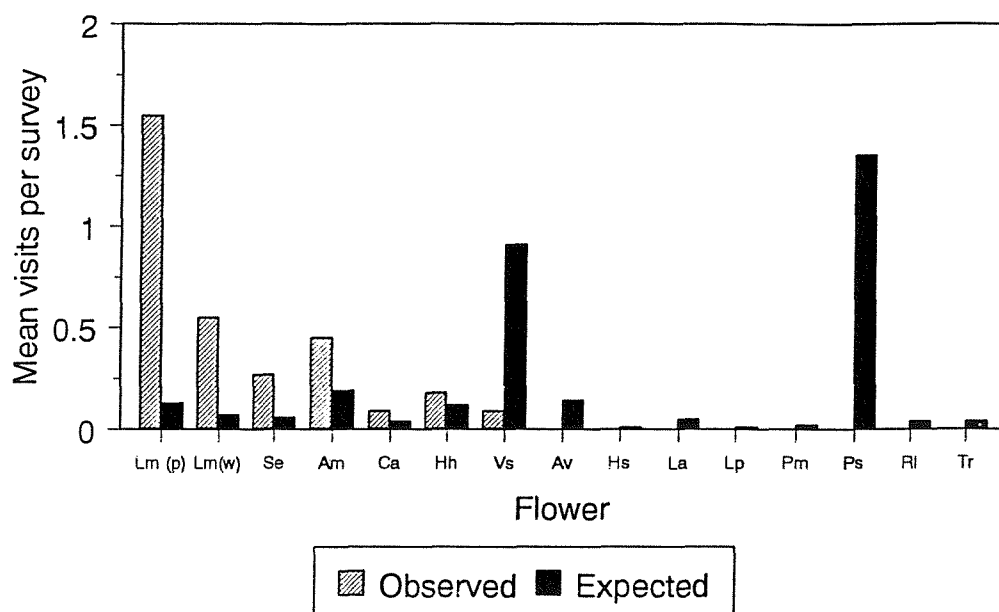


Fig 3.21 Female *Sphaerophoria* spp.  $\beta$  values.

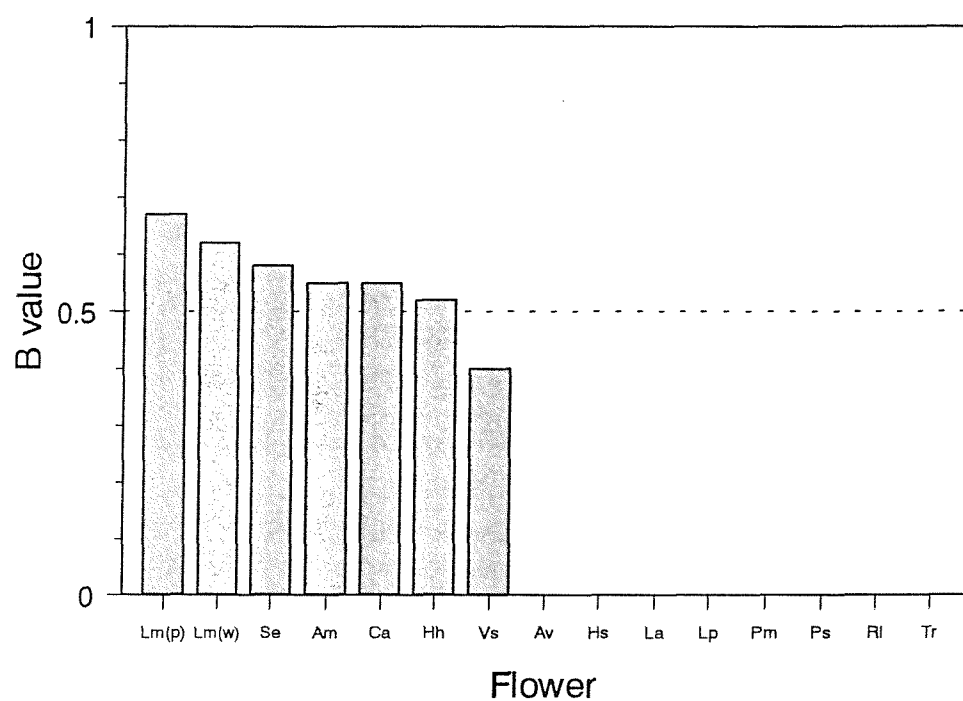


Table 3.3 Syrphidae recorded foraging on *Lobularia maritima* and/or bank flora, August 1991. Larval food source's are also indicated.

Syrphid	<i>L.maritima</i>	Bank flora	Larval food source
<i>Episyrphus balteatus</i>	✓	✓	1
<i>Eristalis arbustorum</i>	0	✓	2
<i>Eristalis tenax</i>	0	✓	2
<i>Helophilus spp.</i>	0	✓	2
<i>Melanostoma mellinum</i>	✓	✓	3
<i>Melanostoma scalare</i>	✓	✓	3
<i>Meliscavea auricollis</i>	✓	0	1
<i>Meliscavea cinctella</i>	0	✓	1
<i>Metasyrphus corollae</i>	✓	✓	1
<i>Metasyrphus luniger</i>	✓	✓	1
<i>Platycheirus albimanus</i>	✓	✓	3
<i>Platycheirus clypeatus</i>	✓	✓	3
<i>Platycheirus peltatus</i>	0	✓	3
<i>Platycheirus scutatus</i>	✓	✓	3
<i>Scaeva pyrastris</i>	✓	✓	1
<i>Sphaerophoria scripta</i>	✓	✓	1
<i>Syritta pipiens</i>	✓	✓	4
<i>Syrphus spp.</i>	✓	✓	1

#### Key

✓ = recorded foraging	0 = not recorded foraging	1 = aphids
2 = filtered from water	3 = aphids or rotting leaves	4 = decaying matter

*Lobularia maritima* (either white or purple varieties) consistently had the highest  $\beta$  values for any of the flower resources available, for both males and females of all five of the most abundant syrphid genera, except for *Scaeva pyrastris* L. (Figs 3.11 & 3.13).

Wilcoxon's signed rank tests (Sokal & Rohlf, 1981) were used to compare  $\beta$  values for each flower species within syrphid genera, between sexes, of the most abundant Syrphidae. There were no significant differences in the median  $\beta$  values between sexes; *Episyrphus balteatus* T=27, n=12, NS; *Metasyrphus* spp. T=21, n=12, NS; *Melanostoma* spp. T=36, n=13, NS; *Spaerophoria* spp. T=7, n=9, NS; *Scaeva pyrastris* T=6, n=7, NS. These statistics imply a similarity of resource use between sexes.

A number of similarities in the way syrphid genera utilise floral resources can be detected from Figs. 3.2 to 3.21. *Artemisia vulgaris*, *V. sativa*, *L. album* and *L. purpureum* were either not foraged upon or were consistently fed upon by all genera less than would be expected from their abundance in the environment. *Convolvulus arvensis*, *L. maritima* (cv. Carpet of Snow) or *L. maritima* (cv. Royal Carpet) were consistently foraged upon by all genera more than would be expected from their abundance in the environment, except for *S. pyrastris*. *Plantago major* was fed upon only by *Melanostoma* spp. which are known as specialist pollen feeders on grasses and plantains (Gilbert, 1986). The remaining flora were foraged upon with varying degrees of selectivity by the syrphids present.

#### Laboratory choice experiment

There were a combined total of 277 forage visits made to the white- and purple-flowered varieties of *L. maritima* by *E. balteatus* in the culture box during 8 one-hour observation periods. There were no significant differences in the median number of visits, per 100 flowers, to either of the white flowered specimens, in each of the one-hour periods of observation (Mann Whitney U-test) U= 0.44, NS; or to either of the purple flowered specimens U= 0.42, NS. However the median number of forage visits to the white coloured variety was significantly higher than the median number of visits to the purple coloured variety (U= 2.89, P<0.01). This result is consistent with the results from field observations which showed that during 16 surveys *E. balteatus* showed higher  $\beta$  values or preference for the white cultivar compared with the purple cultivar (Figs 3.3 and 3.5).

## DISCUSSION

At least 13 species of Syrphidae were recorded using *Lobularia maritima* as

a food resource during the study. The five most abundant Syrphidae utilised *L.maritima* selectively, with an economically important species of syrphid (Cowgill, 1991) visiting it more frequently than any other resource in the investigation. Neither sex of *Scaeva pyrastris* was recorded foraging on white flowered *L.maritima*, while both sexes did feed from the purple flowered variety, but to a lesser extent than would be expected from its abundance in the environment. Chesson (1978) wrote that selective predation occurs when the relative frequency of a prey item in a predator's diet differs from the frequency in the environment. In this study, the frequency of prey (flora) in the diet was taken as the frequency of flower visits. Although indicating which flowers are constituents of the diet of a particular syrphid species, quantity (Percival, 1956) and quality of both pollen (Stanley & Liskens, 1974; Baker & Baker, 1979) and nectar (Corbet, Unwin & Prys-Jones, 1979) vary between flower species. The absolute amounts and proportions of different pollens and nectars available to Syrphidae were not assessed in this study. Instead total floral area was used as a measure of resource availability. Resource availability may be measured by two methods,

- i) counting discrete prey individuals or food items (e.g. prey for predators; food plants for herbivores) (Hurlbert, 1978) or;
- ii) comparing the energy represented by each resource (e.g. number of plants available to a herbivore multiplied by the energy content of each plant).

Although energy supplied by different items may ultimately influence the evolution of foraging tactics, it may be only one of many criteria by which individuals discriminate among resources. Where resources occur in discrete units, counting the units (e.g. flowers) is more likely to reveal any degree of discrimination than are values calculated from energy content of items (Feinsinger, Spears & Poole, 1981). Counting flowers is also much less labour intensive than quantifying nectar and pollen production by flowers (Zimmerman & Pleasants, 1982).

In a study of syrphid foraging on Cruciferae (Brassicaceae) weeds, such as *Sinapis arvensis* L. (charlock) and *S.alba* L. (white mustard) in Poland, Wnuk & Wojciechowicz-Zytka (1991) concluded that crucifers seem not to be very attractive for Syrphidae. The findings of the present study contradict this, at least with respect to one crucifer, *L.maritima*. *Lobularia maritima* is often used as an edging plant in gardens and has fragrant nectar-bearing flowers which are frequently visited by small insects (Clapham, *et al.* 1962). Despite this, Rupert & Klingauf (1988) (cited by

Wnuk & Wojciechowicz-Zytka, 1991) stated that "wild plants are more attractive to adult syrphids than garden ones". The present study found otherwise. During observational studies, Wilson (1992) recorded the highest densities of Syrphidae on a range of ornamental flowers, including *L.maritima*, when investigating floral attraction of arable weeds and ornamental flowers.

The most commonly recorded Syrphidae in this study foraged upon a range of floral resources. Gilbert (1981), Ruppert & Molthan (1991) and Cowgill *et al.* (1993a) used observational methods to study syrphid use of flora. They all found that syrphids use flora selectively. This study supports the previous data and in addition was able to show non-significant differences between sexes. The current study also identified a non-native floral resource that is highly ranked, using a selectivity index, for a number of important syrphid species and genera with aphidophagous larvae.

Using another selectivity index (Murdoch's Index C, (Murdoch, 1969)), Cowgill *et al.* (1993a) illustrated that during observational studies on *E.balteatus* in agricultural land from June until August, a floral species' selectivity index changed through time. This was attributed to the changing pollen and nectar contents of the flowers through the season. Cowgill *et al.* (1993a) did not distinguish between male and female *E.balteatus* during their investigation. Haslett (1989a) investigated syrphid feeding during a five month period between May and September, but did not use direct observational techniques. Syrphids were captured and dissected. Contents of the crop were examined microscopically and measurements made of the pollen and nectar content. Female *Rhingia campestris* were shown to switch from a diet consisting chiefly of nectar to that of pollen and back to nectar over the period. The switching was linked to egg development, with most pollen ingestion occurring while yolk deposition was taking place prior to egg maturation. Nectar utilisation related to flight activity. The first period of high nectar content in the diet coincided with mate searching, while the second nectar period coincided with finding oviposition sites. The present study was undertaken over a much shorter time period, and between-date differences in selectivity index were not examined.

Gilbert (1981) classified *E.balteatus* as a generalist feeder, reporting the species having fed from 122 plant species, while *Metasyrphus corollae*, also a generalist, fed from 67 plant species. Within the small area of the grassy bank and *L.maritima* plots, most available resources were used, at least to a certain degree, by Syrphidae.

The between-resource selectivity demonstrated by each of the syrphid groups examined could have been due to physical or biological attributes of resources concerned such as attractiveness to each species from a distance e.g. colour of petals or physical dimensions of inflorescences. The present study found that most Syrphidae selected white *L.maritima* more often than the purple variety. There have been a number of investigations which have included comment on the colour preferences of Syrphidae with respect to the flora they visit. Ilse (1949) suggested that *Eristalis tenax* L. preferred yellow flowers. Kay (1976) stated that *E.tenax* preferred yellow or white flowers. Haslett (1982) suggested however that *E.tenax* preferred red and blue coloured flowers, while *Eristalis pertinax* Scop. preferred white and yellow flowers. *Cheilosia albitarsis* preferred yellow, with low reflectance of ultra-violet (Haslett 1989b). *Rhingia campestris* favoured blue and purple flowers (Gilbert, 1981; Haslett, 1989b). Flowers foraged upon by *E.balteatus*, with high selectivity indices, in the study by Cowgill *et al.* (1993a) were white, yellow, white and yellow, and purple. The latter investigation shows, when considered with the conflicting conclusions from previous studies, that colour is not a factor that should be considered exclusively when predicting the attractiveness of a flower to syrphid species, especially to *E.balteatus*. Flower density may also have been important; the evenly spaced dense patches of *L.maritima* were unique compared with the random, mixed distribution of flora on the bank (such factors will be considered in more detail in Chapter 5). Pollen and nectar content would also be an important factor (see above).

Although this work shows that *L.maritima* is selectively foraged upon by a number of syrphid genera and species with aphidophagous larvae, there was a considerable amount of labour required to maintain the *L.maritima* in a healthy state, and prevent it being overgrown by weeds. As such, it is concluded that unless more hardy and competitive varieties of *L.maritima* are developed, which can compete with arable weeds, it is unlikely that growing *L.maritima* around arable fields, as part of a management scheme to influence syrphid distribution and potentially influence syrphid oviposition, will be developed further in the UK. However *L.maritima* has been used on a commercial farm in the USA where it was sown around fields of sweetcorn which were intercropped with spinach, as part of an integrated pest management scheme in California (S.Wratten, pers. comm.).

Related projects in the UK with a greater likelihood of commercial success include those which use existing techniques to manage field boundaries, but use such



include those which use existing techniques to manage field boundaries, but use such techniques to enhance native herbaceous flora for Syrphidae and other beneficial arthropods. Field boundary management techniques were investigated by Harwood *et al.* (1992). Use of selective herbicides and a restricted mowing regime of a field boundary resulted in greater floral diversity and consequently higher numbers of Syrphidae at the boundary. However non-native plants are still being investigated for use as possible resources for Syrphidae e.g. *Phacelia tanacetifolia* is still under investigation for use around UK cereal fields (Hickman & Wratten, 1994). Other non-native plants which may be used as resources for Syrphidae and are being investigated for commercial use as crops are considered in Chapter 4.

## CHAPTER FOUR

### SYRPHID FORAGING ON ALTERNATIVE CROPS

#### INTRODUCTION

Flowers in hedgerows and field margins are often the only available sources of pollen and nectar for insects on arable land (Pollard, 1971). Supplementing existing sources of pollen and nectar with additional resources or, in the case of heavy herbicide use providing the only source of these resources, may enhance the potential for biological control by manipulating the distribution and local population size of beneficial insects, such as Syrphidae and parasitoids, about crops on a field scale.

The previous chapter showed that the garden ornamental *Lobularia maritima* was selectively foraged upon by a range of important aphidophagous Syrphidae. However, the labour required to sustain the healthy *L.maritima* in an arable environment was a major factor preventing it being used in further field experiments on a larger scale in attempts to manipulate the distribution of Syrphidae. Flora that require little maintenance in an arable environment, yet are foraged upon by beneficial Syrphidae would be more suitable candidates for such large scale field experimentation. Cowgill *et al.* (1993a) listed several arable weeds that were selectively foraged upon by *Episyrphus balteatus*. The encouragement of such weeds in a crop is possible by the selective use and timing of herbicide application, in the development of "Conservation Headlands" (Rands & Sotherton, 1987). However following the recommended techniques for conservation headlands does not guarantee the flourishing development of many arable weeds in the margins of cereal fields (J. Holland pers. comm.). A more active, and costly, alternative would be the sowing of wild flowers around field margins (Harwood *et al.*, 1992). However, plants that are foraged upon by Syrphidae, and could be harvested for economic rewards are more likely to be favoured by farm managers. Such plants could be the novel or alternative crops that are currently under investigation in the UK and elsewhere.

#### Alternative crops

Interest in alternative and novel crops has been stimulated in recent years by

surpluses in production of major crops (Freer, 1990) and the need for farmers to diversify their interests. Potatoes, turnips, oilseed rape and sugarbeet are the major crops that have been introduced into northern Europe in the last 300 years, but none of these are truly new crops (Williams, 1978). Alternative crops that are being investigated are not only potential food and/or fodder crops, but include crops grown for oil production (Table 4.1).

Increasing oil prices have pushed up industry's raw material costs and have led to the search for alternative oil sources (Long, 1990; Freer, 1990). Oils from plant seeds, with varying levels and content of fatty acids, form the basis of several chemical feed stocks for manufacturing processes (von Eierdanz & Hirsinger, 1990). With new technology, new cultivars and a genuine need to find alternatives to cereals, alternative sources for some oils are developing. Support for alternative crops is usually high during times of agricultural surpluses since producers are willing to experiment with new products (Hirsinger, 1989).

As well as oilseed crops, alternative food crops are being experimentally grown in the UK (Table 4.1). Currently there is pressure on farm managers to diversify their cropping (Freer, 1990) and growing alternative crops would enable them to do this. If UK temperatures rise due to global warming, the chances of growing alternative crops successfully in the UK will improve (Freer, 1990). However, higher temperatures are not necessarily required for all alternative crops to be grown successfully. Cold adapted, dwarf varieties of sunflower are already being grown commercially in the UK (Long, 1991).

Insects have been recorded foraging on alternative crops, taking pollen and/or nectar from flowers. In Japan, *Apis* spp. have been recorded foraging on commercial crops of buckwheat (Hamakawa, 1986) and on sunflowers (Banaszak, 1984; du Toit, 1990). In India, *Apis florea* F. is the main insect visitor to coriander (Baswana, 1984). Beneficial predatory insects have been recorded foraging on alternative crops, Syrphidae and Chrysopidae were observed feeding on coriander (Baswana, 1984); and Syrphidae were recorded foraging on buckwheat in Poland (Namai, 1986). High numbers of Syrphidae were recorded in sweep net sampling of buckwheat and coriander in New Zealand by Hodgson & Lövei (1993).

Table 4.1 Potential alternative crops for UK agriculture and their uses.		
Crop	Use	Reference
Amaranthus <i>Amaranthus</i> spp. L	Possible grain crop, fed direct to livestock or used in human foods	Long, 1990
Borage <i>Borago officinalis</i> L.	Not new, but demand is increasing, oil used in pharmaceuticals	Long, 1990 Freer, 1990
Buckwheat <i>Fagopyrum esculentum</i> Moench.	New to UK, used as a course flour in making biscuits & for breakfast cereals, livestock feed, also used in pharmaceuticals, game cover crop.	Tahir & Farooq, 1988; de Rougemont 1989
Calendula <i>Calendula officinalis</i> L.	Oils for nylon production	Long, 1990; *1
Coriander <i>Coriandrum sativum</i> L.	New to UK, traditionally used as a culinary ingredient, recently in pharmaceuticals, livestock feed, oils for chemical industry	Ridley, 1912; *1; *2
Echium <i>Echium</i> spp. L.	Oils especially steridonic acid for industry, human foods e.g. honey	B. Bland (pers. comm.)
Evening primrose <i>Oenothera biennis</i> L.	Oils; $\gamma$ -linolenic acid	Freer, 1990, *3
Gold of Pleasure <i>Camelina sativa</i> L. (Crantz)	Oils for cosmetics industry	Freer, 1990
Meadowfoam <i>Limnanthes alba</i> Benth.	Oils for industry, manufacture of waxes, surfactants, water repellents, cosmetics	Long, 1990; *2, *3
Niger <i>Guizotia abyssinica</i> (L.f.) Cass.	Game cover crop, oils used for manufacture of soaps, foods	de Rougemont 1989, *3
Oilseed poppy <i>Papaver somniferum</i> L.	Oils as culinary ingredient, pharmaceuticals, other industrial uses including paint ingredient	de Rougemont 1989, *3
Quinoa <i>Chenopodium quinoa</i> Willd.	Specialist human diets, game cover crop, animal feed	Rideout <i>et al.</i> , 1991; Freer, 1990
Safflower <i>Carthamus tinctorius</i> L.	Paints, varnishes, oils in margarine and salad dressings	Röbbelen <i>et al.</i> , 1989
Sunflower <i>Helianthus annuus</i> L.	Small area grown in UK already, expanding market, oils and fats for food & industry	Williams, 1978 Jones, 1987 Long, 1991
Texsel green <i>Brassica carinata</i> Braun	Game cover crop	de Rougemont 1989

\*1 = Meier-zu-Beerentrup & Röbbelen (1987) \*2 = von Eirdanz & Hirsinger (1990)

\*3 = Röbbelen *et al.* (1989)

### Distribution of beneficial insects about floral resources

Leius (1967b) showed a higher incidence of parasitoid attack by *Scambus buolinae* (Htg.) (Hymenoptera: Ichneumonidae) on tent caterpillars and codling moths near sites of floral richness compared with florally depleted sites. However because adults visit flowers before egg maturation (van Emden, 1963) and then go on to search for hosts, it has not always been possible to show a causative link between increased parasitoid attack and increased floral resources (Pollard, 1971).

Working with Syrphidae, Chandler (1968c) did not show any influence of *Senecio jacobaea* flowers on syrphid oviposition in Brussels sprouts. However, there is some evidence of differences in distribution of adult Syrphidae between sites of differing floral resources. Harwood *et al.* (1992) recorded significantly more *Metasyrphus corollae*, *Melanostoma scalare* Fab. and *Platycheirus* spp. in yellow water traps extending into winter wheat from margins drilled with wild flowers than in yellow traps extending from unmanaged margins. Comparing abundance of Syrphidae along two field margins with different types of vegetation composition, Lagerlöf and Wallin (1993) found more adult Syrphidae and significantly more larval Syrphidae in a margin with a high diversity of plant species, compared with a margin sown with a mixture of Leguminosae. Other work that has attributed differences in distribution of Syrphidae to provision of floral resources in field margins includes Klinger (1987), Sengonca and Frings (1988), Molthan and Rupert (1988) and Molthan (1990).

### Aims of this chapter

The work in this chapter aimed to determine whether Syrphidae forage on potential alternative crops in the UK and to find whether an alternative crop could be used to manipulate the distribution of Syrphidae in an arable environment on a field scale.

## **MATERIALS AND METHODS**

### Observational study of Syrphidae foraging on alternative crops: Summer 1991

Alternative crops were grown at Bridgets EHF (Experimental Husbandry Farm), a MAFF ADAS (Agricultural Development & Advisory Service) establishment of 419ha, on silty clay loam in Northern Hampshire (Grid ref SU 518 341). Eight alternative crops (*Borago officinalis* (borage), *Calendula officinalis* (dwarf marigold),

*Camelina sativa* (gold of pleasure), *Chenopodium quinoa* (quinoa), *Coriandrum sativum* (coriander), *Fagopyrum esculentum* (buckwheat), *Helianthus annuus* (sunflower) and *Limnanthes alba* (meadowfoam) were sown by MAFF staff in mid-May 1991, in contiguous plots 6m x 12m in a linear design. There was no replication. The plots were primarily used as demonstration plots (B. Freer, pers. comm.) and had not been originally designed as part of this study. The crops were enclosed by black plastic netting (mesh size 1.5cm), which prevented damage to the crops by pigeons. The plots were first inspected on 19 July, by which time *Camelina sativa* and *Limnanthes alba* had begun to senesce. The remaining crops were in flower. On four dates (23 & 31 July and 12 & 21 August) syrphid foraging activity was observed at each crop except quinoa. Quinoa was omitted because no syrphid foraging had been observed on the crop during the preliminary visit and the small wind pollinated flowers were thought not suitable for syrphid foraging. The netting prevented the observer from carrying out a standard census walk (*sensu* Gilbert, 1981). Instead 1m<sup>2</sup> of each crop was observed for a ten minute period in rotation, five times on each date, except on July 23 when wind and rain prevented more than two sets of observations being recorded. Such a method had previously been used by Namai (1986). Syrphidae in a 1m<sup>2</sup> patch of a 2m x 30m patch of buckwheat, grown outside the netting, as part of another MAFF study, were also observed. Comparison of the syrphid foraging on buckwheat with and without net cover allowed any effect of the netting to be detected. Individual Syrphidae seen in the 1m<sup>2</sup> area of crop being observed were watched and if seen feeding on either pollen or nectar from the crop, were identified to species and sexed where possible. Results were recorded onto a micro-cassette recorder. Recordings started between 06:30 BST and 08:00 and ended between 14:30 and 16:00. Because of the time interval between repeat observations of crops on any day, it was assumed that the same syrphid would not be seen foraging on a crop that it had previously been observed on. Such an assumption is considered in more detail in Chapter Five.

#### Field trial of an alternative crop: Summer 1992

Having determined from observations in 1991 that buckwheat (*Fagopyrum esculentum*) and coriander (*Coriandrum sativum*) were alternative crops that beneficial Syrphidae foraged upon, coriander was selected for a field scale investigation in 1992. Coriander was preferred to buckwheat for agronomic reasons.

Buckwheat is susceptible to lodging (Koblev, 1986; Campbell, 1987) and to late spring frosts (S. Wratten, pers. comm) while coriander is more tolerant to frosts, with a critical root temperature of  $-8^{\circ}\text{C}$  and critical leaf temperature of  $-13^{\circ}\text{C}$  (Sergeeva & Sil'chenko, 1984).

### Experimental design

#### Establishing a strip of coriander

The field trial was carried out in Field 13 (F13), a 19ha field on the Leckford Estates in Northern Hampshire. The field had been sown with winter wheat (cv. Galahad) to the field boundaries in October 1991, without leaving a boundary strip, as defined by Greaves & Marshall (1987).

To allow room for a strip of coriander to be sown along two edges of the field, a hand held CP15 sprayer was used to spray Fusilade-5 (fluazifop-P-butyl) at recommended field rate ( $250\text{g AI ha}^{-1}$ ) on the outermost 2m of crop on the northern and western boundaries on 22 March, 1992. As the sprayer progressed along the headland, applying the herbicide, an assistant held a square polythene barrier 1.5m x 1.5m at right angles to the sprayer to prevent Fusilade drifting further into the crop than the area intended to be sprayed.

The northern and western field boundaries of F13 and the western field boundary of the control field (F25), were hedges of *Crataegus monogyna*, with annual grasses and herbs in the hedge bottom e.g. *Heracleum sphondylium*, *Torilis arvensis* (Huds.) Link, *Galium aparine*, *Rubus fruticosus*, *Cirsium arvense* (L.) Scop., *Lapsana communis* L., *Sonchus oleraceus* L., *Papaver rhoeas* L. and *Convolvulus arvensis*. The northern field boundary of F25 was a post and wire fence with annual grasses at the base of the fence.

Recommended sowing rate for coriander is  $25\text{kg ha}^{-1}$  (Kamla-Singh *et al.*, 1987), with 800 rows per 100m (Bhati, 1988) which is equivalent to 3.125g per 10m row. Seeds of coriander were weighed into 20ml plastic beakers, approx. 3.13g per beaker, and sealed. On 31 March, coriander was sown into the boundary strip - the area that had been previously sprayed with herbicide to kill the wheat. Three parallel shallow furrows, approx. 5cm deep, and 200m long were made using a hand held hoe in both northern and western boundaries. The boundary strips were marked with bamboo canes at 10m intervals from the north-western corner of F13. The coriander seed was sown by hand into the furrows, one beaker of seed per furrow, per 10m.

The seeds in the furrows were then covered with previously excavated soil and compacted by foot. This method of sowing ensured a more even distribution of coriander seeds than may have otherwise resulted from alternative hand sowing techniques.

Coriander began to flower on 15 June. On 13 dates from 17 June to 26 July, an estimate of the proportion of coriander in flower was made. The number of coriander plants with closed and open buds in four randomly selected 10m sections of the western 200m strip was counted. The percentage abundance was calculated as :

$$\% \text{ flowering} = (\text{No} / \text{No} + \text{Nc}) * 100$$

Where, No = number of plants with open buds

Nc = number of plants with closed buds

#### Trapping Syrphidae in water traps

Fluorescent yellow water traps had trapped the highest number of Syrphidae during tests of differently coloured water traps, used to capture cabbage root fly, (*Delia radicum* L) (Finch, 1977). Consequently, circular, brown, plastic, flowerpot-saucers, 19cm in diameter were converted into fluorescent yellow water traps. They were first prepared by scouring the internal surfaces with a coarse grade aluminium oxide woodworking cloth (scale F2-120). The scouring was used to provide a key to which coats of paint could adhere. It had been found that paint on smooth, un-scoured saucers flaked off. The saucers were washed in detergent to remove dust and grease before white undercoat (Brilliant-white Undercoat, B&Q Ltd., Eastleigh) was applied. Two coats of white undercoat were applied to the internal surfaces of the saucers. Two coats of "Glocote foundation base" (Coo-var Ltd., Hull) were applied as a foundation base primer before two final coats of "Glocote yellow," (Coo-var Ltd.) a yellow fluorescent paint were applied.

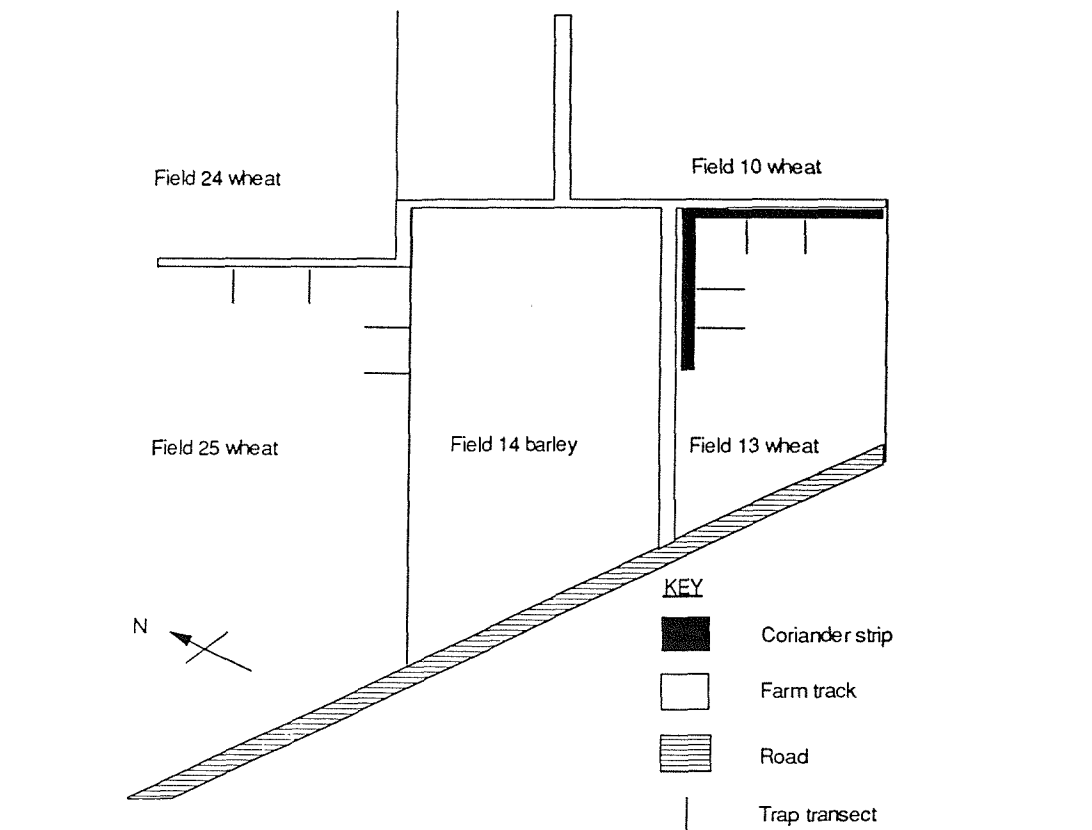
Four transects of yellow traps were arranged in F13, the experimental field and four transects of traps in Field 25 (F25), a 33.2ha field of winter wheat (cv. Galahad) that was not sown with coriander boundary strips and which was used as the control field. Each line of yellow traps was positioned at right angles to the nearest field boundary, with traps positioned at 1m, 5m, 15m, 25m and 50m from the boundary into the field (Fig 4.1). Umbelliferae and other flowers on which Syrphidae



could feed were cut down around the control field by hand.

Each trap consisted of a fluorescent yellow painted saucer which sat inside a shallow 24cm diameter flower pot saucer, that was fixed to a wooden stake in the ground. Wooden stakes, 1.5m long, had been hammered into the ground using a sledge hammer, so that each stake was approx. 1.3m high. A 24cm saucer was fixed on top of each stake using a brass screw. The yellow traps were first set out in F13 and F25 on June 14 1992, when the coriander began to flower. 500ml of a 5% aqueous solution of detergent (Fairy Liquid, Procter & Gamble Ltd., Newcastle-Upon-Tyne) was put into each yellow trap. Each water trap in F13 and F25 was emptied on 11 dates between 17 June and 26 July, when the coriander stopped flowering. Each time a water trap was emptied, Syrphidae in the trap were removed using forceps and placed into a 20ml specimen tube containing 70% alcohol and a pencil-written label. The remaining contents of the trap were discarded and the trap reset with a fresh detergent solution. Syrphidae were identified in the laboratory following Stubbs & Falk (1983).

Fig 4.1 Diagrammatic layout of field trial with coriander - summer 1992.



### Aphid counts

On 14 June, ten randomly chosen wheat plants were selected around each yellow trap in field F13 and F25. The plants were marked by placing numbered jewellers' tags over the emerging ears at crop growth-stage (GS) 57 (Zadoks, Chang & Konzak, 1974). On each date that the yellow traps were emptied, the number of aphids on each marked ear was recorded. In addition, aphid counts were conducted on 19 June and 24 June although yellow traps were not emptied. Aphid counts stopped after 17 July, when the field population of aphids crashed. Marked ears were also examined for syrphid eggs or larvae on each date aphid counts were made.

### Census walks

On 7 July, a census of Syrphidae foraging on the flowering coriander was carried out in F13. From 06:30 BST until 12:30, 24 standard walks were carried out along the 200m strip of coriander on the western boundary of F13. Syrphidae among the strip were observed by slowly walking adjacently to the coriander strip. Walks lasted 15min. Syrphidae that were observed were identified to species where possible and sexed. Their activity when first observed was also recorded as either resting / basking, feeding, or flying if in close proximity (within approx. 50cm) to coriander. Results were recorded onto a micro-cassette recorder.

Six standard walks were conducted along the eastern boundary of F25 on 8 July, from 07:30 BST but were stopped at 09:00; during this period very few Syrphidae were recorded.

### Bait plants

On 13 July, twenty 11cm diameter pots containing John Innes No. 2 compost were sown with barley (cv. Atom) and maintained in the university glasshouses. After seven days, the barley was at GS 11. Each pot was then infested with laboratory cultures of *Sitobion avenae*. Infested barley seedlings from culture were cut and placed onto uninfested barley in the pots. After 24h aphids had transferred and settled on the new barley. Such infested bait plants were then transferred to F13 and F25 on 21 July, where one pot of infested plants was placed on the ground by each yellow trap in two of the rows of yellow traps in F13 and F25. The bait plants were examined on 22 & 26 July for aphids, syrphid eggs and syrphid larvae.

## RESULTS

### Observational study of Syrphidae foraging on alternative crops: Summer 1991

A total of 601 recordings of forage visits to four crops inside and one crop (buckwheat) both inside and outside the netting was made during seventeen surveys on four dates. Eleven syrphid genera and 16 species were observed feeding on alternative crops. 73.5% of individuals recorded were from species with obligate or facultative aphidophagous larvae. The most commonly observed species was *Episyrphus balteatus* which comprised 32.8% of all individuals seen.

To determine whether the netting influenced the ability of different sized Syrphidae to penetrate and reach the alternative crops, Syrphidae were classified as small (e.g. *Melanostoma* spp. and *Syritta* spp.), medium (e.g. *E. balteatus* and *Metasyrphus* spp.) or large (e.g. *Eristalis* spp.) and a G-test carried out on numbers in each class seen foraging on buckwheat inside and outside the netting. There was no significant association between syrphid size class and the numbers recorded foraging on buckwheat inside or outside the netting ( $G_{adj} = 3.27$ , 2DF, NS).

Kruskal-Wallis non-parametric ANOVA's were conducted on rank ordered data (number of individuals foraging on each crop per survey) for *E. balteatus* and the three other most common genera recorded foraging on alternative crops. There were significant differences in the median number of forage visits to each crop m<sup>-2</sup> in three of the four taxa tested; *E. balteatus*,  $K = 18.79$ ,  $DF = 4$ ,  $P < 0.001$ , *Eristalis* spp.  $K = 20.87$ ,  $DF = 4$ ,  $P < 0.001$ , *Melanostoma* spp.,  $K = 25.29$ ,  $DF = 4$ ,  $P < 0.001$ , *Syrphus*  $K = 7.72$ ,  $DF = 4$  NS.

To determine which crops were foraged upon significantly differently, multiple Mann-Whitney U tests were performed on data from *E. balteatus*, *Eristalis* spp. and *Melanostoma* spp.. U- tests were also carried out on *Syrphus* spp. to see if patterns approaching significance emerged, although no overall significance had previously been shown by the Kruskal-Wallis test. Results are shown in tables 4.2 - 4.5. Because of the many planned comparisons made, a conservative experimentwise error rate of 0.005 was calculated as the appropriate level of significance, below which tests could validly be considered as significant (Sokal & Rohlf, 1981).

Table 4.2 Mann-Whitney U test results comparing foraging by *E.balteatus* on alternative crops.

Crops	Borage	Coriander	Buckwheat	Sunflower
Calendula	0.91 (NS)	2.25 (NS)	2.93 *	0.79 (NS)
Sunflower	1.75 (NS)	2.80 *	3.56 *	-
Buckwheat	2.18 (NS)	0.33 (NS)	-	-
Coriander	1.54 (NS)	-	-	-

NS = not significant \* =  $P < 0.005$

Table 4.3 Mann-Whitney U test results comparing foraging by *Syrphus* spp. on alternative crops.

Crops	Borage	Coriander	Buckwheat	Sunflower
Calendula	0.60 (NS)	1.36 (NS)	1.86 (NS)	0.93 (NS)
Sunflower	1.48 (NS)	0.53 (NS)	0.87 (NS)	-
Buckwheat	2.42 (NS)	0.32 (NS)	-	-
Coriander	1.84 (NS)	-	-	-

NS = not significant

Table 4.4 Mann-Whitney U test results comparing foraging by *Eristalis* spp. on alternative crops.

Crops	Borage	Coriander	Buckwheat	Sunflower
Calendula	3.65 *	0.78 (NS)	1.08 (NS)	1.93 (NS)
Sunflower	2.06 (NS)	1.77 (NS)	2.52 (NS)	-
Buckwheat	3.86 *	0.82 (NS)	-	-
Coriander	3.39 *	-	-	-

NS = not significant \* =  $P < 0.005$

Table 4.5 Mann-Whitney U test results comparing foraging by *Melanostoma* spp. on alternative crops.

Crops	Borage	Coriander	Buckwheat	Sunflower
Calendula	0.03 (NS)	2.59 (NS)	3.25 *	0.56 (NS)
Sunflower	0.60 (NS)	2.97 *	3.54 *	-
Buckwheat	3.08 *	0.82 (NS)	-	-
Coriander	2.46 (NS)	-	-	-

NS = not significant \* =  $P < 0.005$

Bees were seen foraging on borage, and there may have been competition for pollen or nectar between bees and Syrphidae. No quantitative recording of bee density or behaviour was made during the observations of syrphids on alternative crops.

Coriander was further investigated as a pollen and nectar resource used by Syrphidae during the summer of 1992. Although buckwheat had been favourably foraged upon by Syrphidae, for agronomic reasons given in the materials and methods section, it was not investigated in 1992.

#### Field trial of an alternative crop: Summer 1992

##### Trapping Syrphidae in water traps

Between 15 June and 26 July, 726 Syrphidae from seven genera and nine species were caught and identified from the water traps in F13 (the field with a coriander boundary strip); and 1075 syrphids in the same genera and species from F25 (the control field). *Episyrphus balteatus* and *M.corollae* comprised the majority of all species caught in either field (F13: *E.balteatus* = 52.8%, *M.corollae* = 34.7%; F25: *E.balteatus* = 53.2%, *M.corollae* = 35.6%) during the study period. Figs 4.2 and 4.3 show that most Syrphidae were caught between 17 July and 26 July in either field. There were 4 dates (July 10, 17, 22 and 26) when 10 or more individuals from the same species (*E.balteatus* or *M.corollae*) were caught by yellow water traps in both fields and it is data from these dates that have been statistically analysed. Analysis was carried out using repeated-measure ANOVA of  $\log_{10}(x+1)$  transformed

data on the separate numbers of males and females *E.balteatus* and *M.corollae* caught in yellow traps at different trap-distances in either field on 10 July, 17 July, 22 July and 26 July. Syrphidae caught on these dates comprised 92.4% of all Syrphidae caught in F13 and 91.7% of Syrphidae caught in F25, during the entire trapping period (15 June to 26 July).

There were no significant differences in the number or sex of either *E.balteatus* or *M.corollae* captured in yellow traps between fields i.e. there was no significant enhancement or redistribution of common syrphids, shown by data from yellow traps, in the field using coriander as a treatment around F13 (Tables 4.6 to 4.9).

There were no significant differences in the distribution of numbers of *E.balteatus* or *M.corollae* in yellow traps at different distances from each field margin (Tables 4.6 to 4.9). However there was an interaction between the effect of field treatment and distance of yellow trap from the field boundary, shown by female *M.corollae* (Table 4.9). Inspection of data showed that more female *M.corollae* were caught in the traps at 1m from the field boundary of F25 than in traps at the same distance from the boundary of F13.

The only factor which was consistently statistically significant during the trapping period was date of trap emptying. This was highly significant for both sexes of *E.balteatus* and *M.corollae*. Figs 4.2 and 4.3 show that relatively large numbers of *E.balteatus* and *M.corollae* were caught on 22 and 26 July. Having found using repeated-measure ANOVA that 'date' was a significant factor, single-factor ANOVA was carried out using pooled data from each field with date as the single factor; mean number of each species and sex caught in yellow traps on each date are given in Table 4.10

Figs 4.4 to 4.7 show the percentage distribution of male and female *E.balteatus* and *M.corollae* caught in yellow traps at distances from the hedgerows around F13 and F25 on each date after 6 July when numbers caught began to rise. Figs 4.4 and 4.5 illustrate that greater proportions of *E.balteatus* were caught in yellow traps closer to the hedge, in both fields, up to 13 July, and that after this date the proportions caught at each distance were more evenly distributed. A similar pattern is shown by *M.corollae*, except that an even distribution over each distance does not occur until 22 July.

Table 4.6 Repeated measure ANOVA results for male *E.balteatus*; yellow water trap data ( $\log_{10} (x+1)$  transformed). F-ratio and significance level results with field treatment, distance and date as factors.

Source of variation	DF	Sums of squares	Mean square	F-ratio	P
<u>Between Fields</u>					
Treatment	1	0.28	0.28	0.91	NS
Residual	6	1.85	0.31		
<u>Between traps in fields</u>					
Distance	4	0.27	0.07	1.03	NS
Treatment by distance	4	0.37	0.09	1.37	NS
Residual	24	1.60	0.07		
<u>Within traps in fields</u>					
Date	3	10.74	3.58	40.64	**
Treatment by Date	3	0.19	0.06	0.71	NS
Date by Distance	12	0.82	0.07	1.28	NS
Treatment by Date by Distance	12	0.32	0.03	0.50	NS
Residual	72	3.82	0.05		
TOTAL	141	20.26	0.14		

Key: NS = Not significant ( $P > 0.05$ ); \*\* = Highly significant ( $P < 0.01$ )

Table 4.7 Repeated measure ANOVA results for female *E.balteatus*; yellow water trap data ( $\log_{10}(x+1)$  transformed). F-ratio and significance level results with field treatment, distance and date as factors.

Source of variation	DF	Sums of squares	Mean square	F-ratio	P
<u>Between Fields</u>					
Treatment	1	0.00	0.00	0.01	NS
Residual	6	1.56	0.26		
<u>Between traps in fields</u>					
Distance	4	0.34	0.09	1.21	NS
Treatment by Distance	4	0.75	0.19	2.63	NS
Residual	24	1.70	0.07		
<u>Within traps in fields</u>					
Date	3	5.66	1.89	15.53	**
Treatment by Date	3	0.11	0.04	0.30	NS
Time by Distance	12	0.90	0.07	1.48	NS
Treatment by Date by Distance	12	0.66	0.06	1.10	NS
Residual	72	3.63	0.05		
TOTAL	141	14.75	0.10		

Key: NS = Not significant ( $P > 0.05$ ); \*\* = Highly significant ( $P < 0.01$ )



Table 4.8 Repeated measure ANOVA results for male *M.corollae*; yellow water trap data ( $\log_{10} (x+1)$  transformed). F-ratio and significance level results with field treatment, distance and date as factors.

Source of variation	DF	Sums of squares	Mean square	F-ratio	<i>P</i>
<u>Between Fields</u>					
Treatment	1	0.47	0.47	2.67	NS
Residual	6	1.05	0.17		
<u>Between traps in fields</u>					
Distance	4	0.17	0.04	0.84	NS
Treatment by Distance	4	0.04	0.01	0.17	NS
Residual	24	1.24	0.05		
<u>Within traps in fields</u>					
Time	3	12.93	4.31	43.95	**
Treatment by Date	3	0.16	0.05	0.54	NS
Time by Distance	12	0.49	0.04	0.59	NS
Treatment by Date by Distance	12	1.13	0.09	1.36	NS
Residual	72	4.98	0.07		
TOTAL	141	22.66	0.16		

Key: NS = Not significant ( $P > 0.05$ ); \*\* = Highly significant ( $P < 0.01$ )

Table 4.9 Repeated measure ANOVA results for female *M.corollae*; yellow water trap data ( $\log_{10} (x+1)$  transformed). F-ratio and significance level results with field treatment, distance and date as factors.

Source of variation	DF	Sums of squares	Mean square	F-ratio	P
<u>Between Fields</u>					
Treatment	1	0.00	0.00	0.00	NS
Residual	6	0.73	0.12		
<u>Between traps in fields</u>					
Distance	4	0.06	0.01	0.63	NS
Treatment by Distance	4	0.47	0.12	5.28	**
Residual	24	0.53	0.02		
<u>Within traps in fields</u>					
Time	3	3.80	1.27	21.55	**
Treatment by Date	3	0.09	0.03	0.54	NS
Time by Distance	12	0.34	0.03	0.89	NS
Treatment by Date by Distance	12	0.47	0.04	1.22	NS
Residual	72	2.31	0.03		
TOTAL	141	8.80	0.06		

Key: NS = Not significant ( $P > 0.05$ ); \*\* = Highly significant ( $P < 0.01$ )

Fig 4.2 Composition of Syrphidae in water traps in the coriander bordered field (F13).

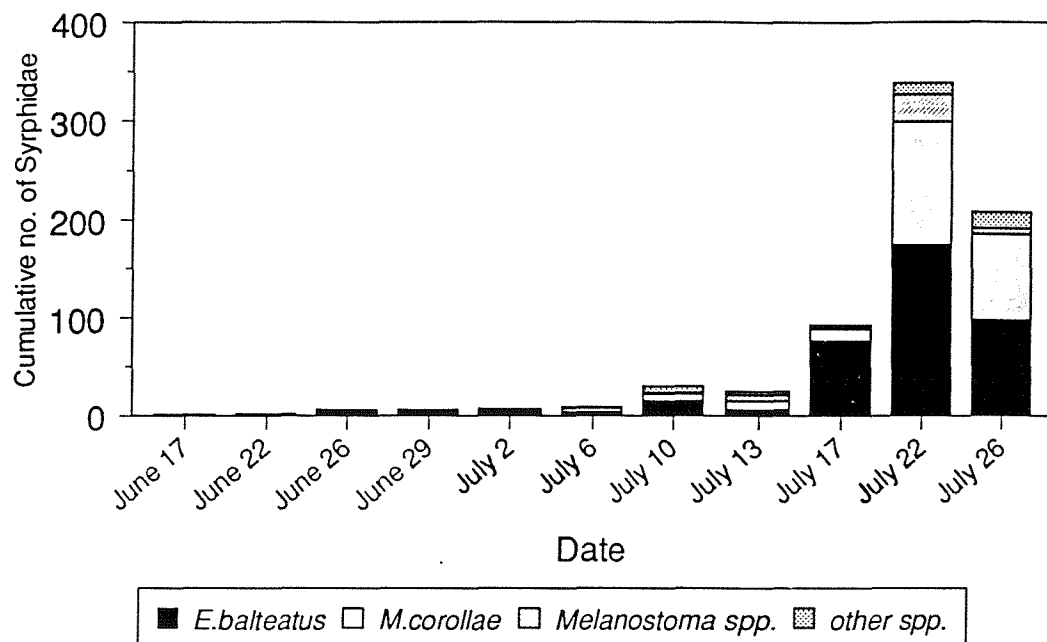


Fig 4.3 Composition of Syrphidae in water traps in the control field (F25)

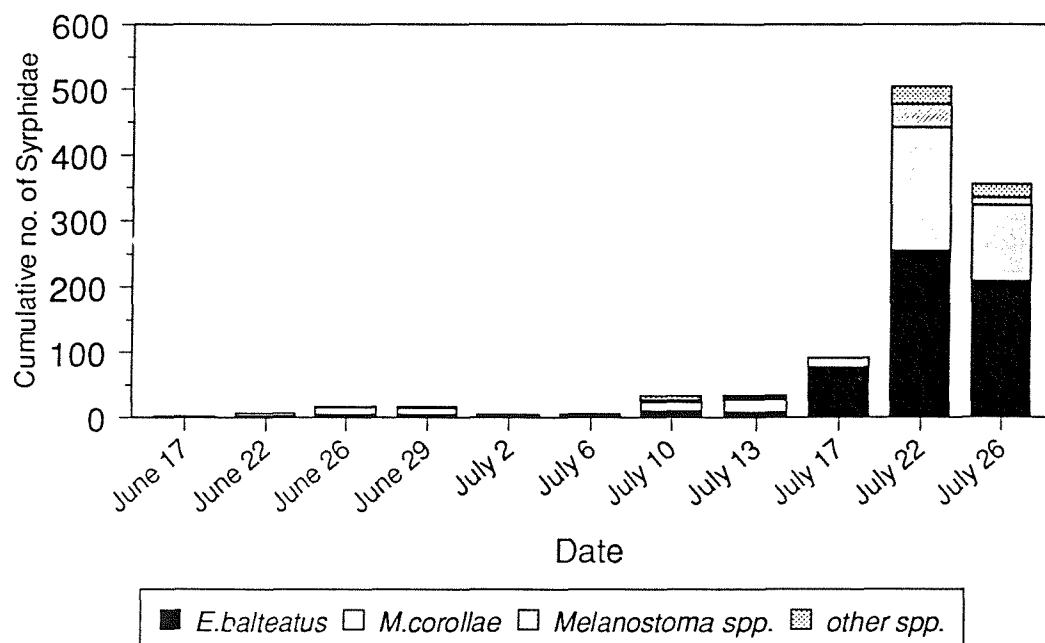


Fig 4.4 Distribution of *E.balteatus* in yellow water traps in F13 with a coriander boundary strip (females and males shown separately).

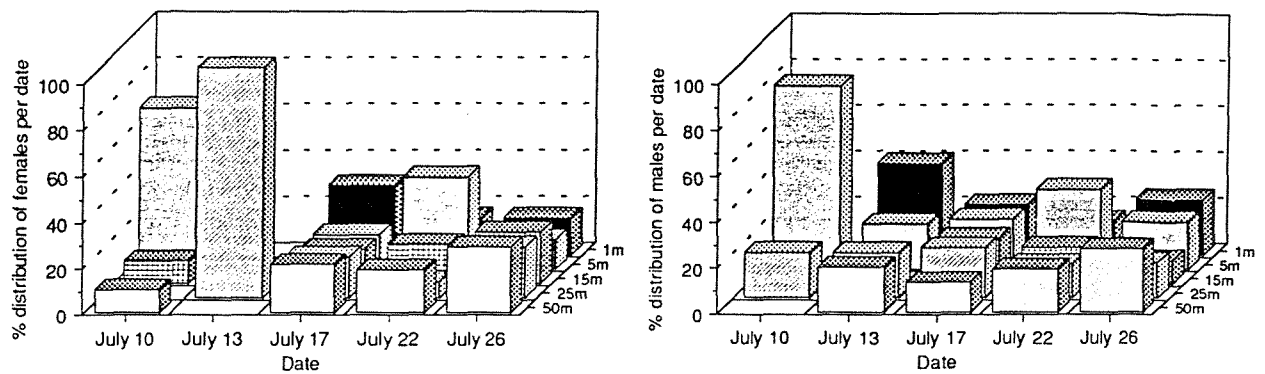


Fig 4.5 Distribution of *E.balteatus* in yellow water traps in F25 without additional resources in the field boundary (females and males shown separately).

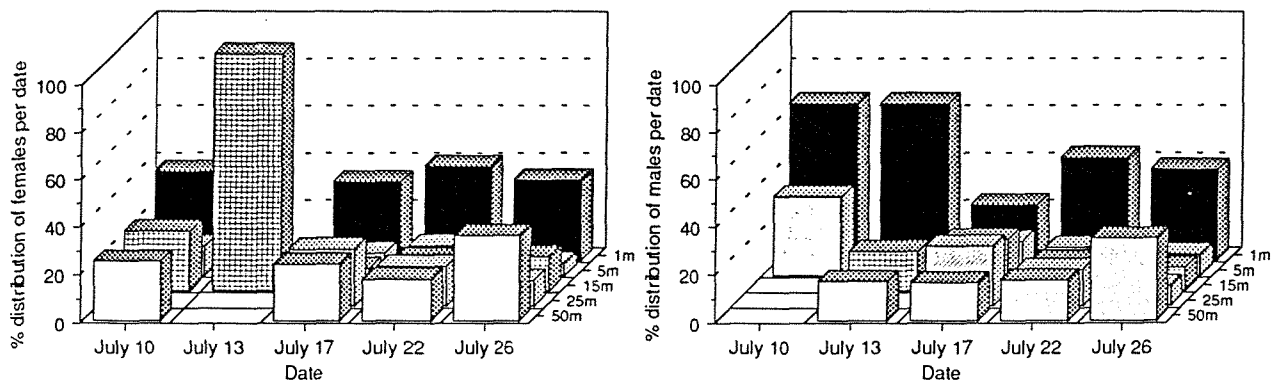


Fig 4.6 Distribution of *M.corollae* in yellow water traps in F13 with a coriander boundary strip (females and males shown seperately).

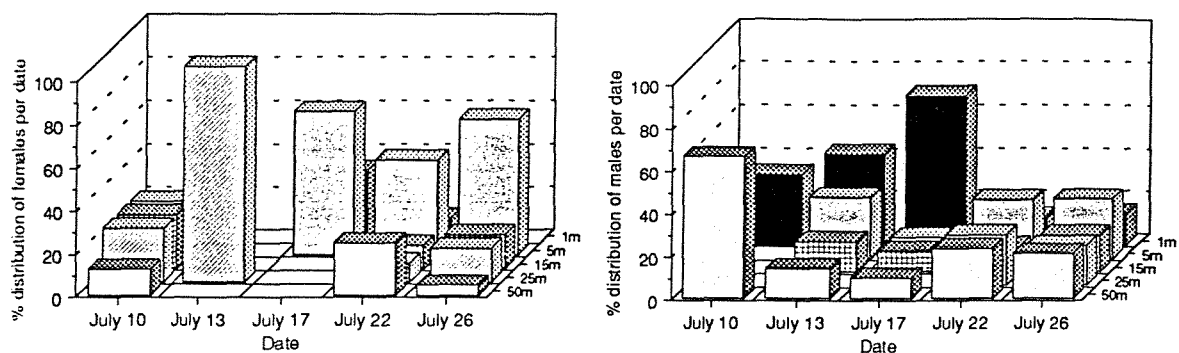


Fig 4.7 Distribution of *M.corollae* in yellow water traps in F25 without additional resources in the field boundary (females and males shown seperately).

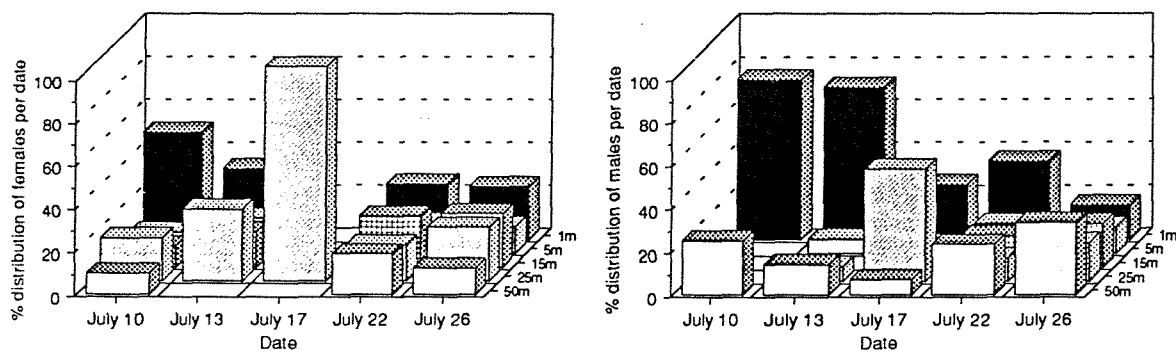


Table 4.10 Mean number of male and female *E.balteatus* and *M.corollae* in yellow traps on key dates in July. Data in the same column sharing the same letter do not significantly differ (Tukey HSD following ANOVA of  $\log_{10} (x+1)$  transformed data)

Date	<i>E.balteatus</i>		<i>M.corollae</i>	
	Male	Female	Male	Female
July 10	0.40 a	0.90 a	0.35 a	0.90 ab
July 17	5.05 b	2.70 b	1.85 a	0.30 a
July 22	12.30 c	9.15 c	10.20 b	4.35 c
July 26	9.50 bc	4.35 b	10.20 b	1.75 b

#### Census walks

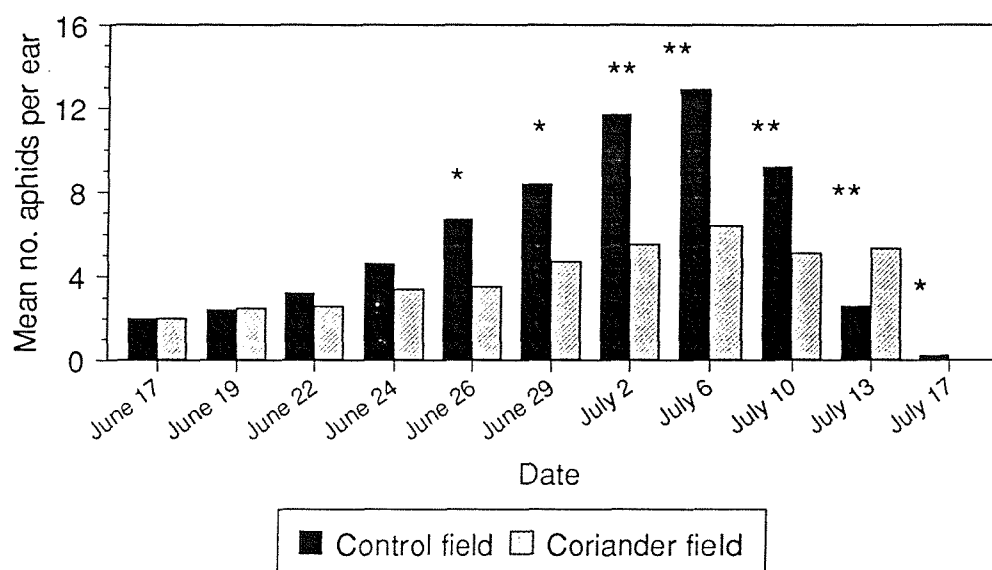
During 24 walks, along a 200m strip of coriander in F13, the mean number of *E.balteatus* seen resting or feeding on coriander ( $\pm 95\%$  C.L.) was  $21.8 \pm 5.0$ ; and the mean number seen flying near coriander was  $16.5 \pm 3.1$ . When 6 census walks were conducted along a 200m strip of the boundary strip of F25 at the same time the next day, under similar weather conditions, the mean number of *E.balteatus* seen resting or basking on vegetation ( $\pm 95\%$  C.L.) was  $1.4 \pm 0.8$  and the mean number seen flying was  $2.3 \pm 1.1$ .

Since census walks were carried out in F25 between only 07:30 and 09:00, and syrphid activity can be related to time of day and local climatic conditions (Cowgill, 1991), comparisons between F13 and F25 censuses were also made with data collected only between 07:30 and 09:00 on each day. There were significantly more *E.balteatus* observed in F13 than in F25 during the same period on consecutive days ( $t = 4.27$ ,  $DF = 10$ ,  $P < 0.01$ ). In F13, the mean number of *E.balteatus* observed was  $38.5 \pm 16.3$ , and the mean number observed in F25 during the same period, the next day was  $3.6 \pm 1.5$ .

### Aphid counts

The mean number of aphids on marked ears, in each field, through time, is shown in Fig 4.8. The recommended aphid spray threshold of 66% infestation (one or more aphid per ear) between GS 61 and GS 73 (Anon., 1988) was not reached in either field. Significant statistical differences in mean numbers of aphids on marked ears were found, from June 26, between field types. Except on July 13, there were consistently greater mean numbers of aphids on wheat ears in F25 (the control field) than in F13 (the field with coriander boundary strips). Two-way ANOVA of  $\log_{10}(x+1)$  transformed data performed on the mean number of aphids per marked ear around each yellow trap, with field and trap as factors, gave the following results; 17 June,  $F_{1,19}=1.17$ , NS; 19 June,  $F_{1,19}=1.05$ , NS; 22 June,  $F_{1,19}=1.60$ , NS; 24 June,  $F_{1,19}=2.62$ , NS; 26 June,  $F_{1,19}=6.97$ ,  $P < 0.05$ ; 29 June,  $F_{1,19}=8.08$ ,  $P < 0.05$ ; 2 July,  $F_{1,19}=15.72$ ,  $P < 0.01$ ; 6 July,  $F_{1,19}=15.13$ ,  $P < 0.01$ ; 10 July,  $F_{1,19}=15.32$ ,  $P < 0.01$ ; 13 July,  $F_{1,19}=11.22$ ,  $P < 0.01$ ; 17 July,  $F_{1,19}=5.78$ ,  $P < 0.05$ .

Fig 4.8 Mean number of aphids per marked wheat ear in control and coriander fields.



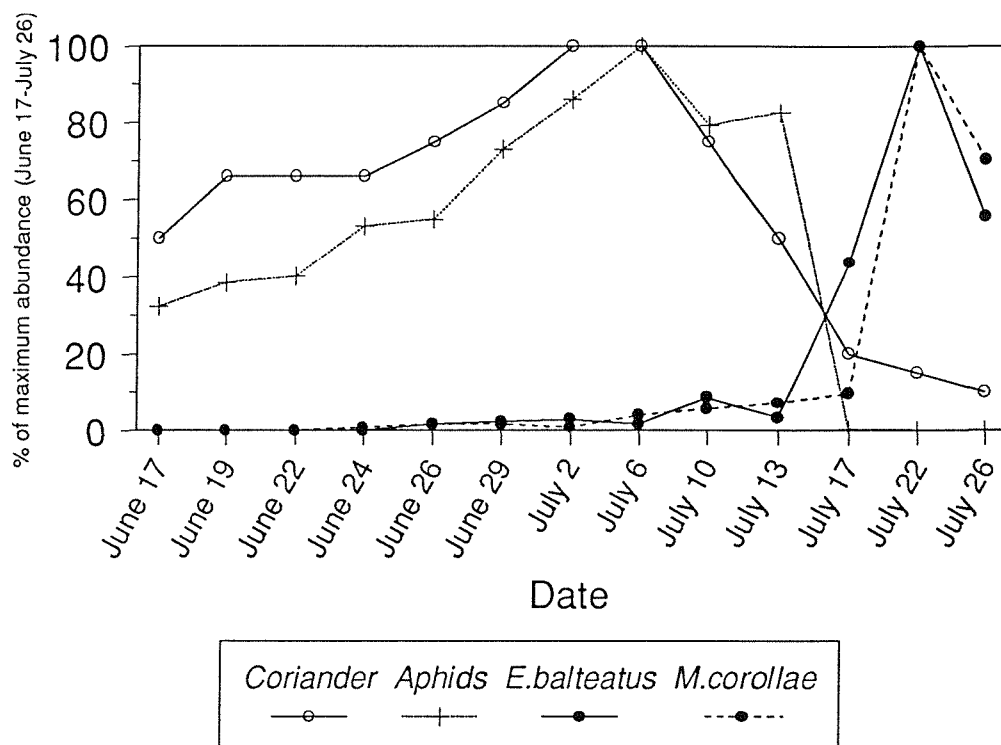
Asterisks indicate significant differences in the mean number of aphids between fields on specific dates ( \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ).

No syrphid eggs were spotted on marked ears in either F13 or F25. On 6 July one third instar *E. balteatus* larva was found on an ear in F13 around trap 16, 1m from the

field margin.

The timing of maximum abundance of aphids, *E.balteatus* and *M.corollae* in F13 is illustrated in Fig 4.9. Fig 4.9 also shows when the maximum amount of coriander was in flower. The peak aphid abundance occurred on 6 July (crop GS 71), this coincided with maximum coriander flowering. Maximum abundance of the common syrphid adults did not occur until 22 July.

Fig 4.9 An illustration of the relationship between timing of maximum abundance of aphids, common syrphid species and coriander flowering in F13.



### Bait plants

The natural aphid population in crop plants crashed before the maximum occurrence of adult Syrphidae (Fig 4.9). Bait plants were then used to simulate suitable oviposition sites for Syrphidae with aphidophagous larvae, however no syrphid eggs or larvae were recorded on any bait plants in either field on 22 or 26 July.

## DISCUSSION

Syrphid species common in the agricultural environment were recorded



foraging on a range of potential alternative crops while the crops were in flower. *Episyrphus balteatus* was recorded foraging on all crops observed, but was most commonly recorded on either buckwheat or coriander. Flowers of buckwheat and coriander are white, the colour of many of the preferred food plants of *E.balteatus* (Cowgill, 1991). The structure of buckwheat and coriander inflorescences, with short corolla tubes was also suitable for foraging by Syrphidae such as *E.balteatus* which has a short proboscis (Gilbert, 1980). The open arrangement of buckwheat and coriander inflorescences was also conducive to syrphid foraging, enabling Syrphidae to walk or fly easily between inflorescences. Foraging by Syrphidae with short probosci was also recorded in other crops with very different floral structures such as borage. Syrphids were seen to climb into the deep corollae of borage flowers to reach nectar. Movement between borage flowers is assumed to be more difficult or time consuming for syrphids due to the structure of the inflorescences.

Not only did syrphids take pollen from the anthers of flowers of alternative crops, but also from pollen which had fallen onto leaves. Some pollen which had been knocked from the anthers of sunflowers, probably by bees, landed on sunflower leaves from where it was observed being taken by *E.balteatus* and *Eristalis* spp.. Holloway (1976) has previously described feeding on pollen, not taken from anthers directly, by *Eristalis tenax*. She described *E.tenax* using the front and back tarsi to comb pollen, which had collected on body hairs, into pollen particles which were transferred to pollen-retaining bristles on the front tarsi where pollen particles could be reached by the proboscis and ingested.

As well as Syrphidae, bees were seen foraging on alternative crops. Whether there was competition over floral resources was not investigated by this study. Previously, Morse (1981) showed that the bee *Bombus terrestris* Smith displaced the syrphids *Melanostoma mellinum* L. and *Toxomerus marginatus* Say when bees and syrphids were foraging on *Rosa carolina* L.. When bees were prevented from foraging on *R.carolina*, *M.mellinum* foraged 41% longer at each flower.

The preliminary study in 1991 recorded foraging at different times of the day. Cowgill (1991) recorded diurnal activity of syrphidae on agricultural land and found peak activity of *E.balteatus* before 10:00 BST. There were not enough data collected in the present study to show if feeding activity changed through the day on alternative crops. Hamakawa (1986) studied *Apis* spp. foraging on buckwheat and found maximum foraging lagged behind timing of nectar secretion. Nectar secretion

occurred from 08:00 until 12:00 and most foraging occurred between 09:00 and 13:00. Corbet (1978) and Corbet *et al.* (1979) studied diel changes in nectar in flowers visited by bumblebees. The pattern of visits by bumblebees to *Tilia europaea* L. and *Echium vulgare* L. through time, were related to changing concentration of sugar in the nectar.

When coriander was used in a large scale field trial, there was only one instance where significant differences in the mean numbers of Syrphidae caught in fields with and without coriander in boundary strips was recorded, and in that instance, more male *M.corollae* were found in the control field. However significantly more *E.balteatus* were observed in the boundary strip of F13, with coriander, than in the boundary strip of F25, but the differences in numbers of observed syrphids was not reflected in yellow trap data i.e. there was no redistribution of *E.balteatus* shown by yellow trap catches of Syrphidae. For the majority of the study, the incidence of syrphid capture was low, only after peak flowering did large numbers of Syrphidae get caught in yellow traps. Low incidence of capture early in the season could have been due to the phenology of the syrphids, the early trapping period being between generations and the high numbers caught in traps after July 22 could have been due to either recent emergence of adults or possibly migration of adults into the region, or a combination of both of these events.

If the high numbers of Syrphidae captured in traps had come from a generation that had recently emerged from crops in F13 or F25, then the eggs they emerged from would have coincided with the peak abundance of aphids in those fields, with hatching larvae abundant just after the aphid peak.

Adult Syrphidae are very mobile and feeding sites may be considerable distances from ovipositional sites (Pollard, 1971). It is possible that the 1992 experiment was conducted on too small a scale to show any redistribution effects as a result of manipulating adult food resources. Syrphidae could have fed in the coriander boundary strips of F13 and then dispersed to other fields in the area (including F25) where they were caught in yellow traps.

Significantly more aphids in F25 than in F13, at a time when syrphid numbers in yellow traps were increasing, may have also contributed to a lack of significant differences in numbers of adult female Syrphidae being caught in the two fields. The higher densities of aphids in F25 may have attracted gravid females from F13 or other surrounding fields into F25 to oviposit. Syrphid oviposition response to aphid

densities has been reported by many authors in the past including Schneider (1948), George, (1957), Chandler (1968a), Kan (1988a, b, 1989) and Cowgill *et al.* (1993b). Ruppert and Molthan (1991) reported higher numbers of adult syrphids from plots in cereal fields, where there were higher aphid densities. Gravid females would have responded to aphid densities as ovipositional stimulants, and males which had not previously mated could have been searching amongst the females for a partner to mate with.

In addition to the mobility of Syrphidae and differences in aphid densities between fields, contributing to a lack of significant differences in Syrphidae caught between fields, yellow traps in either field may not have been equally as effective at trapping syrphids. It is possible that syrphid visitation rates to yellow traps in F25 and subsequent capture efficiency could have been higher than visitation rates and capture by traps in F13, because floral resources had been cut down around F25. Proportionally more Syrphidae in F25 may have visited yellow traps anticipating that they were flowers, but were caught in the water. Syrphidae, in F13 had more (real) resources available and consequently yellow water traps may have attracted proportionally less Syrphidae than the traps than in F25.

It had been hoped that data from the 1992 experiment would illustrate an "edge effect", with more Syrphidae caught in traps closer to field boundary flowers or hedges, than in traps at greater distances, but no such effect was seen in either field. Harwood *et al.* (1992) reported an edge effect for *Eristalis* spp. in an experiment comparing numbers of Syrphidae caught in yellow traps at distances from managed and unmanaged field boundaries. Significantly more *Eristalis* spp. were caught 1m from florally rich boundaries than at greater distances, up to 100m, from the boundaries. However, in the same experiment Harwood *et al.* (1992) could not show any similar edge effect for *E.balteatus*. If any edge effect is to be illustrated, for *E.balteatus*, in future, it may be necessary to have traps extending much further into the crop, since the width of any edge effect may be variable between species, and larger for *E.balteatus* than for *Eristalis* spp.

The incidence of detecting syrphid larvae during the study was low. Only one larva was found on a marked ear. One larva on 200 ears per field, on each date, could be an underestimate of the density of syrphid larvae. The underestimate may have resulted from larvae which were present, not being recognised. Syrphid larvae are active at night in cereals (Vickerman & Sunderland, 1975; Holmes 1984). They

use crypsis as a primary defence mechanism and hide in sites which provide maximum concealment during the day (Rotheray, 1986) e.g. between spikelets on ears. Lapchin *et al.* (1987) compared three sampling techniques used to count aphid predators in cereals. The three techniques were, i) rapid searches and counts of predators in small plots, ii) proportionally longer searches and counts in larger plots, and iii) destructive sampling, where crop plants were removed and searched in the laboratory. It was found that the third technique was the most accurate method for assessing densities of syrphid larvae. However such a technique could not have been used on marked ears since temporal changes in aphids' numbers were being recorded on those ears.

No syrphid eggs were found on marked ears during the study; perhaps this reflected the low numbers of adults, and the consequent low number of gravid females caught, during most of the study. When high numbers of syrphids began to get captured in yellow traps, and bait plants were put out, syrphid eggs were not recorded on bait plants in either F13 or F25. This could have been due to gravid females not detecting the bait plants. However, such a technique has been used successfully in cereals in the past (J. Hickman, pers. comm.). Cultured aphids did not remain on the bait plants in the field. On inspection staphylinid beetles (*Tachyporus hypnorum*) were found in the pots and could have predated on the aphids. The compost the barley was growing in was also very dry when inspected and barley plants wilted in the field. Consequently, aphids could have left the barley to find alternative host plants.

There have been examples where plants have been sown in an agricultural environment and successfully influenced the distribution of Syrphidae (Lövei *et al.*, 1992; Hickman & Wratten, in prep.) on a field scale. In New Zealand, Lövei *et al.*, (1992) sowed *Phacelia tanacetifolia* (Hydrophalaceae) in strips within cereal fields and captured three to eight times as many Syrphidae in fields with flowering strips than in adjacent fields without strips. Also working in New Zealand and using *P.tanacetifolia*, White *et al.*, (1994) captured significantly more Syrphidae in plots of cabbages surrounded by flowering *P.tanacetifolia* than in plots without such flowering borders.

The next chapter goes on to investigate possible underlying mechanisms resulting in redistribution of Syrphidae about floral resources on arable land.

## CHAPTER FIVE

### FACTORS INFLUENCING THE DISTRIBUTION OF SYRPHIDAE BETWEEN RICH AND POOR FLORAL RESOURCES ON ARABLE LAND

#### INTRODUCTION

There is some evidence that floral resources can be managed to influence the distribution of Syrphidae in agricultural ecosystems (Klinger, 1987; Harwood *et al.*, 1992; Cowgill *et al.*, 1993b; Lagerlof & Wallin, 1993 and Hickman & Wratten, 1994). These investigations have shown differences in adult or larval syrphid densities between sites of high (rich) and low (poor) floral diversity in agricultural land; habitat manipulation in each of these studies resulted in higher numbers of Syrphidae being recorded at the richer, more diverse sites. Although these papers quantified syrphid numbers at floristically contrasting sites the possible mechanisms causing differences in syrphid distribution were not investigated.

Cowgill *et al.* (1993b) demonstrated that greater proportions of syrphids and a greater diversity of syrphids were observed in the regions of a cereal field that had been established as "Conservation Headlands" following guidelines by The Game Conservancy Trust (Rands & Sotherton, 1987) when compared with field margins that followed normal farm practice with respect to pesticide application. The distribution of *E. balteatus* and *M. corollae* between the two differently treated areas was significantly different and related to the total floral area of the weeds present in the study plots; more annual weeds being present in the Conservation Headland plots.

A possible reason that such investigations have been predominantly descriptive and have not examined mechanisms causing differences in syrphid distribution, is the difficulty in working with species which are highly mobile. Cowgill (1991) marked 2910 *E. balteatus* over a 23-day period and only 19 (<1% of the total marked) were ever resighted. The low rate of resightings may have been due to the dispersal of the majority of marked flies, assumed to be newly emerged, from the marking site (Cowgill, 1991).

Two possible mechanisms which would cause differences in abundance of Syrphidae at sites of floral richness are; (i) differential rates of attraction of Syrphidae into the sites; and (ii) differential affinities that Syrphidae have for sites once they are

in them. Mechanism (ii) could also be described as differential rates of retentiveness of Syrphidae by the sites. The work described in this chapter attempted to answer which of these two mechanisms were responsible for observed differences in syrphid distribution at sites of varying floral richness.

#### (i) Syrphid attraction into a florally rich site

Syrphidae could be classed as attracted to one of two sites when more individuals were recorded moving into that site than would be expected via trivial (non-migratory) movement alone. Movement into the site would be non-random, the Syrphidae being attracted to the site after detecting it from a distance. Detection may be by visual stimulus of the compound eye or by chemical stimulus of the antennae.

Larger blossoms are seen at greater distances, by pollinating insects, than are smaller blossoms (Clements & Long, 1923). This seems intuitively correct if the colour of the blossom is within the visual spectrum of the observer. However, the colour of a flower must also have sufficient contrast with its background to enable it to be discriminated at a distance (A. Dafni & P. Kevan, pers. comm.). Kugler (1943) found that the distance at which a flower visually attracts bumble bees is proportional to the flower's diameter. Collett and Land (1975) filmed the syrphid *Syritta pipiens* (L.) approaching Compositae inflorescences and by studying the film, frame by frame, suggested that the blossoms were first seen when the cruising flight path of the syrphid altered towards the inflorescences. The distance from the inflorescences at which a flight path was altered was not given. That the approach to flowers is a purely optical response was concluded by Daumann (1932, 1935; cited by Cowgill, 1991). Daumann (1932, 1935) also showed that Syrphidae can distinguish the shapes of flowers. The important characteristics a flower uses to advertise itself, enabling it to be seen by potential pollinators, include flower colour, size, shape and brightness; each of which has been widely researched, and reviews include those by Kevan (1978), Faegri & van der Pijl (1979) and Real (1983). Such floral characteristics also enables anthophiles (flower-loving organisms) to distinguish between flower species at a distance (Kevan, 1978).

Ilse (1949) investigated colour vision and colour preference in *Eristalis tenax*. He made model flowers from Ostwald Standard Colour Series paper. This paper is available in 24 different colours; each colour has four coded intensities. Different colours sharing the same intensity code have the same colour intensity and differ only

in colour. (Colour is determined by the wavelength of electromagnetic radiation, intensity is proportional to the amplitude of the wave of electromagnetic radiation). Each model flower had a sugar solution in the centre of the flower. Ilse (1949) provided flowers of the same light intensity, but of different colour, and after recording that 94% of flower visits were to yellow flowers and 6% were to blue flowers, it was concluded that *E. tenax* had colour vision. Horridge, Mimura & Tsukahara (1975) discovered photoreceptors from *E. tenax* which gave maximum response in electrophysiological experiments when stimulated by radiation at 350nm (ultra-violet) and 450nm (blue) and also concluded that *E. tenax* had colour vision. Starvenga (1979) investigated visual pigments in *E. balteatus* and also found two peaks in the action-spectra, one at 490-500nm (blue-green) and another at 450nm (blue). Electrophysiological experiments with the blowfly *Calliphora erythrocephala* (Meig.) produced action spectra which showed that specimens responded to intensity contrast (wave amplitude) rather than spectral (wavelength) contrast.

The visual acuity (resolving power) of insects is not as great as that of humans. The resolving power - that is the angle subtended by a small object which can just be determined visually (Collocott, 1971) - of *Musca domestica* L. is  $4.0^\circ$  (Mazokhin-Porshnyakov, 1969) and that of *Apis mellifera* L. about  $2.5^\circ$  (Laughlin & Horridge, 1971), whereas for humans it is  $0.84'$  (Land, 1990). There are no figures in the literature about the visual acuity of Syrphidae, but a syrphid is likely to see a blossom when the blossom subtends one ommatidial acceptance angle (M. Land, pers. comm.). An ommatidial acceptance angle is the angle at which light enters a single ommatidium in the compound eye to illicit a response. M. Land (pers. comm.) suggested that  $1^\circ$  is an appropriate figure for the acceptance angle for Syrphidae. Using trigonometry, this would imply that a flower with a diameter of 1cm is seen at 57cm, and a flower with a diameter of 10cm is detected at 5.7m by a syrphid observing the blossom en-face (at right angles to the plane of the flower's mouth) (Appendix IX). However if the acceptance angle of  $1^\circ$  is used in equations devised by Dafni & Kevan (pers. comm.) a syrphid would detect a flower with a diameter of 1cm at approximately 120cm and a 10cm diameter flower at 12.0m (Appendix X), more than twice the distances suggested by Land. Given these relatively short distances between a syrphid and a flower before the flower is observed, the hypothesis that syrphids have been attracted into a floristically rich habitat by being visually stimulated and then flying towards the site seems unlikely when distances

between flower patches on a farm can be hundreds of metres.

However, it may not be necessary for Syrphidae to be able to detect individual blossoms on a flower before being attracted towards a floral site. A mass of flowers in a patch may act as a single visual stimulus resulting in a syrphid flying towards it. Only when the syrphid approaches to within a few metres are individual blossoms then differentiated. Sih & Baltus (1987) observed patches of cat-mint (*Nepeta cataria* L.) containing different numbers of flowers, for ten-minute periods between 10:00 and 14:00. They found that as the numbers of flowers in a patch increased, so did the number of visits to the patch by pollinators such as Syrphidae, Lepidoptera and Hymenoptera. Despite these findings however, the composite visual image of patches has received little attention. If a circular patch of flowers, 5m in diameter can be viewed as a single stimulus by a syrphid with a visual acuity of  $1^\circ$  then the 5m patch will be detected at a distance of between approx. 285m (calculated from Land, Appendix IX) and 600m (calculated from Dafni & Kevan, Appendix X), if the patch is viewed en-face. Over such distances visual attractiveness may be an important factor in the mechanism of distributing syrphids on a farm scale.

However flying Syrphidae do not necessarily fly at right angles to the planar surface of flowers. Instead, the angle of approach will vary and the area of any flower patch seen by a syrphid will be less than the maximum area of the flower, but proportional to the sine angle at which the flower patch was approached.

Most studies which have considered the size of a flower with respect to its anthophile visitors, have measured the surface area of a flower, as viewed en-face, the view at right angles to the plane of the flower's mouth (Dafni, 1994). However the area of the profile of some flower species can be significantly greater than the area en-face (Dafni, 1994). Such flower species are able to advertise their presence to potential pollinators which do not view such flowers predominantly en-face.

Chemoreception by antennae, eliciting an olfactory response, could work over long distances with scent from scent glands or nectar attracting syrphids into an area. Some parasitoids are known to show an olfactory response to the flowers on which their hosts are found (Shahjahan, 1974). Pollen and nectar aromas were studied by Dobson (1987) in the laboratory. He showed that olfactory stimulus played a role in guiding foraging bees to flowers, at least at close range. The scale at which such odours work is unknown but would depend upon factors such as sensitivity of receptive antennae, wind conditions and humidity (P.Howse, pers. comm). Other



chemical stimuli include synomones (plant chemicals which affect insect behaviour). The chrysopid *Chrysoperla carnea* (van Emden & Hagen, 1976) and the coccinellid *Hippodamia* spp. are attracted to aphid colonies by chemical volatiles from aphid honeydew. It is unknown over what scale such synomones work, but pheromones from the female gypsy moth *Lymantria dispar* L. have attracted males from 3.72km (Dethier & Chadwick, 1948).

If Syrphidae are not attracted into a site, then an alternative mechanism determining syrphid distribution about floral resources could be that Syrphidae move randomly and the recorded differences in distribution at sites of differing floral abundance are due to Syrphidae remaining at sites they came across randomly for longer periods i.e. they are retained at a site.

#### (ii) Retentiveness of a floral site

Retentiveness in this context is the ability of floral resources to keep a syrphid within the vicinity of the resource. Syrphids that come across a floral resource by chance, or are drawn to a resource from very short distances would be classed as being retained there if they tended to remain in the vicinity of the resource for longer periods than they would be expected to remain there by chance alone.

Time spent by Syrphidae at floral resources would depend upon a number of abiotic and biotic factors. A syrphid must first be able to reach pollen and/or nectar from a given flower for that flower to be of nutritional value. Gilbert (1981, 1985) suggested that morphological differences between syrphid species were responsible for differences in feeding from different floral resources (see also Chapter Three). The handling time of each resource would be another factor determining retentiveness. A syrphid with a short proboscis may take longer to take a given amount of pollen and/or nectar from a flower with a deep corolla compared with a syrphid with a longer proboscis, which is able to feed more easily. The nutritional state of an individual would also be important in determining the retentiveness of an area. A starved individual is more likely to spend more time at a feeding site than a satiated individual. The quality and quantity of food resource is yet another factor to consider. Stanley & Liskens (1974) and Baker & Baker (1979) reported differences in the nutritional value of pollens from different flower species. Cowgill (1991) reported that some flower species with pollen readily available were completely ignored by foraging Syrphidae, possibly because the pollen was of poor nutritional quality. Spending

longer at a particular site may not indicate a preference for feeding at that site, but that it is a necessary requirement i.e. a syrphid at a particular feeding site within a habitat with overall poor resource availability may spend proportionally longer at the few flowers available, compared with a syrphid in a habitat with rich resources, where the individual syrphid is able to move easily between flowers.

The important difference between the mechanism of (i) attraction and (ii) retention, is that in (i) Syrphidae locate the site and move towards it, whereas in (ii) Syrphidae come across the site by chance and remain there for longer periods of time compared with alternative sites.

The mechanism causing differences in distribution could also be a combination of (i) and (ii).

Similar work which investigated host plant location by aphids and the aphids subsequent distribution among host and non-host plants was carried out by Kennedy *inter alia* in the 1940's and 1950's. Kennedy, Booth & Kershaw (1959) recorded garden observations of *Myzus persicae* and *Aphis fabae* returning to their respective overwintering host plants of peach (*Prunus persica* L) and spindle-tree (*Euonymus europaeus* L). Both aphid species were found to alight apparently indiscriminately on either tree with no significant difference between the aphid species composition on either tree. However there were significant differences in the rate of departure by each aphid species from host plants, thus *M.persicae* remained for significantly longer on peach tree leaves than on spindle-tree leaves, while the opposite was found with *A.fabae*. It was concluded that the significant difference in departure rates from host and non-host plants led to the differences in distribution of aphid species on host plants. Thus a retention mechanism was attributed as the behavioural action which caused differences in distribution of aphids.

Observing marked syrphids at sites with different floral resources available could allow the possible mechanisms determining syrphid distribution to be understood.

### Marking Techniques

Mark-release-recapture methods have previously been used to study dispersal in Diptera. Most studies have examined vectors of disease or direct crop pests. Gillies (1961) used paints and the radioisotopes  $^{32}\text{P}$  and  $^{35}\text{S}$  to mark mosquitoes *Anopheles gambiae sensu lato*. Radioisotopes were also used by Davies (1965) in

studies of *Culicoides* spp.. Fluorescent dusts were used by Brenner (1984) to stain screwworms (Calliphoridae). More recently, Hopper and Woolson (1990) used trace elements in mark-release-recapture experiments with Hymenoptera. MacLeod & Donnely (1957) compared painting, dusting and radio-isotope labelling techniques for marking Diptera. There were disadvantages with each method. Small paint spots did not always mark the chitin of the thorax, but formed a blob on fine thoracic microchaetae. The microchaetae broke off and the paint was lost as a marker. Dust marks were not retained as long as were either paint or radiolabel, and the introduction of radiolabels had to be carried out on laboratory-reared specimens (MacLeod & Donnely, 1957). If carefully applied, paints remain a simple method of marking Diptera in the field (Cowgill, 1991).

Paints have been used by Nielsen (1969) to mark syrphids in a study of population size. Holloway and McCafferey (1990) marked 1223 *Eristalis pertinax* using paints, of which 345 were resighted, in a study of habitat utilization and dispersion. In previous work which involved marking syrphids, species studied have been numerous in local patches such as woodland glades, woodland clearings or rides and although mobile, remained in discrete locations during the study. Cowgill (1991) showed that enamel paints were non-toxic to laboratory-cultured *E. balteatus* and used these paints to mark Syrphidae in cereals. Investigations were carried out to investigate habitat use, but due to low numbers of resightings, she found it was difficult to draw any meaningful conclusions.

#### Aims of this chapter

The following experiments, using marking techniques, were carried out to determine if there was an attractiveness mechanism and/or a retentiveness mechanism responsible for the differences in distribution of Syrphidae about a boundary supplemented with floral resources, compared with an existing boundary with no additional resources provided beyond that which were naturally available. The retentiveness of a site was to be assessed by observing and recording the time spent by Syrphidae at different sites, while results from yellow trapping were used in a simple mathematical expression to determine whether attractiveness also played a role in determining syrphid distribution (see Appendix XI). In addition, bait plants were used to investigate whether oviposition was enhanced at sites of greater floral richness.

## MATERIALS AND METHODS

### Description of the field site

The experiments were carried out in Field 14 (F14) a 20ha field sown to spring barley (cv. Alexis) on the Leckford Estate. The field was surrounded on all sides with hedges of *Crataegus monogyna* (Fig. 5.2). A farm track between the hedge and crop on two sides of the field provided access for farm vehicles to other parts of the estate. The hedge forming the north-eastern boundary to the field consisted of hawthorn with a grassy bottom and herbaceous layer of *Cirsium arvense*, *Convolvulus arvensis*, *Galium aparine*, *Heracleum sphondylium*, *Lapsana communis*, *Papaver rhoeas*, *Rubus fruticosus*, *Silene alba* (Mill.) Krause and *Torilis japonica* (Hout.) D.C.,

### Establishing a strip of alternative crops

Alternative crops (Chapter 4) were used to provide enhanced floral resources along one part of a field boundary. Seeds of thirteen potential alternative crops were obtained from J.K. King & Sons Ltd. (Coggeshall, Essex UK) and ADAS Bridgets (Winchester, Hampshire UK). The 1000-seed weight of each crop was measured (1000-seed weight is a common unit used to determine appropriate sowing rates) and is shown in Table 5.1 together with sowing rates used for each crop. By arrangement with the farm manager, a boundary strip (Greaves & Marshall, 1987) was established along the north-western side of the field, adjacent to the hedge, in April 1993, after the field had been sown. The outer 2m of the crop was ploughed, leaving a 2m strip between the edge of the remaining crop and the existing hedgerow. Each of the alternative crop species seed was weighed as indicated in Table 5.1 and placed into 24 plastic tubs 10cm x 4.5cm. The tubs were each fitted with a lid and sealed with sticky tape to prevent spillage and loss of seed during transit between the laboratory and field site.

The day before sowing the alternative crops, 240m of the boundary strip was cultivated by hand and raked over. Large flints were removed. Bamboo poles were used to mark 10m plots along the length of the 240m strip. The 'alternative crop' seeds were sown on 16 April 1993. Just before sowing, the tubs containing the seed mixture for each 10m length were shaken up to mix the contents in case any settling had occurred, with smaller seeds sinking to the bottom of the tub, thereby preventing an even mix of the seed when sown. The seed was broadcast by hand between the



bamboo poles marking each 10m section of the 240m strip over an area 10m x approx 0.75m, then gently raked over using a garden rake.

During May and June the strip was weeded by hand to remove mainly *Convolvulus arvensis* and *Sonchus oleraceus*.

Fig. 5.1 Field plan investigating the mechanism of syrphid distribution at sites of contrasting floral richness (summer 1993).

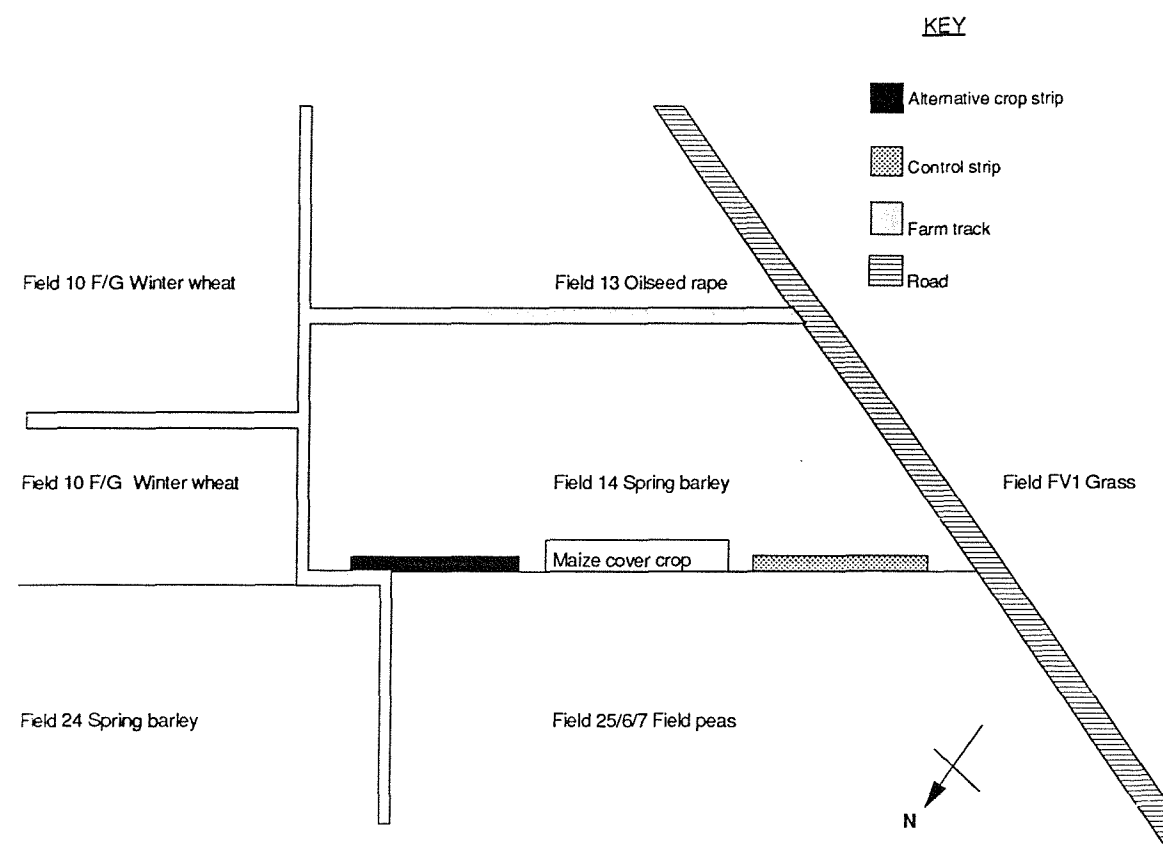


Table 5.1 : Potential alternative crops in UK agriculture sown adjacent to an existing hedgerow to provide additional floral resources. Crops whose seeds were available only in small amounts are indicated with an asterisk ( \* ). Scientific names for alternative crops are given in Chapter Four - Table 4.1

Alternative Crop	1000 seed weight(g)	Seed rate (g) per 10m	No. seeds per 10m
Amaranthus	0.94	0.45	480
Buckwheat *	26.20	3.00	115*
Calendula *	8.52	0.87	100*
Coriander	12.63	6.00	480
Echium	2.61	1.25	480
Gold of Pleasure	1.92	0.92	480
Linseed *	9.22	3.00	325*
Meadowfoam *	10.63	3.00	280*
Niger	2.04	0.98	480
Oil-seed Poppy	0.52	0.25	480
Quinoa	2.58	1.24	480
Safflower *	34.18	0.31	9*
Texsel (Abyssinian cabbage)	4.02	1.93	480

It was unknown which of the alternative crops would grow in the chalky soil or how long it would take to reach flowering of those that did grow. Very high seed rates were applied in an attempt to provide adequate floral resources for syrphids from any of the crops which did grow.

#### Measuring floral abundance

The abundance of alternative crops and hedgerow plants in flower at the enhanced site and the abundance of hedgerow plants in flower at the control site were measured on eight dates between 16 June and 11 August. Depending upon the arrangement of inflorescences on the species, plants' floral abundance was assessed either by i) counting individual inflorescences along the length of each 240m strip (such a method was used, for example, with calendula and oil-seed poppy, or ii) counting the individual inflorescences in a 10m-strip and using that number to

estimate the number in each other 10m strip making up the whole 240m strip of the control and experimental sites. Dimensions of a sample of flowers in each species were measured with a ruler and the area presented by the inflorescence estimated by approximating the shape of the flower to a circle or regular polygon. Total area presented at both strips by each species was estimated by multiplying mean area by the estimated total number of inflorescences.

#### Marking syrphids with paint

Syrphidae were first marked with enamel paints at 11:00 BST on 16 June when some of the alternative crops had started to flower. The 240m enhanced strip was slowly patrolled and any syrphids seen were approached, identified to species when possible and sexed. A fine paint brush (size 00) was used to mark individual Syrphidae with a small dot of enamel paint on their thorax or abdomen. The method had been practised previously at other fields on the Leckford Estate earlier in June, but there had been few Syrphidae in those fields. It was found that marking syrphids directly with a paintbrush was difficult. Syrphids tended to fly away when the brush approached to within a few centimetres of them. Thus it became very time consuming to mark successfully even a small number of Syrphidae.

On marking dates between 24 June and 1 July, a toothbrush was used to mark Syrphidae with a fine spray of enamel paint. A toothbrush, with stiff bristles could be charged with paint from a small tin of modelling paint (Humbrol enamel) and using thumb or forefinger, the bristles could be pushed backwards and upon release would spring forwards throwing a fine spray of paint forwards. Using such a method it was not necessary to get as close to the syrphids to mark them as had previously been required with a paint brush. Syrphidae could be marked with a toothbrush from a distance of 10cm and even during flight. A much higher marking rate was achieved using this method, but there was probably more disturbance caused to marked flies using this method. The paint spray could not be controlled and sometimes spots of paint were seen to land on the wings of syrphids. Although many syrphids were only temporarily disturbed, some did not seem to respond at all and continued to behave as they did before marking, it was not possible to guarantee behaviour was unaffected.

From 3 July, when there were higher numbers of syrphids, the paintbrush method was used again. With more Syrphidae at each site, it was found that

substantial numbers of syrphids could in fact be marked *in situ*, with practice, without disturbing them.

Syrphids were marked on the thorax or abdomen or sometimes along the leading edge of the wing. The position where a spot of paint was placed onto a syrphid depended upon the orientation of the syrphid on a flower when it was marked. After marking, a syrphid was observed for a few seconds to see if any behavioural changes were noted.

Enamel paints dried very quickly and both toothbrushes and paintbrushes had to be cleaned frequently to keep them in good order. Acrylic paints (organic pigments in a water emulsion of a polymer resin (Crawshaw, 1994)) were used after 30 June. A six-well artist's water colour pallet was used to carry paint and water. Brushes could be cleaned in the water, keeping them in good condition and paints could also be thinned with the water, preventing the paint drying up.

After syrphids had been marked, the area of the strip in which markings had been made was surveyed to count the number of Syrphidae that remained within the marking zone. Marked individuals were also sexed. As the experiment progressed, it became clear that the possibility of re-sighting a previously marked syrphid depended upon the time interval between marking and returning to the zone where marking had taken place, to carry out a survey. To reduce the time between marking and surveys, the size of the marking zones was reduced. At the start of the experiment (16 June) the entire 240m strip of alternative crops was inspected to mark any *E.balteatus*. This was reduced to a 50m strip on 6 July and to a 20m strip on 7 July, then a 10m strip on 10 July. *Episyrphus balteatus* in the hedgerow strip that had been supplemented with alternative crops were marked and surveyed on nine dates between 16 June and 13 July; *E.balteatus* in the control strip were marked and surveyed on six dates between 16 June and 11 July. Marking took place on dry, still mornings between 08:00 and 11:00, finishing up to two hours later depending on the length of strip marked. A different colour paint was used on each date syrphids were marked. Surveys of marking zones were carried out 15min to 2hr after marking during the early attempts to resight marked Syrphidae, but the time between marking and surveys was reduced to zero from 7 July when it became clear that individuals were rapidly dispersing from the marking zones.



### Marking syrphids to investigate movement within treatment sites

On four dates in July, paints were used to mark syrphids in two adjacent 10m plots within the control and enhanced treatment sites (Table 5.2). A different colour of paint was used in each 10m plot. Fifteen minutes were spent marking Syrphidae in the adjacent plots, immediately after which four consecutive 15-min surveys were carried out to record the number and colour of each marked syrphid observed within the 20m area in which they had been marked. Without the assistance of another observer, concurrent observations at both sites could not be carried out. The weather on each date of this study was similar, with dry and sunny conditions.

Table 5.2 Dates and times details for paint marked Syrphidae to show within-site movement.

Date (1993)	Site	Time of marking (BST)	Time of 4 surveys after marking
7 July	Control	08:45 - 09:00	09:00 - 10:00
7 July	Control	10:45 - 11:00	11:00 - 12:00
11 July	Control	10:45 - 11:00	11:00 - 12:00
10 July	Enhanced	10:45 - 11:00	11:00 - 12:00
13 July	Enhanced	10:00 - 10:15	10:15 - 11:15

### Watching marked individuals

As well as carrying out repeated surveys of an area containing marked Syrphidae to determine how long they were retained by a specific habitat, an alternative approach would be to watch marked individuals and measure the time spent in an observed area. Time recorded from the moment the individual was first noted to the time it left or was no longer visible in the area could be used to determine the areas "retentiveness". This approach was taken on nine occasions at the enhanced/alternative crop strip between 13 July and 2 August and on two occasions at the control strip on 14 July and 20 July. The floral resources available at the control site were very limited after 20 July. It was not possible to observe Syrphidae for any sustained period at the control site after this date as observed Syrphidae flew out of the area too quickly. Most effort was therefore used to gather

data at the alternative crop (enhanced) strip.

A 3m patch of flowers either at the alternative crop strip or control strip were chosen in which *E.balteatus* were observed. Sites were selected within the strips that had a range of flower species available and whose flowers had not completed flowering. When observing syrphids at the control site, there were so few areas with flowering herbs, where syrphids could be observed for any length of time, that regions of the control were not randomly selected, but deliberately chosen for their floral content. Thus at least some measure of duration by *E.balteatus* in the control site could be made.

The observer stood 1m out from the middle of the patch selected for study and waited until a single *E.balteatus* was seen entering the site and feeding on a flower in the patch. The syrphid was then marked with an acrylic paint. The time at which the individual was first seen was recorded. The marked syrphid would then be observed until it either moved out of the 3m patch or was lost from view within the patch. Another *E.balteatus* would then be observed in the same manner. With experience it was found that two or three marked individuals could be observed at once, especially if one or more of them was feeding on pollen from oil-seed poppy flowers, since Syrphidae tended to spend many minutes feeding at individual poppies. To successfully watch more than one syrphid at a time, it was necessary to spend 5-10s watching each in rotation. The observer remained as motionless as possible during the observation periods.

#### Trapping syrphids in water traps

Fluorescent yellow painted flowerpot saucers (as described in Chapter Four) each containing a 500ml water and detergent solution were used to trap syrphids at the two sites between 23 June and 11 August. Eight such traps were set up in both the enhanced strip and control strip. The first trap in each strip was 20m from the start of the strip and then one trap was placed every 25m along the length of the strip. Each yellow trap was placed in a 30cm diameter plastic dish fixed to a 2.5cm x 2.5cm x 120cm wooden stake by a metal wood-screw and washer. The wooden stakes had been fixed into the ground using a sledgehammer.

Water traps were first filled on 23 June and emptied once a week until 11 August. When emptying the traps on the first two dates, it was possible to remove Syrphidae from the water with fine forceps and place them into labelled specimen

tubes containing alcohol, without a great time interval between examining the first and last traps, because of the low number of syrphids caught. However after 7 July the number of syrphids in each trap was much higher and to prevent large time intervals between emptying traps, trap contents were poured into labelled white plastic beakers with lids being attached and syrphids stored until sorting in the laboratory the next day.

Contents from yellow water traps in the white beakers were returned to the laboratory where they were emptied into a white plastic tray 45cm x 35cm x 8cm. Syrphids were picked out using fine forceps and transferred into specimen tubes containing 70% alcohol. They were identified to species following Stubbs & Falk (1983) and sexed.

#### Bait Plants

When gravid *E.balteatus* had begun to be caught in the yellow traps, bait plants, as used during the summer of 1992 and described in Chapter Four, were used. One pot of barley (cv. Atom) at GS 11, infested with laboratory cultures of *S.avenae* was placed at the bottom of each of three yellow traps in the enhanced and control sites on 21 July. On 28 July the bait plants were collected from F14. The leaves of bait plants from each pot were cut at soil level, and the leaves placed into plastic bags, one bag per pot, with pencil written paper labels in each bag. The bags were returned to the laboratory and emptied into a white plastic tray 45cm x 35cm x 8cm. The leaves of bait plants were examined and the number of adult and nymphal aphids, syrphid eggs and syrphid larvae from each bag were recorded. It was not possible to determine the number of aphids on individual leaves because aphids were found loose in the plastic bags and in the white tray.

A second set of bait plants were set out by the yellow traps in F14 on 28 July and collected on 3 August, using the same protocol.

## **RESULTS**

#### Abundance of flowers

Of the thirteen species of alternative crops sown by the hedge at the enhanced floral strip, nine species germinated and eight flowered during the study. The germination success was generally poor. Linseed, meadowfoam, niger and quinoa did not germinate. Amaranthus germinated in some of the plots but did not

reach flowering during the study. Fig 5.2 shows the change in composition of flowers at the enhanced (alternative crops) strip.

The hawthorn hedgerow consisted of a number of species of herbs which came into flower at different times during the period of the study. The change in composition of flowers and the relative abundance of each, at the control site, is shown in Fig 5.3.

#### Syrphid foraging on alternative crops

Of the eight alternative crops which flowered during the study, all were foraged upon to some extent by at least one syrphid genus, and more often by a range of syrphid species (Table 5.3). Only *E.balteatus* was recorded foraging on all alternative crops which flowered. The crops which were recorded being foraged upon by all of the genera in Table 5.3 (buckwheat, coriander, gold of pleasure and texsel) had small (<4mm diameter) white or yellow flowers from which anthers and pollen were easily accessible.

Table 5.3 Syrphidae recorded foraging on alternative crops in flower during the study.

Crop	<i>Episyrphus balteatus</i> *	<i>Metasyrphus corollae</i> *	<i>Syrphus</i> spp. *	<i>Eristalis</i> spp.	<i>Syritta pipiens</i>
Buckwheat	✓	✓	✓	✓	✓
Calendula	✓	○	○	○	○
Coriander	✓	✓	✓	✓	✓
Echium	✓	○	✓	○	○
Gold of Pleasure	✓	✓	✓	✓	✓
Oil-seed poppy	✓	✓	○	○	○
Safflower	✓	○	○	✓	○
Texsel	✓	✓	✓	✓	✓

Key: \* = Syrphidae with aphidophagous larvae ✓ = observed foraging on flower of crop, ○ = not observed foraging on flower of crop,

Fig 5.2 Percentage composition of flora at enhanced strip

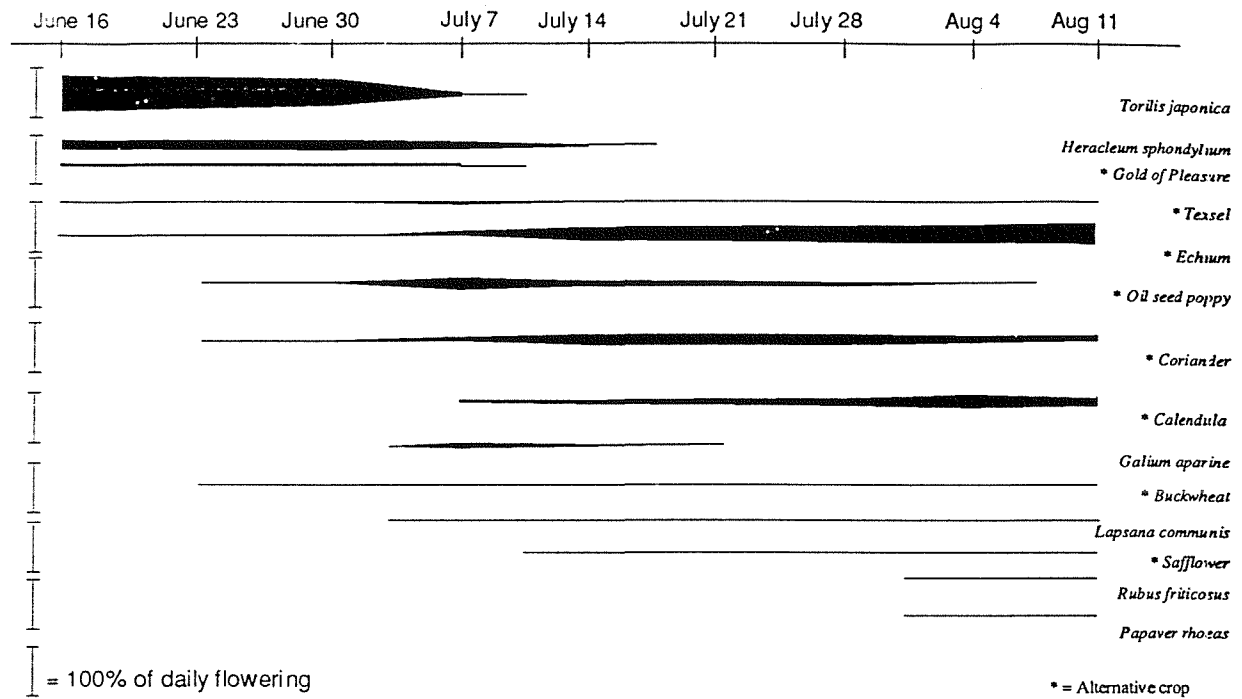
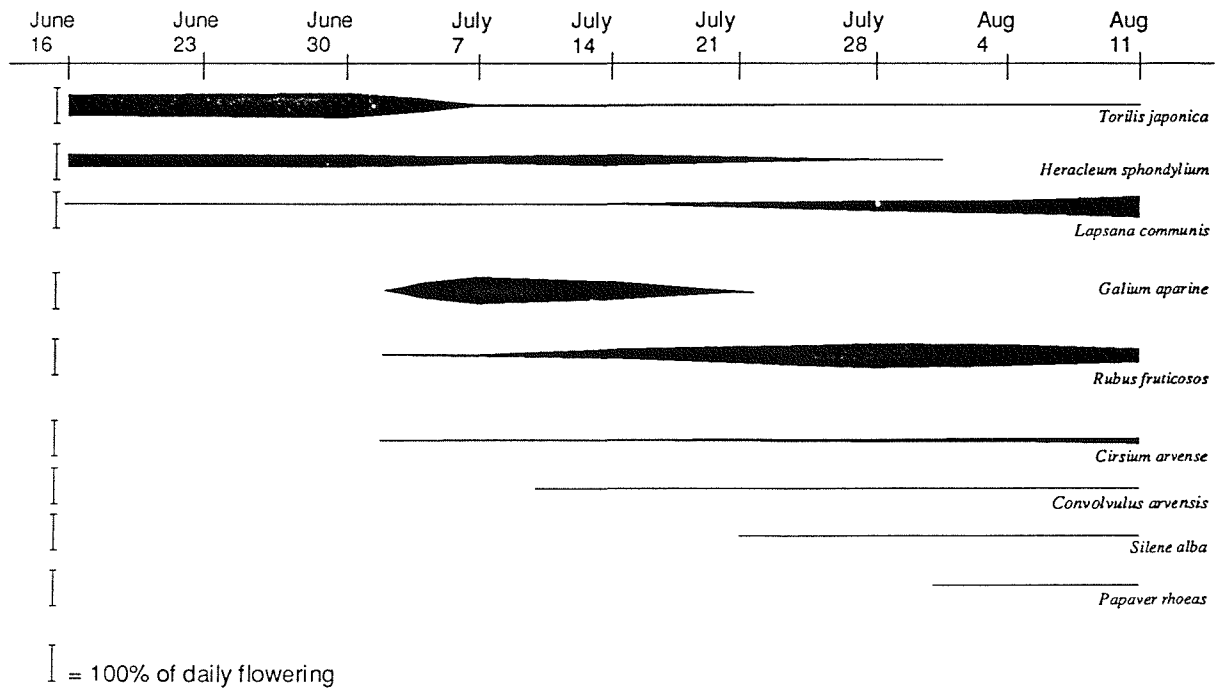


Fig 5.3 Percentage composition of flora at the control strip



### Marking Syrphidae with paint

During the first few weeks of the study (16 June - 7 July), there were relatively few syrphids in F14 and attempts were made to mark any species encountered at either the control or enhanced strip. From 7 July, only *E.balteatus* was marked when this species became the most abundant syrphid at either site. When there were low numbers of Syrphidae, the number seen during marking was recorded (Table 5.4), but when the density of Syrphidae increased (from 30 June) it was not possible to mark and count Syrphidae at the same time.

Marking with paints did not appear to affect the behaviour of the majority of Syrphidae. There were a few occasions early in the experiment when spots of paint dried and stuck an individual's wings together, or stuck wings to the abdomen. Any Syrphidae which were seen to have been adversely affected by marking were not recorded.

Table 5.4 Numbers of Syrphidae seen and successfully marked at the control and enhanced site, and numbers seen during later surveys (16 June - 3 July).

Date	Site	No. Syrphidae seen while marking		Number marked		Number of Syrphidae seen in survey		Number of marked Syrphidae	
		E.b.	other	E.b.	other	E.b.	other	E.b.	other
Jn16	Con	24	2	7	1	0	0	0	0
Jn16	Enh	38	19	9	9	33	13	0	1
Jn17	Enh	64	93	42	55	61	94	4	13
Jn24	Enh	3	2	2	2	0	0	0	0
Jn24	Con	5	3	4	3	0	0	0	0
Jn30	Con	-	-	39	-	13	-	2	-
Jy1	Enh	-	-	32	-	-	-	4	-
Jy3	Enh	-	-	82	-	92	-	3	-
Jy3*	Enh					71	-	2	-

Key : E.b. = *E.balteatus*, other = other syrphid species, Enh = enhanced strip, Con = control strip, - = not recorded, \* = second survey, no additional markings made.

Table 5.4 indicates that low numbers of marked Syrphidae were seen during the surveys in June and the beginning of July, when the entire 240m length of both control

and enhanced strips was surveyed. The low numbers of marked Syrphidae which were resighted led to a change in the protocol and more frequent surveys of shorter plot lengths. This resulted in many more marked Syrphidae being resighted. Between 16 June and 11 July, 70 marked male and 34 marked female *E.balteatus* were resighted after marking during six surveys at the control site. 232 marked male and 130 marked female *E.balteatus* were sighted at the enhanced site during nine surveys between 16 June and 13 July.

The rates of decline in percentage of marked male and female *E.balteatus* from surveyed plots at the control and enhanced site are shown in Figs 5.4 and 5.5. The fitted exponential lines in Figs 5.4 and 5.5 are described by the general formula,

$$Y = Ae^{bx}$$

Such curves can be transformed to straight lines using natural logarithms (base e). Thus,

$$\log_e Y = \log_e A + bx$$

Figs. 5.6 and 5.7 show the transformed data points from Figs 5.4 and 5.5, with fitted linear regressions. Each regression was forced through the point (0, 4.61) which corresponds to 100% marked Syrphidae at time zero. Table 5.5 gives the equations of the model 1 regressions from Figs 5.6 and 5.7.

Fig 5.4 Percentage of marked *E.balteatus* (male) resighted at the enhanced and control site in surveys after marking (with fitted exponential regressions).

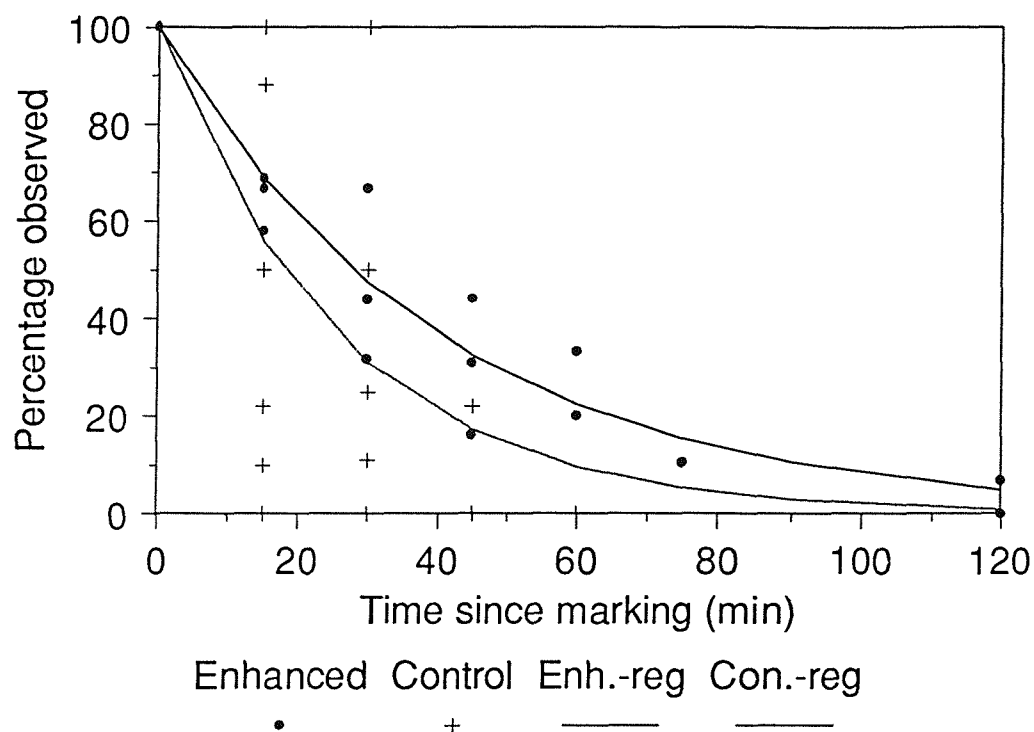


Fig 5.5 Percentage of marked *E.balteatus* (female) resighted at the enhanced and control site in surveys after marking (with fitted exponential regressions).

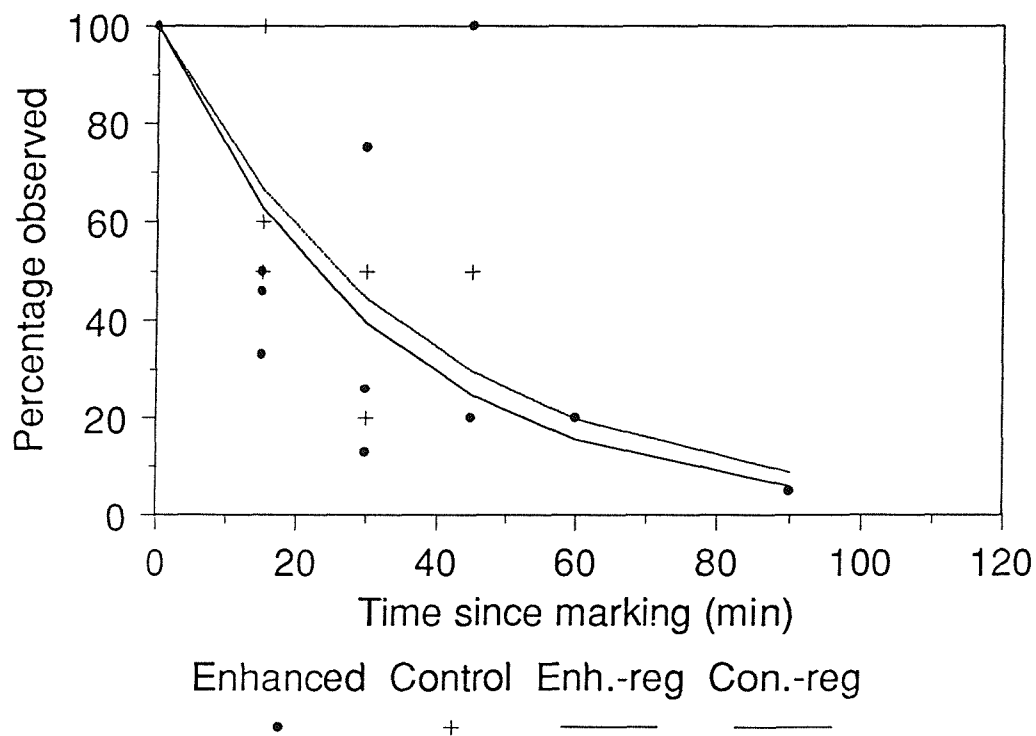




Fig 5.6 Log e percentage of marked male *E.balteatus* remaining and recorded in surveys at two different sites. (Regression lines through 4.61 (100%) at time zero are fitted).

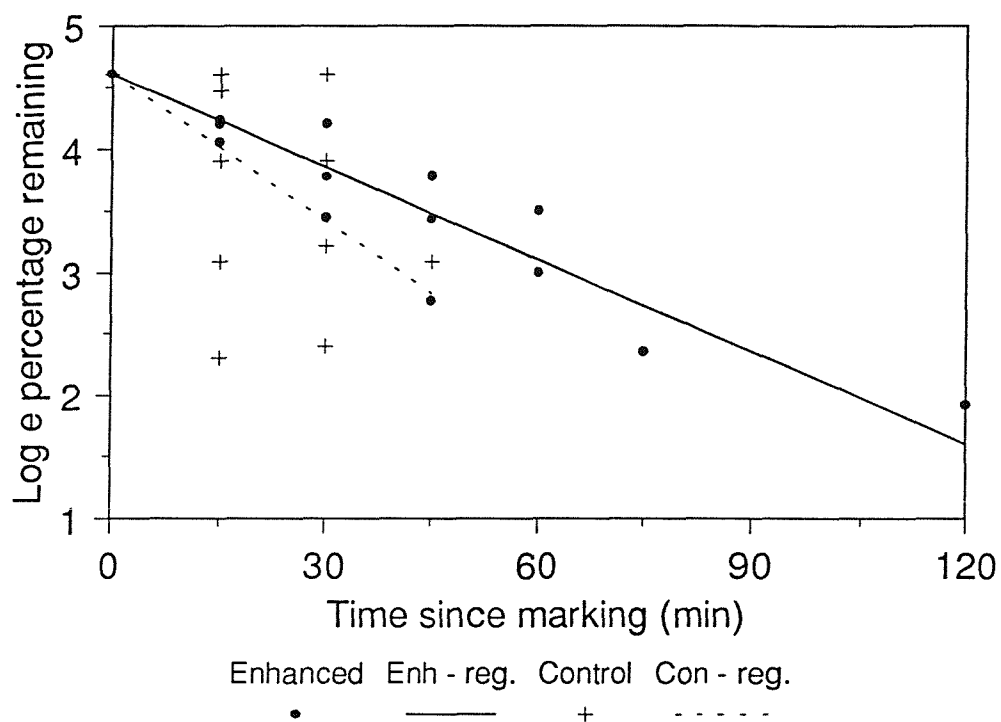


Fig 5.7 Log e percentage of marked female *E.balteatus* remaining and recorded in surveys at two different sites. (Regression lines through 4.61 (100%) at time zero are fitted).

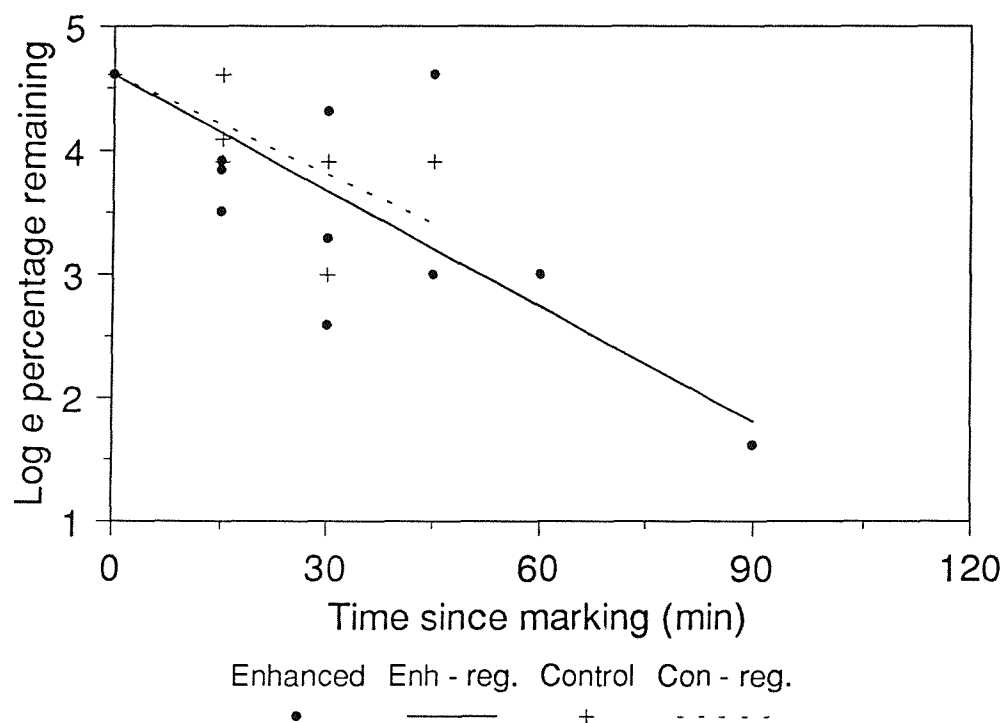


Table 5.5 Regression equations illustrating dispersal of marked male and female *E.balteatus* from sites of differing floral richness. (See Figs 5.6 and 5.7).

Site	Sex	Equation	SE of Y est	SE of X coeff	r <sup>2</sup>	DF
Enhanced	Male	$y = -0.025 x + 4.61$	0.27	0.001	0.89	17
Control	Male	$y = -0.039 x + 4.61$	0.69	0.008	0.34	14
Enhanced	Female	$y = -0.031 x + 4.61$	0.51	0.004	0.68	16
Control	Female	$y = -0.027 x + 4.61$	0.31	0.004	0.57	12

There were no significant differences between the rates at which male *E.balteatus* left the control site compared with the enhanced site (comparison of the gradients of regression lines;  $t = 1.69$ ,  $DF = 31$ , NS); or the rate at which female *E.balteatus* left the control and enhanced sites ( $t = 0.83$ ,  $DF = 28$ , NS).

Comparing dispersal rates from the same sites between sexes, there were no significant differences between the rates at which marked male and female *E.balteatus* were recorded leaving the control site ( $t = 1.37$ ,  $DF = 26$ , NS) or the enhanced site ( $t = 1.61$ ,  $DF = 33$ , NS).

#### Marking *E.balteatus* to investigate movement within each strip

Using two colours of paint to mark *E.balteatus* in adjacent 10m plots, *E.balteatus* was recorded moving between plots at both the control and enhanced sites. During three surveys on 7 July and 11 July at the control strip (Table 5.2), 50 marked *E.balteatus* were recorded in two adjacent plots, 40 of which were recorded in plots where they had originally been marked. (These surveys consisted of four 15-min "sub-surveys", during which double counting of *E.balteatus* would occur, if the same individual was observed during different 15-min "sub-surveys" in either of the adjacent 10m plots).

During two surveys at the enhanced site on 10 July and 13 July, 119 marked *E.balteatus* were recorded, 110 of which were observed in the plots in which they had originally been marked.

The percentage of observed marked individuals remaining in adjacent plots during each sub-survey is shown in Figs 5.8 and 5.9 (solid lines). The percentage of

observed individuals remaining in the plot where they were originally marked, was higher and lasted over a longer period at the enhanced site, than at the control site, implying that marked *E.balteatus* moved at a slower rate between 10m plots along the length of the enhanced site. Comparison of regression lines however, indicated that the difference in this rate was not significant ( $t=1.54$ ,  $DF=16$ , NS).

The movement of marked individuals into adjacent 10m plots is also shown in Figs 5.8 and 5.9 (broken lines). The gradient for movement between plots at the control site was steeper than for the enhanced site, implying that marked *E.balteatus* moved more quickly into adjacent 10m plots at the control site than at the enhanced site. However comparison of the gradients of the regression lines showed that the movement rate between plots was not significantly different ( $t=1.62$ ,  $DF=16$ , NS). It is recognised that the regression lines within Figs 5.8 or 5.9 are not independent, but sum to 100.

#### Watching marked individuals

Male and female *E.balteatus* were watched at both the enhanced and control sites. Observations on 74 males and 45 females were recorded during nine periods on seven dates between 13 July and 2 August. Eighteen males and 19 females were observed at the control site on two dates, 14 July and 20 July. The number of observation days at the control site was less than at the enhanced site because after 22 July there were very few herbs in flower at the control site, on which Syrphidae could feed. The abundance of available floral resources at the control and enhanced site changed throughout the study as previously shown in Figs 5.2 and 5.3. Although syrphids were seen flying near the hedgerow or resting on vegetation in the hedgerow, they could not be successfully observed feeding in a small area of the control site. More effort was therefore put into collecting data at the enhanced site, where flowers were abundant and syrphids could be observed for longer periods.

The time spent by marked individuals within the study area at the two sites were classified into 11 time periods, 0, 2, 4, 6, 8, 10, 15, 30, 45, 60 and 120+ minutes. The data were sorted by date and grouped into the proportions of each sex that remained in the study area for periods of time within the time categories. Thus a decline in proportions of each sex would be seen through time. This would represent the dispersal rate from the 3m study areas for each sex. Figs 5.10 and 5.11 show the raw data from each site with fitted exponential lines of the percentage of

each sex remaining within the study area. Figs 5.12 and 5.13 show the transformed data points from Figs 5.10 and 5.11 with fitted model 1 regression lines. Each regression has been forced through the point (0, 4.61) which corresponds to 100% of the marked Syrphidae in each site at time zero.

Fig 5.8 Percentage of *E. balteatus* sighted on each of three surveys remaining within a 10m plot or moving into an adjacent 10m plot after marking in the control strip.

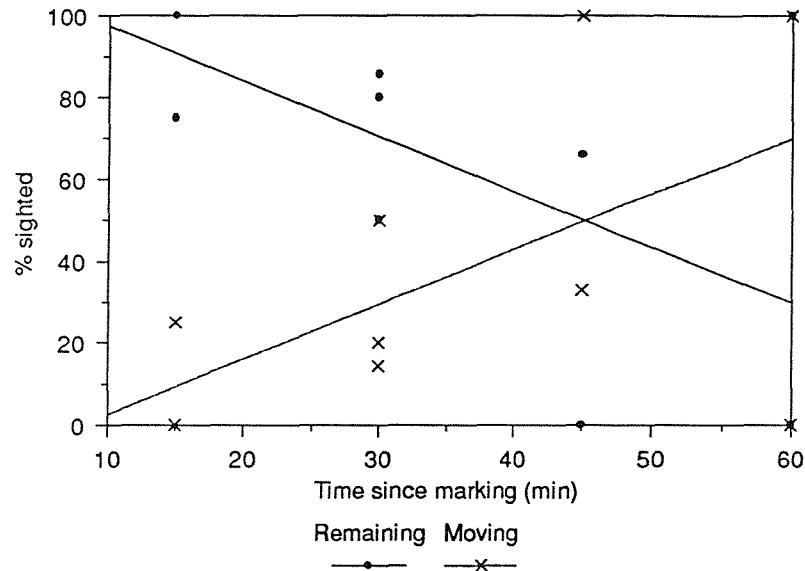


Fig 5.9 Percentage of *E. balteatus* sighted on two surveys remaining within a 10m plot or moving into an adjacent 10m plot after marking in the enhanced strip.

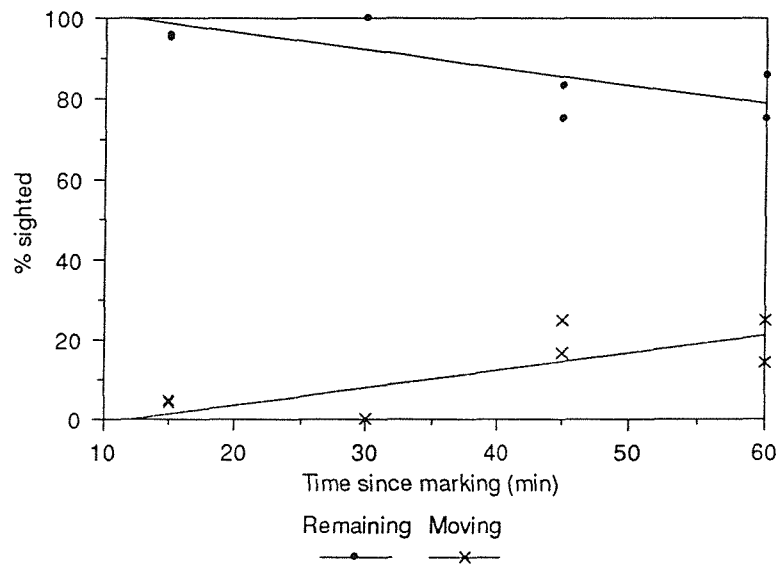


Fig 5.10 Dispersal of observed *E.balteatus* (♂) from control and enhanced sites.

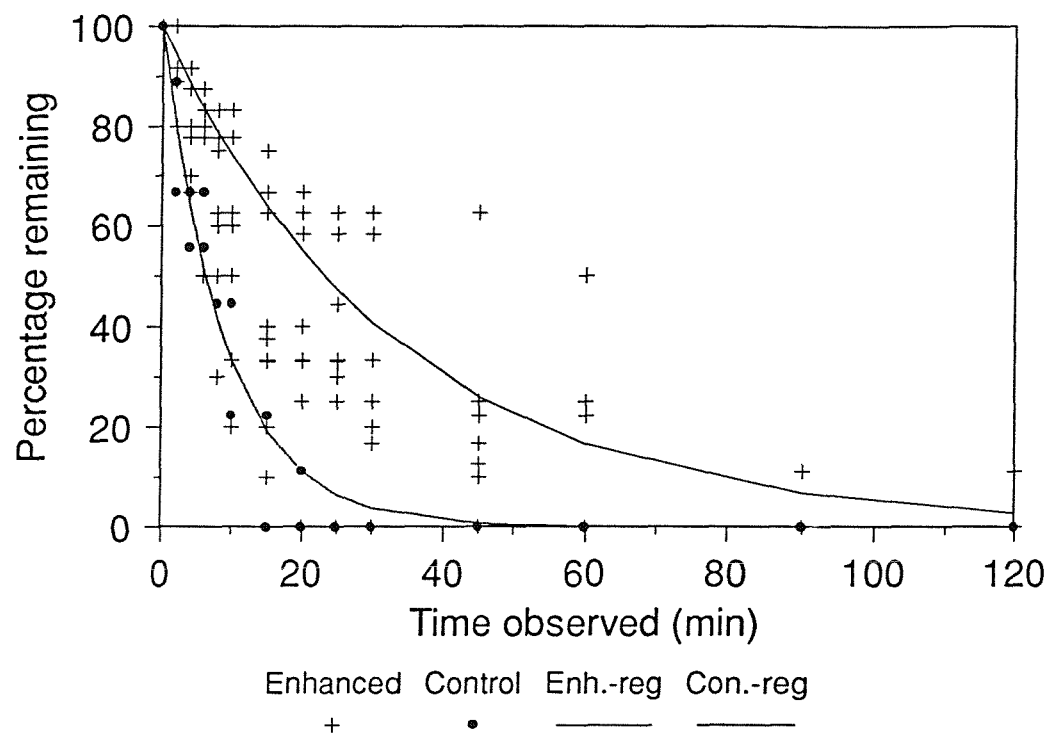


Fig 5.11 Dispersal of observed *E.balteatus* (♀) from control and enhanced sites.

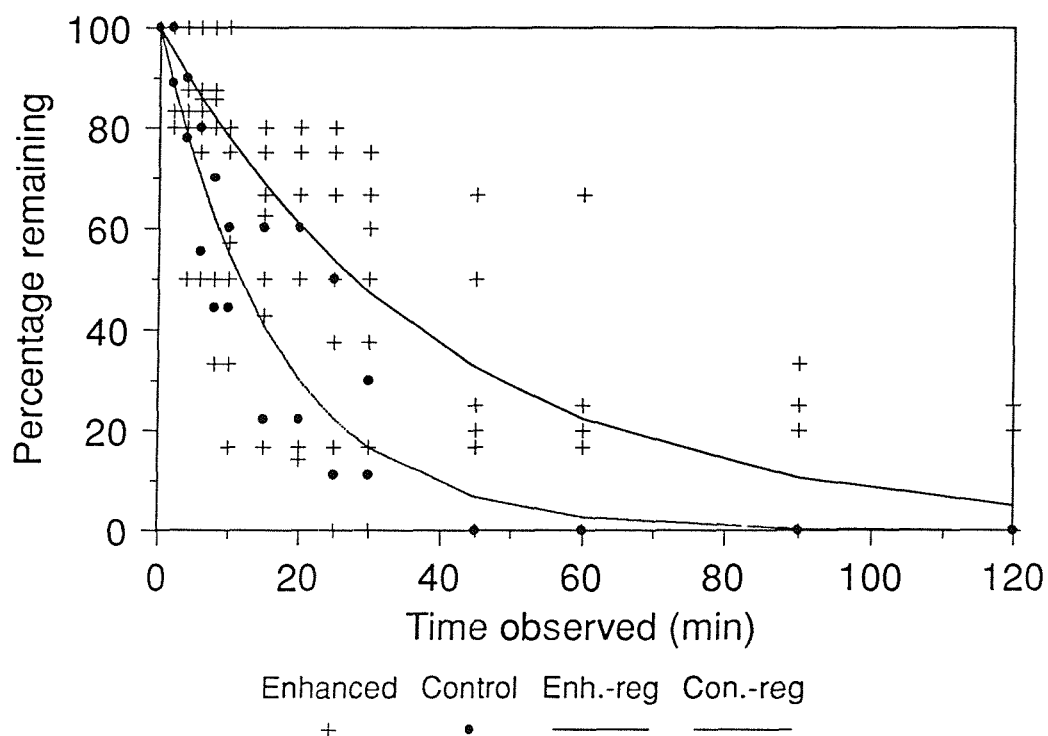


Fig 5.12 Dispersal rates of observed marked *E.balteatus* (male) from control and enhanced sites (Regression lines fitted through 4.61 (100%) at time zero are shown).

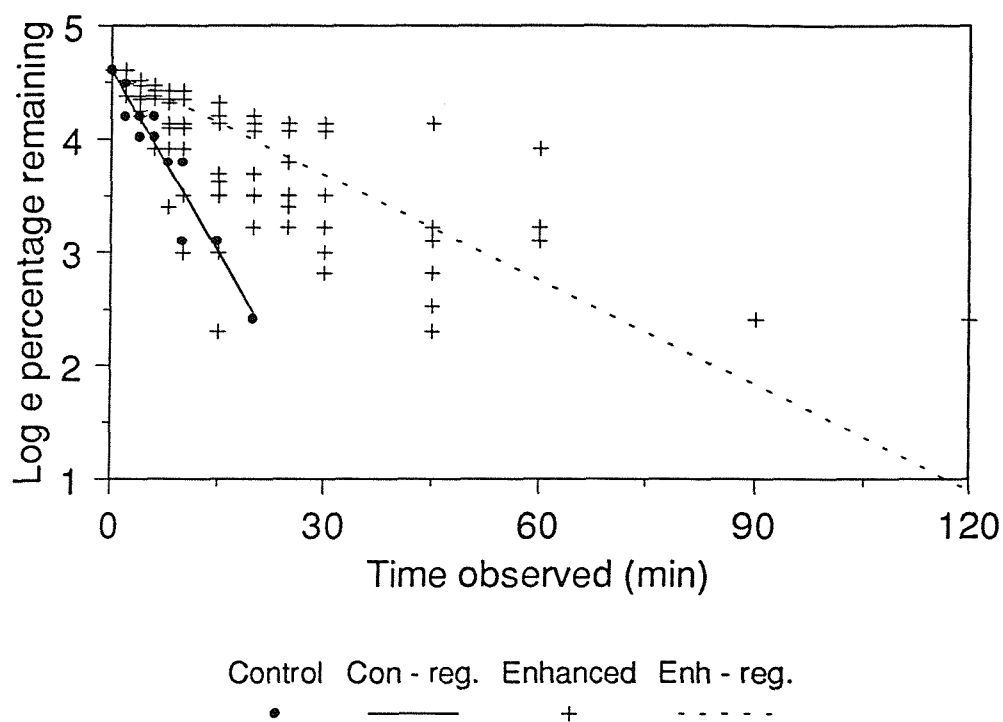
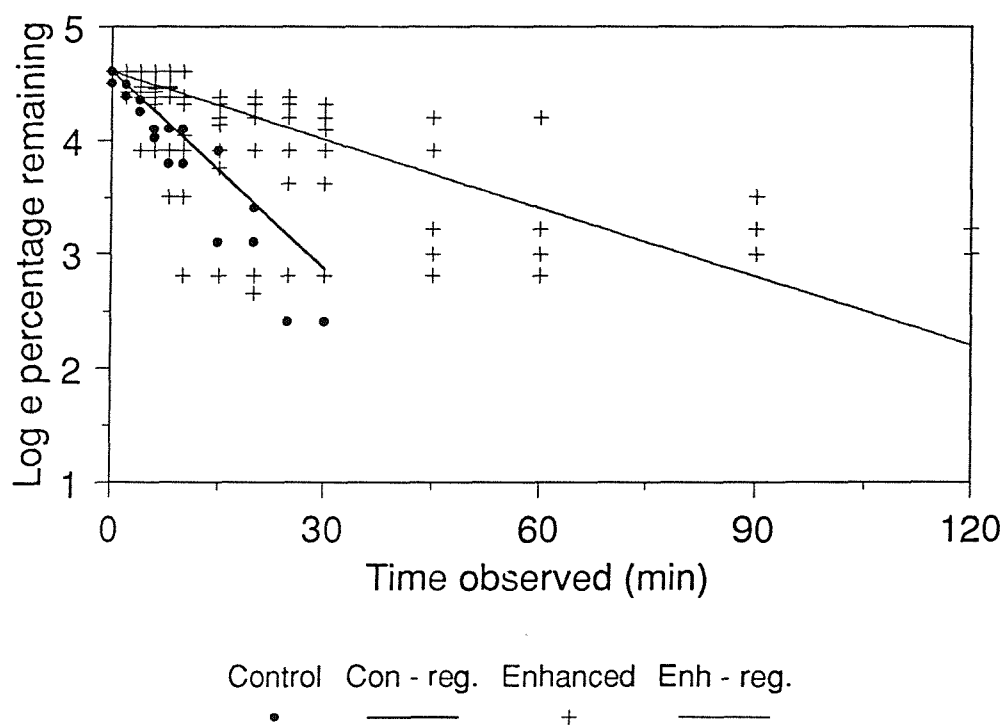


Fig 5.13 Dispersal rates of observed marked *E.balteatus* (female) from control and enhanced sites. (Regression lines fitted through 4.61 (100%) at time zero are shown).



The equations of the regression lines in Figs 5.12 and 5.13 are given in Table 5.6. The gradients of the regression lines were tested for significant differences between treatment sites, within sexes; males,  $t = 13.22$ ,  $DF = 106$ ,  $P < 0.01$ ; females  $t = 6.32$ ,  $DF = 120$ ,  $P < 0.01$ . These results indicate that marked *E. balteatus* left the two sites at highly significantly different rates. Inspection of Figs 5.10 and 5.11 shows that both males and females were slower to leave from the enhanced site than from the control site (the gradients for the enhanced site were less steep for both sexes). When differences in the rate of dispersal from the same sites were examined between sexes, highly significant differences were found; enhanced site,  $t = 4.31$ ,  $DF = 196$ ,  $P < 0.01$ ; control site,  $t = 6.19$ ,  $DF = 30$ ,  $P < 0.01$ . In both cases female *E. balteatus* dispersed at a slower rate than males from the same site.

Table 5.6 Regression equations illustrating dispersal of observed male and female *E. balteatus* from sites of differing floral richness. (See Figs 5.12 and 5.13)

Site	Sex	Equation	SE of Y est	SE of X coeff	$r^2$	DF
Enhanced	Male	$y = -0.03 x + 4.61$	0.49	0.002	0.38	94
Control	Male	$y = -0.11 x + 4.61$	0.18	0.005	0.92	12
Enhanced	Female	$y = -0.02 x + 4.61$	0.56	0.002	0.20	102
Control	Female	$y = -0.06 x + 4.61$	0.40	0.006	0.66	18

#### Yellow traps

Yellow traps caught Araneae, Coleoptera, Diptera, Heteroptera, Hymenoptera and Lepidoptera. Only data concerning Syrphidae are presented.

During 64 days of trapping, a total of 3503 syrphids were caught in eight yellow traps at the florally enhanced site (2252 at the unmanaged control site). Sixteen species and nine genera were represented at the enhanced floral site. *Episyrphus balteatus* comprised 71.8% of all syrphids at this site. Seventeen species and 11 genera were found at the control site with *E. balteatus* comprising 83.3% of all syrphids.

Figures 5.14, 5.15 and 5.16 show the mean number of male and female *E. balteatus*, *M. corollae* and *Eristalis* spp. caught in yellow traps on each date of trap emptying at each site with 95% confidence limits given for males and females of each genus at the enhanced site. The three genera combined made up 95.3% of all syrphids at the enhanced site and 95.0% of syrphids at the control site.

Fig 5.14 Mean number of ♂ and ♀ *E.balteaus* in yellow traps at enhanced and control sites.

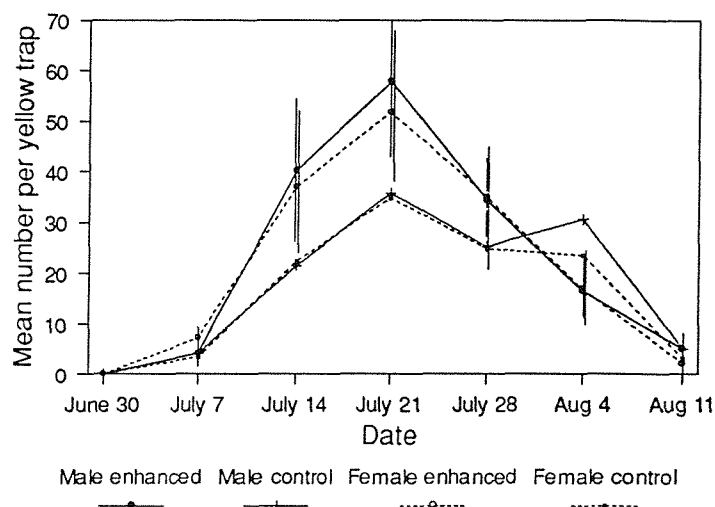


Fig 5.15 Mean number of ♂ and ♀ *M.corollae* in yellow traps at enhanced and control sites.

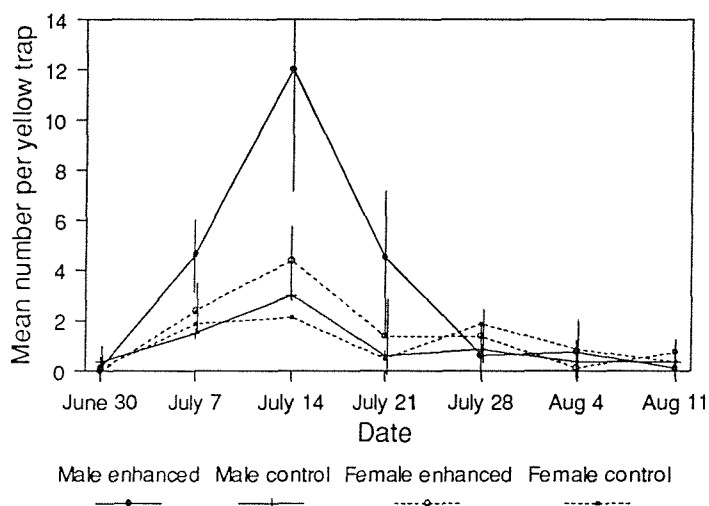
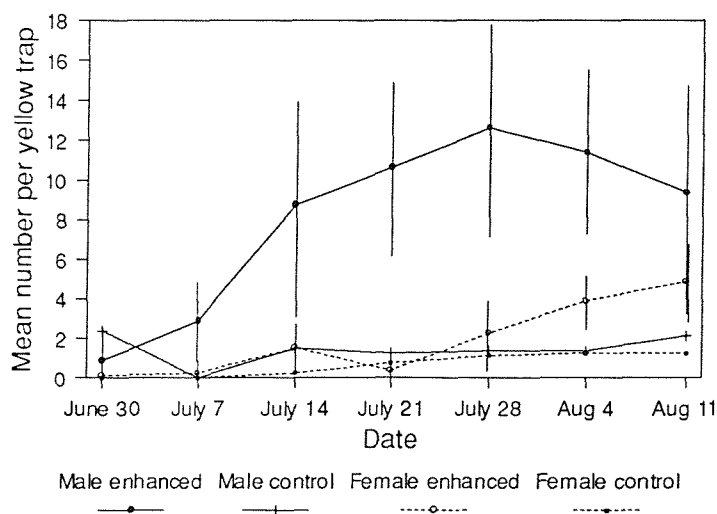


Fig 5.16 Mean number of ♂ and ♀ *Eristalis* spp. in yellow traps at enhanced and control sites.





One way ANOVA of each genus, separating the sexes, shows that there were periods during the study when there were significantly more males and females of each species caught at the enhanced site (Tables 5.7 - 5.9). Timing of the significant differences varied between genera and between sexes within genera, although during the period 7 July to 14 July, there were consistently more of all three genera and of both sexes at the enhanced site.

Table 5.7: Total number of male and female *E.balteatus* in eight yellow water traps from a) the enhanced hedgerow and b) the control hedgerow, with ANOVA results.

Date	Sex	No. at enriched site (a)	No. at control site (b)	Ratio numbers at a:b	ANOVA F-ratio	<i>P</i>
30 June	Male	0	1	0:1	-	-
	Female	0	1	0:1	-	-
7 July	Male	57	33	1.73:1	3.04	NS
	Female	58	27	2.15:1	8.13	<0.05
14 July	Male	321	172	1.87:1	6.14	<0.05
	Female	296	179	1.65:1	4.93	<0.05
21 July	Male	462	286	1.62:1	7.69	<0.05
	Female	414	278	1.49:1	3.48	NS
28 July	Male	275	202	1.36:1	2.53	NS
	Female	280	199	1.41:1	2.92	NS
4 Aug	Male	135	245	0.55:1	3.56	NS
	Female	134	188	0.71:1	3.20	NS
11 Aug	Male	40	40	1:1	0.00	NS
	Female	17	25	0.68:1	0.46	NS

NS = No significant difference at  $P < 0.05$  in the mean number of males or females caught at each site (one way ANOVA with site a, or b, as the factor). DF = 1 and 15 in each case. - = ANOVA not performed.

Table 5.8: Total numbers of male and female *M.corollae* caught in yellow water traps at a florally enhanced site and an unmanaged site, with ANOVA results

Date	Sex	No. at enriched site (a)	No. at control site (b)	ANOVA F-ratio	<i>P</i>
30 June	Male	1	3	-	-
	Female	0	1	-	-
7 July	Male	37	12	17.16	< 0.001
	Female	19	15	0.95	NS
14 July	Male	96	24	11.96	< 0.05
	Female	35	17	6.42	< 0.05
21 July	Male	36	5	8.25	< 0.05
	Female	11	4	3.80	NS
28 July	Male	5	7	0.17	NS
	Female	11	15	0.17	NS
4 Aug	Male	6	3	-	-
	Female	1	7	-	-
11 Aug	Male	1	3	-	-
	Female	6	3	-	-

NS = No significant difference ( $P > 0.05$ ) in the mean number of males or females caught at each site (one way ANOVA with site a, or b, as the factor). DF = 1 and 15 in each case. - = ANOVA not performed.

Table 5.9: Total numbers of *Eristalis* spp. caught in yellow water traps at a florally enriched site and an unmanaged site, with ANOVA results

Date	Sex	No. at enriched site (a)	No. at control site (b)	ANOVA F-ratio	<i>P</i>
30 June	Male	7	19	2.70	NS
	Female	1	0	-	-
7 July	Male	23	0	-	-
	Female	2	0	-	-
14 July	Male	70	12	9.70	< 0.05
	Female	12	2	7.61	< 0.05
21 July	Male	85	10	22.64	< 0.05
	Female	3	6	0.69	NS
28 July	Male	101	11	24.99	< 0.001
	Female	18	9	1.60	NS
4 Aug	Male	91	11	31.15	< 0.001
	Female	31	10	10.61	< 0.01
11 Aug	Male	75	17	8.49	< 0.05
	Female	39	10	14.72	< 0.01

NS = No significant difference ( $P > 0.05$ ) in the mean number of males or females caught at each site (one way ANOVA with site a, or b, as the factor). DF = 1 and 15 in each case. - = ANOVA not performed.

#### Yellow trap ratios and dispersal rates

The number of Syrphidae caught in yellow traps at both the experimental strips would be related to the number of Syrphidae, and the time they spent, in the vicinity of the strips. If equal numbers of Syrphidae spent equal lengths of time at the strips, then one would expect that this would be reflected in approximately equal yellow trap catches. Further, the ratio of time spent at site A to the time spent at site B by Syrphidae should be approximately equal to the ratio of numbers of Syrphidae caught in traps at site A compared to numbers caught at site B (see Appendix XI).

During the course of the experiment, there were three dates, representing 13

trapping days, when there were significant differences in the numbers of either male or female *E.balteatus* at the control and enhanced sites; in each case there were more individuals caught at the enhanced strip.

If the ratios of dispersal rates (as an indication of time spent at each site) are compared with ratios of trap catches at each site, then a higher ratio of trap catches at the enhanced site indicates that i) there are more individuals at the enhanced site or, ii) that the same number of Syrphidae spend substantially longer at the enhanced site or iii) that Syrphidae are being attracted into the enhanced site from a distance (Appendix XI).

Table 5.10 Comparing the ratio of trap catches and dispersal rates for male and female *E.balteatus* at the enhanced and control strips (see also Appendix XI).

Period	Sex	Ratio of total yellow trap catches (Enhanced:Control) ( $N_t / N_c$ )	Ratio of dispersal gradients (Control:Enhanced) ( $\lambda_c / \lambda_t$ )
June 30 - July 13	Male	1.68:1	1.56:1
	Female	2.07:1	0.84:1
July 14 - Aug 2	Male	1.60:1	3.45:1
	Female	1.51:1	2.85:1

For both male and female *E.balteatus*, during the first period, 30 June - 13 July, the ratio of yellow trap catches at each site was higher than the ratio of dispersal rates at each site (Table 5.10). As Appendix XI shows, it follows that between 30 June and 13 July, males and females did not move randomly into the two sites, but moved in greater numbers into the enhanced site, perhaps by visual attraction.

During the second period, 14 July - 2 August, the ratio of yellow trap catches for both sexes is higher than the ratio of dispersal gradients and the Null hypothesis that the rate of immigration to both sites is the same, cannot be rejected. The difference in numbers of *E.balteatus* caught at either site is due to individuals' spending longer at the enhanced site; hence they are more likely to be captured by yellow traps.

### Gravid females and bait plants

There was a combined total of 46 gravid *E.balteatus* caught in yellow traps from both sites during the study (*M.corollae* combined total = 28, all other species combined total = 31). There were no significant differences in the proportions of gravid *E.balteatus* or *M.corollae* in yellow traps at either site ( $t=1.49$ ,  $DF=12$ , NS and  $t=1.89$ ,  $DF=12$ , NS respectively ( $\sqrt{\text{arcsine transformed proportions}}$ )).

Table 5.11 shows the number of aphids, syrphid eggs and larvae found on bait plants between July 21 and August 11. There were significantly fewer apterous aphids on bait plants during the first period, when no eggs were found on bait plants at either site, than during the second week ( $t=2.71$ ,  $DF=10$ ,  $P<0.05$ ;  $\log_{10} x+1$  transformed data).

Table 5.11 The number of alate and apterous aphids, syrphid eggs and larvae from pots of bait plants in F14 at control and enhanced sites. Bait plants were in F14 between July 21 and July 28 (Period 1) and July 28 and August 3 (Period 2).

Period	Site / trap	Aphids		Syrphidae	
		Alate	Apterous	Eggs	Larvae
1	Control 1	1	4	0	1
1	Control 2	2	24	0	4
1	Control 3	1	15	0	0
1	Enhanced 1	5	26	0	5
1	Enhanced 2	1	24	0	1
1	Enhanced 3	3	59	0	0
2	Control 1	3	113	4	0
2	Control 2	5	211	0	0
2	Control 3	3	164	4	0
2	Enhanced 1	1	21	0	2
2	Enhanced 2	1	27	0	0
2	Enhanced 3	2	163	6	0

## DISCUSSION

There were six flowering species of the hedgerow common to both control and enhanced sites. These were fed upon by Syrphidae at both sites. However, the majority of Syrphidae at the enhanced site were recorded foraging on alternative crops. Most alternative crops were in flower when Syrphidae were relatively abundant in F14. *Episyrphus balteatus*, *Metasyrphus corollae*, *Syrpitta pipiens*, *Syrphus* spp., and *Eristalis* spp. are all considered generalist feeders (Gilbert, 1981), feeding on flowers of different colours and structures. The alternative crops which flowered were foraged upon to a greater or lesser extent by all these syrphid species.

To have an appreciable effect on field populations of aphids, the flowering of alternative crops and maximal abundance of females should occur just as aphid populations are beginning to build up, or between cereal GS 61 and GS 73 when most economic aphid damage occurs to cereals (Anon., 1988). In this experiment there was poor synchrony between flowering of alternative crops, appearance of gravid Syrphidae and appropriate cereal crop growth stage. Most crops flowered after July 7 (GS 73) and aphids on cereals after this time cause little economic damage. The experiment though does provide a model system to illustrate a possible mechanism which causes differences in distribution of Syrphidae on a field scale.

The differences in abundance of syrphids about areas of differing floral richness can be due to a number of factors, including the time spent at each site. Thomson (1981) reported that solitary bees and flies concentrated in patches where there were more resources available because of an increased turning rate within rich patches. The time spent at either the control site or enhanced site by Syrphidae would be related to the resources provided at the site and the resource needs of the individual. Diel changes in the sugar concentration in nectar of *Crataegus* and *Echium* (Corbet, 1978; Corbet *et al.*, 1979) may have influenced the time spent by Syrphidae at the experimental sites, but it was not possible to measure changes in dispersal rate from the site at different times of the day, or to correlate dispersal rate with flowers' nectar concentrations because of the number of repeat observations required to gather such data.

To determine whether attraction into a florally-rich site was a factor in influencing syrphid distribution at flower sites, a simple mathematical model was used to describe the numbers of Syrphidae which could be expected at a particular site

(Appendix XI). A number of assumptions were made by the model,

Assumptions

- i) Syrphids moved randomly and had the same probability of coming across either of the two sites by chance i.e. immigration rate to either site was the same,
- ii) Yellow traps at both sites were equally efficient and captured Syrphidae in proportion to their abundance and time spent at the different sites,
- iii) The syrphids remain at the sites for a period of time and leave (disperse) at different rates i.e. emigration rates were different.

If movement rates into the two sites were the same i.e. assumption i) was correct, then the ratio of trap catches from each site should approximately equal the inverse of the ratio of dispersal rates from each site; since dispersal rate is a measure of the time spent at the sites, given that condition ii) is correct.

During the early part of the experiment, when repeated surveys were carried out rather than individuals being watched, the ratio of numbers of *E.balteatus* captured by yellow traps at the enhanced strip to numbers caught at the control strip, was higher than the ratio of dispersal rates from the two sites. Dispersal rates were not significantly different between sites at this time i.e. *E.balteatus* stayed for approximately the same time at each site. According to the model in Appendix XI, this indicates that movement by male or female *E.balteatus* into the enhanced floral site was non-random. This could have been for a number of reasons,

- i) The two sexes may have been attracted into the area from an unknown distance by visual or chemical stimuli,
- ii) Local populations of *E.balteatus* could have pupated at a number of sites which were all closer to the enhanced strip. Consequently the probability of their reaching either of the two strips was not equal.

iii) Climatic factors at the two sites may have been significantly different. Temperature, relative humidity, exposure to sun and shade cover as well as wind speed affect a number of behavioural activities of *E.balteatus* (Cowgill, 1991). Differences in such factors between the sites could have affected their capture rates by the yellow traps. However the length of the plots would have reduced such environmental effects. Replicating the experiment over a number of fields may have overcome such problems but the experiment was too labour intensive to enlarge it to such a scale.

A major assumption in the interpretation of the results is that the yellow traps

were equally efficient at capturing syrphids at the control and enhanced sites (assumption ii). This is not an entirely safe assumption and needs further consideration. Fluorescent yellow water traps were used to mimic flowers and to entice Syrphidae to land on them where they would be trapped. Syrphidae foraging at the enhanced site had many sources of pollen and nectar available and would perhaps not visit yellow traps as frequently as Syrphidae at the control site. At the control site, there were fewer floral resources available, consequently the yellow traps constituted a greater proportion of the items that Syrphidae may have visited. The proportion of visits to yellow traps by Syrphidae at the control site may have been much higher than at the enhanced site. This would result in higher numbers of Syrphidae being caught at the control site with a resultant reduction in differences between mean number of Syrphidae caught between the sites when ANOVA's were carried out. This would result in conservative conclusions being drawn. Despite this however, there were some dates when significant differences occurred between sites, but there may have been more occasions when significantly more syrphids were caught at the enhanced site, had the yellow traps caught equal proportions of available Syrphidae at each site.

The syrphids at both the enhanced strip and control strip were seen to move along the strips in both directions (north-east to south-west and vice versa). This was demonstrated in the colour mixing experiment. Although not significantly different, the rates of colour mixing between adjacent plots was higher at the control site than at the enhanced site. This indicates a potential higher movement rate along the length of the control site, perhaps due to syrphids' requiring to move greater distances while searching between the fewer floral resources available at the control site.

Although Syrphidae are strong fliers and can be caught in fields by yellow traps tens or hundreds of metres from hedgerows (Hickman & Wratten, 1994) syrphids may have been using the hedge as a corridor for movement as well as a source for nutrients. Dover (1989) made observational studies of Lepidoptera on arable land, to record their distribution and movement around hedgerows. Butterflies were recorded moving along the length of hedgerows, parallel to them and within a few metres. It appeared that the butterflies used the hedgerows as movement corridors. The influence of hedgerows and other linear features in the landscape on syrphid movement is considered further in Chapter 6.

In contrast to what was found in the earlier part of the experiment, the later



period of the experiment revealed that male and female *E.balteatus* remained for significantly longer periods at the enhanced site than at the control site, with females remaining longer than males at both sites. Females spent longer at the enriched site, perhaps because of the greater need that they have to feed on pollen (Schneider, 1948; Haslett, 1989b). Males will feed on pollen and nectar but because males invest less in reproductive tissue and spend more time hovering (Haslett, 1989b) pollen feeding is less important and less time will be spent feeding compared to females. Spending longer at the enhanced site than at the control site, (female *E.balteatus* spent 2.85 times longer; males 3.45 times longer) during the second part of the study did not result in an equal and proportionate rise in the number of male and female *E.balteatus* being caught in yellow traps at the enhanced site. The proportion of *E.balteatus* captured at the enhanced site compared with control site was less than the ratio of emigration rate from each site. A greater increase in immigration to the enhanced site could therefore not be shown, and differences in numbers caught at each site could be entirely due to the different rates of emigration.

Significant differences in the time that *E.balteatus* remained at the contrasting sites between the first and second part of the experiment could have been due to a change in quality of the floral resources available at each site between the two periods or over time or due to differences in the protocol used in the first and second part of the experiment.

*Episyrphus balteatus* was the most abundant syrphid at both sites. There were not enough *M.corollae* or *Eristalis* spp. in the vicinity of the strips to carry out marking and observational studies. However differences in the numbers of both males and females of these genera caught in traps at both sites probably resulted from similar mechanisms influencing distribution of *E.balteatus*.

A criticism of the study is the lack of replication between fields, and that Syrphidae at the enhanced and control sites were not observed under exactly the same environmental conditions at exactly the same time. Such observations were not possible since only one observer carried out the work. However, data were pooled from the days on which observations were conducted and analysis carried out on the data as a whole to reduce effects caused by environmental factors such as temperature or humidity which may have affected syrphid behaviour (Cowgill, 1991). Regions of the control site in which syrphids were observed were not randomly selected, but deliberately chosen for their floral content. This meant that the regions

of the control site observed were not entirely representative of the control strip, and would have resulted in any differences between emigration rates from the enhanced and control sites being minimised, hence conclusions drawn from such experimentation are conservative. Nevertheless, significant differences in the rates of immigration, and rates of emigration from sites of contrasting floral richness were obtained for *E. balteatus*. The difference in these rates help to explain the differences in distribution of Syrphidae at sites of differing floral richness.

#### Egg distribution

There were no significant differences in the number of gravid females in yellow traps at either site. Fewer than ten syrphid eggs were found on bait plants at either site. The distance between the enhanced and control sites may have been too small to detect any influence that flowers may have in differences in oviposition by females. Cowgill (1991) and Hickman (pers. comm.) suggest that differences in syrphid oviposition between sites, as a result of manipulating suitable floral resources will only be detected on a larger scale, with whole fields or entire farms as replicates.

## CHAPTER SIX

### SYRPHID MOVEMENT WITH RESPECT TO LINEAR FEATURES IN AN AGRICULTURAL LANDSCAPE<sup>1</sup>

#### INTRODUCTION

The investigation of movement by animals with respect to managed features in the landscape has received great attention in recent years. Mammals (Tew, 1994; Tew, Todd & MacDonald, 1994) and macro-invertebrates (Den Boer, 1977; Dover, 1990; Duelli, Studer, Marchand & Jakob, 1990; Frampton, Cilgi, Fry & Wratten, 1995) have been studied on farmland, with respect to their interaction with linear features (hedgerows, tracks, roads, *inter alia*) in the farming landscape.

Hedgerows can act as corridors for movement of carabids (Burel, 1989; Burel & Baudry, 1990) and butterflies (Dover, 1990, 1994). However, as well as providing channels for movement along the length of fields, facilitating movement within fields, such features can also prevent or reduce movement between fields (Fry & Robson, 1994). Observational studies in Norway showed that butterfly movement between fields over barriers, representing hedges 3m tall, was reduced by more than three times, compared with butterfly movement at a site with no physical barrier (Fry & Robson, 1994). Even barriers 1m tall had a significant effect on reducing the numbers of butterflies crossing between fields over such barriers.

Other linear features such as roads and tracks can also inhibit movement of butterflies and other fauna at the landscape scale (Mader, 1984; Dennis, 1986; Mader, Schell & Kornacher, 1990; Munguira & Thomas, 1992). Working in Germany, Mader (1984) studied the effect of four types of road on the movement of wood mice and carabids. The widest, busiest roads (6m wide, 250 vehicles h<sup>-1</sup>) caused the greatest inhibition of movement of fauna, and even a forest road, closed to public traffic (3m wide, two vehicles h<sup>-1</sup>) caused a significant reduction in the movement of fauna between two sites, compared to movement at a site without a road.

Using mark, release, recapture techniques, carabid movement across hedges and grassy banks, acting as field boundaries, have been investigated by Frampton *et al.*, 1994) and Mauremootoo & Wratten (1994). These studies found that the

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<sup>1</sup>This chapter resulted from an idea originally formulated by J.Hickman.

permeability (rate of movement through the linear feature) was variable between species, and significantly different from movement rates over the same distances in control fields, without such linear features. Movement by linyphiid spiders has also been shown to be inhibited by hedgerows (Thomas, 1992).

Such information about arthropod movement between fields has been used in computer simulation models which simulate the persistence of invertebrate fauna in fields in an agro-ecosystem, with each field liable to receive periodic perturbation in the form of pesticide applications or cultivations (Sherratt & Jepson, 1993). The permeability of field boundaries could have a significant effect on recolonisation rates of depleted habitats after such perturbation (Jepson, 1994).

Earlier work investigating the distribution and movement of aerial insect fauna over linear features such as hedgerows, windbreaks and fences found on farmland includes research by Lewis in the 1960's. Collecting aerial fauna in suction traps, Lewis (1965) found 2 to 27 times as many insects on the leeward side of such linear features than on the windward side. Weaker flying insects (Aphididae and Cecidomyiidae) were thought to be susceptible to being carried in air currents and being deposited fairly evenly on the leeward side at distances from linear features. Stronger flyers such as Syrphidae were found much closer to the features, where there was greater shelter. The angle at which air currents were incident to linear features had a significant effect on distribution of insects on the sheltered side of features. At a shallow angle of incidence ( $0^{\circ}$  -  $30^{\circ}$ ), catches of Aphididae and Cecidomyiidae were much lower in shelter, than catches made in shelter when the wind was incident at steeper angles ( $60^{\circ}$  -  $90^{\circ}$ ) (Lewis, 1966). The horizontal motion of air was the most important component affecting distribution of some airborne insects about a windbreak feature according to Lewis & Dibley (1970). Patterns of diversity of aerial fauna on either side of a windbreak feature resembled the pattern of shelter produced by the windbreak (Lewis, 1969).

Lewis & Stephenson (1966) investigated the effect of permeability of windbreaks to movement and distribution of aerial insect fauna. Artificial windbreaks of varying gappiness were used to represent hedges. For most taxa caught in suction traps, the more solid the barrier, the higher the number caught on the leeward side of the fence. Maximum aerial density of insects coincided with maximum shelter. The work by Lewis was concerned with physical characteristics and conditions of the linear features examined, and the ability of insect fauna to move across such features

was attributed to these physical characteristics and conditions. However, Bowden & Dean (1977) suggested that rather than factors such as air turbulence, wind speed or permeability determining comparative richness of insects at distances from hedgerows, the vegetation surrounding trapping sites would determine insect richness. However it is likely that physical characteristics and biological characteristics of linear features will combine to determine insect distribution and neither are mutually exclusive. Around a florally rich hedgerow, with complex structure, the biological component of a hedgerow will have a greater effect on the insect distribution than any windbreak effects, conversely around a florally poor hedgerow, with a simple structure, the windbreak effect will have greater influence (Bowden & Dean, 1977). Previous studies concerning the distribution of insects, including Syrphidae, about sites of varying floral richness has already been considered in Chapters 3, 4 & 5.

Syrphids are strong flyers and a number of species (*Episyrphus balteatus*, *Metasyrphus corollae*, *Scavea pyrastris* *inter alia*) have been recorded migrating in Sweden (Svenson & Janzon, 1984) England (Owen, 1956; Sutton, 1969; Johnson, 1980) and through the Pyrenees (Lack & Lack, 1951). Poehling, Tenhumberg & Groeger (1991, cited by Cowgill, 1991) considered that *E. balteatus* may migrate from Southern Germany to Northern Germany, but stated that further research was required before firm conclusions could be drawn. With such seemingly strong powers of dispersal, it could be thought that landscape features would not inhibit syrphid movement, which is perhaps why, with the exception of Wratten, Hickman, Bowie & Lovei, (in prep) who concluded that shelter belts inhibit movement of Syrphidae, there has been little research conducted on this subject to date. However flight activity can be divided into two categories;

i) trivial (appetitive) flight: this occurs locally, with many other types of behaviour displayed in between flying. Trivial flights can vary greatly in duration and direction (Johnson, 1969).

ii) migratory flight: this occurs when flights are much longer and other behaviours are suppressed; flight behaviour predominates. Migratory flight does not show such variability in duration or direction as trivial flight. Migratory flight is a dispersal mechanism which always includes females, but not necessarily males (Chapman, 1985).

Previous reports of movement involving trivial flight by Syrphidae include those by Cowgill (1991) who marked *E. balteatus* with enamel paints on arable land. Two

days after marking, a marked individual was recorded 2.5km from the marking site. Schneider (1958) reported *S.pyrastris* travelling from a site of overnight rest to a feeding location, then returning to the same rest spot in the early evening covering 5km during the day. Lyons (1965) recorded *E.balteatus* flying 10km per day.

Information about trivial flight and local movement of Syrphidae on a farm scale is of use if beneficial Syrphidae are to be successfully manipulated in the agroecosystem using floral resources provided as part of a program of IPM i.e. decisions of where to sow attractive floral resources and the between-patch distance in relation to fixed features of semi-natural vegetation could be influenced by any surrounding linear features.

#### Aims of this chapter

This chapter aimed to discover whether linear features, typical of an arable farm, acted as an impediment to syrphid movement. The work in this chapter was carried out in New Zealand, during the southern hemisphere's summer (December 1992 - March 1993). A brief introduction to Syrphidae found on arable land in New Zealand is given below.

The diversity of syrphid species found on arable land in New Zealand is limited because there are relatively few species of hoverfly found in the country. (Anon.,1977). Two predominant native species are found on agricultural land; these are *Melanostoma fasciatum* (Macquart) and *Melangyna novaezealandiae* (Macquart). *Eristalis tenax* is also found in agricultural land but is not native to New Zealand and it does not have predatory larvae.

Syrphid predation of pests in New Zealand, was recognised as economically beneficial by Miller & Watt (1915) and Miller (1918). *Melanostoma fasciatum* and *M.novaezealandiae* larvae are not obligatorily aphidophagous but can be an important component in biological control of pests. *Melanostoma fasciatum* larvae have been found to contribute to 58% of total arthropod predation on white butterfly larvae on brassicas (Thomas, 1977). As in Europe, Syrphidae are a component of the natural enemies of cereal aphids in New Zealand. Cereals are widely cultivated in New Zealand with around 200,000ha grown each season, providing some of the highest yields per hectare in the world (Scott, 1984). Five aphid species are found in New Zealand cereals. These are, *Metopolophium dirhodum* and *Rhopalosiphum padi*,

which are also common to UK cereals, *R. maidis* (Fitch) which is of little economic importance, since it occurs in low numbers, and *Sitobion miscanthi* (Takahashi) (Scott, 1984). *Sitobion fragariae* (Walk.) also occurs but it is not common and its life cycle is not known there (J. Farrell, pers. comm.). *Metopolophium dirhodum* and *R. padi* are the most important aphid pests of New Zealand cereals (Scott, 1984).

## MATERIALS AND METHODS

### The study site

The work was carried out at Flock House Agricultural Centre, a 1200ha farm with a diversity of interests, including cereal production on Rangitikei and Manawatu sandy loams, near Bulls in the south-west of the North Island of New Zealand. The study was carried out in New Zealand because of a developing interest in New Zealand Syrphidae; the convenience that an additional summer's field work would allow for the completion of the overall aims of this thesis and because the opportunity was provided to me.

### Experimental Design

The experiment to investigate syrphid movement across linear features relied on Syrphidae feeding on pollen on one side of various linear features, then dispersing in different directions, with a proportion of those containing pollen being caught in yellow water-traps on the opposite side of the features. Pollen was to be provided in the form of strips of flowering *Phacelia tanacetifolia*, a North American annual in the family Hydrophyllaceae, and a plant known to be used as a pollen resource by Syrphidae in New Zealand (Lövei *et al.*, 1992). When viewed under a microscope, *P. tanacetifolia* pollen may be distinguished from other local pollens by its distinctive shape, which has been described by Constance & Chuang (1983). Syrphidae caught in traps and, upon dissection, found to contain *P. tanacetifolia* pollen would have been assumed to have crossed the linear feature from the nearest source of *P. tanacetifolia* pollen.

Four types of linear feature on the Flock House estate were available for study. They comprised i) an 8m tall windbreak hedge, ii) a freshwater creek with an adjacent 3m tall hedge, iii) an asphalt road with a grassy verge, and iv) a dirt farm

track between post and wire fences. Two control sites were available which had no physical linear feature acting as a barrier; a 3.2ha field of spring wheat (cv. Norseman) and a 3.5ha field that had been recently ploughed and consisted of bare ground for the duration of the study.

Five metre strips of *P.tanacetifolia* were sown adjacent to each type of linear feature. Two rows of traps were used at each site, one row on each side of the linear feature examined. Each row of traps consisted of four yellow water-traps. Two different types of yellow water-trap were used at the tall hedge, creek and ploughed field sites because there was not enough of one single type of water-trap available. Some traps were made from circular flowerpot saucers (diameter 19cm) painted yellow, while other traps were made from yellow plastic tubs (17 x 17 x 8.5cm). Two of each type of trap were used in each row of traps. The traps were fixed on wooden stakes at a height of approx. 1.25m. There were two replicated strips of *P.tanacetifolia* and water-traps at the creek and in the ploughed field. There were four replicates at the track, road and tall hedge sites and three replicates at the wheat field control. Both the ploughed field and wheat field strips of *P.tanacetifolia* were 13.5m long, having been sown as part of another study.

#### Description of each linear feature

##### i) Tall hedge

Two 8m tall windbreak hedges, of *Chamaecyparis lawsoniana* (A. Murr), 80m long on opposite sides of the same paddock were used, with two replicates at each hedge. *Dactylis glomerata* and *Bromus catharticus* (Vahl.) made up the vegetative layer at the base of the hedge. Wheat plants (cv. Norseman) were removed from two areas 5m x 0.5m in the margin of a 1.5ha spring wheat field on the opposite side of one of the tall hedges, to provide space for *P.tanacetifolia* seed to be sown. Before sowing, the ground was cultivated by hand then smoothed with a rake. 3.5g of *P.tanacetifolia* seed was then scattered by hand on the cleared area (equivalent to 14kg ha<sup>-1</sup>). The *P.tanacetifolia* strips used at replicates 3 and 4 were established in a pasture, which was occasionally grazed by cows and/or sheep on the opposite side to the paddock at the second tall hedge. Two areas of the grazed pasture 5m x 0.5m and approx. 1.5m from the tall hedge were mown and cultivated by hand, then sown with *P.tanacetifolia* seed as described previously. The *P.tanacetifolia* was protected from grazing by a portable electric fence. Two rows of traps were set up at each



replicate; the first row was 1m from the *P.tanacetifolia*, between the sown seed and hedge. The second row of traps at each replicate was on the other side of the hedge 15m from the *P.tanacetifolia* (Fig 6.1 i).

ii) Freshwater creek and short hedge

Two 5m strips of *P.tanacetifolia* were sown at the margin of a 7.3ha spring wheat field (cv Norseman), adjacent to a shallow freshwater creek. The seed was sown as described previously. The creek was 3m wide, and had a 2.5m hedge of *Phormium tenax* (Forst. et Forst f.) on the opposite bank. The banks of the creek were dominated by *H.lanatus*. Traps on the other side of the creek and hedge were in a 8.2ha field of *Trifolium* spp. and *L.perenne* (Fig 6.1 ii).

iii) Asphalt Road

Four replicates were situated next to a main road of asphalt and road chippings. The road verge consisted of *Agrostis tenuis* Sibth., *Paspalum dilatatum* Poir., *H.lanatus*, *L. perenne*, *Poa* spp. and *Festuca* spp. Four sections of the verge 5m x 0.5m were mown and cultivated by hand then sown with *P.tanacetifolia* seed as described previously. On the opposite side of the road was a grassy verge of mainly *H.lanatus*, *D.glomerata*, *Bromus* spp. *Trifolium* spp. *L.perenne* and *Rumex* spp. before a post and wire fence surrounding a field of maize. The first row of traps (at 1m) was on the first grassy verge, the second (15m) were on the second grassy verge but before the maize field (not Flock House land) (Fig 6.1 iv).

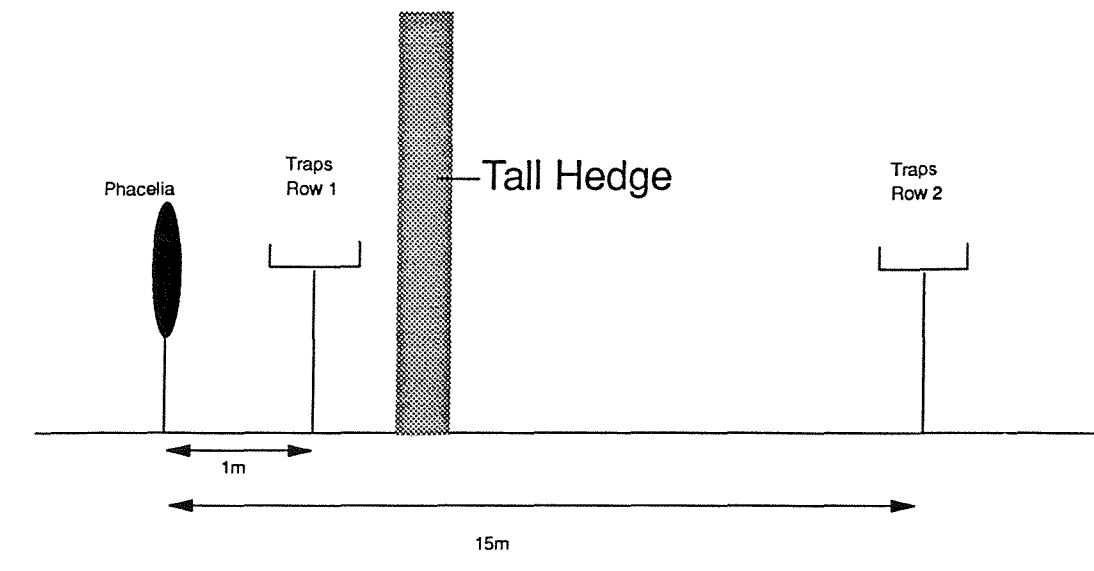
iv) Farm track

Four replicates were situated along a gravel farm track. The *P.tanacetifolia* strips were sown adjacent to the track which ran between two post and wire electric fences enclosing a 3.5ha pasture of *Lolium* spp. and *Trifolium* spp.. The *P.tanacetifolia* was sown in four sections of the grassy verge, in areas 5m x 0.5m, which had been mown and cultivated by hand. On the other side of the track of replicates 1 and 2 was a verge of *Lolium* and *H.lanatus* before a post and wire fence then a field of spring wheat (cv. Norseman). On the other side of the track of replicates 3 and 4 there was similar vegetation, a post and wire fence then a pasture of *Lolium* and *Trifolium*.

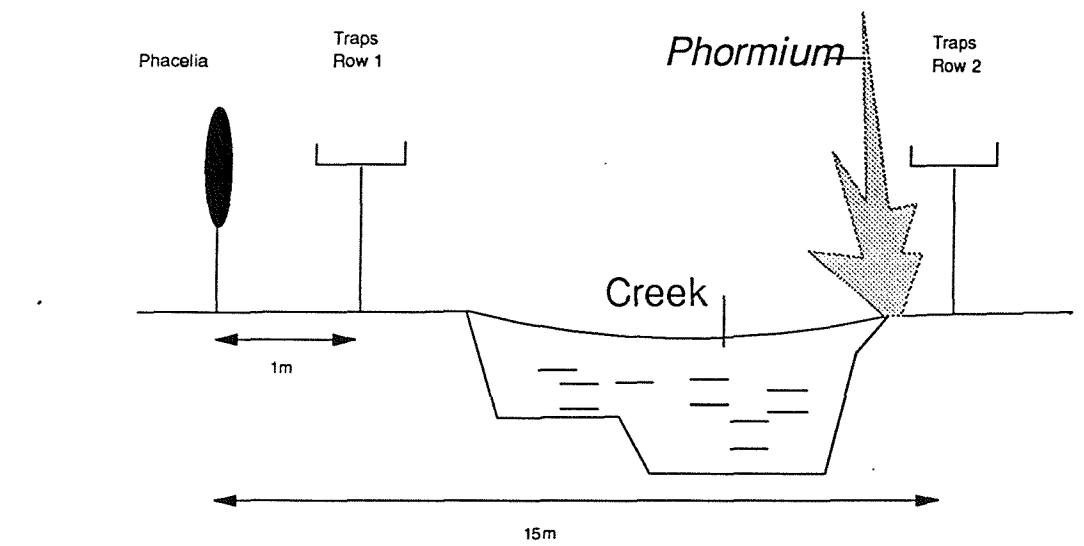
In each replicate, the first row of traps were on the first grassy verge before

Fig 6.1 Diagram of trap layout on each side of linear features.

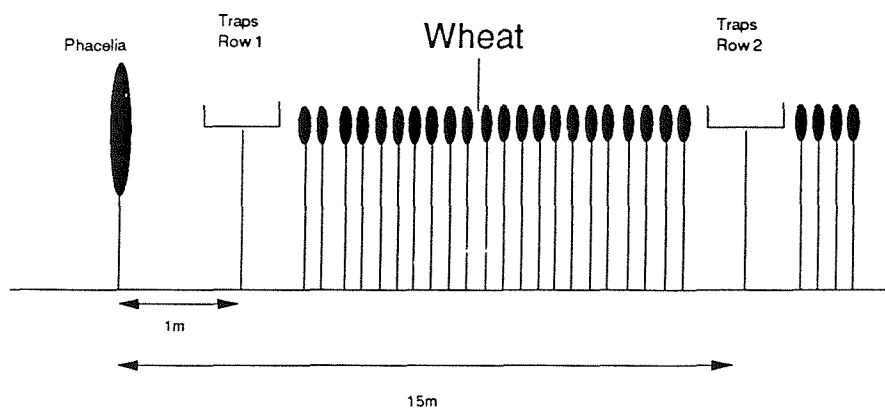
i) Tall Hedge



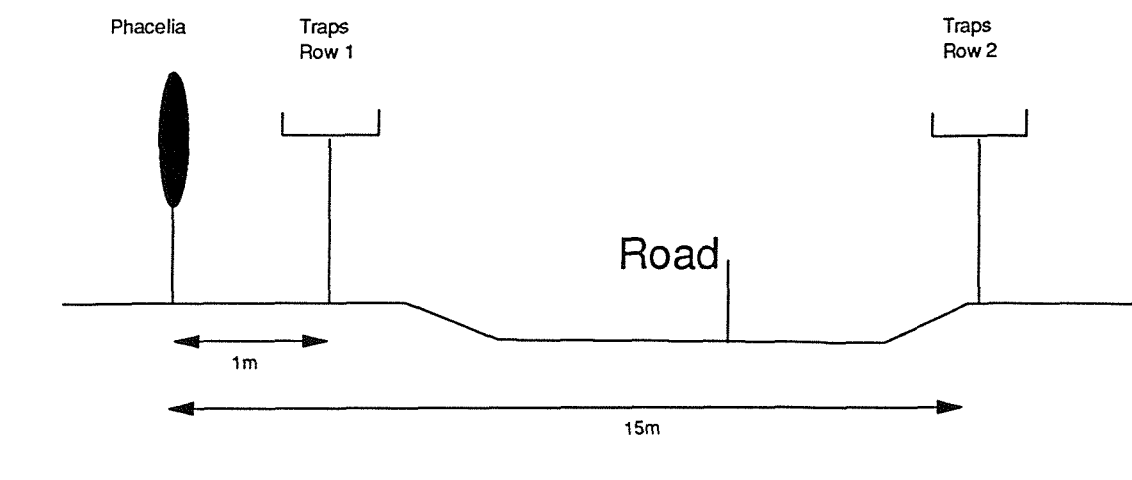
ii) Creek



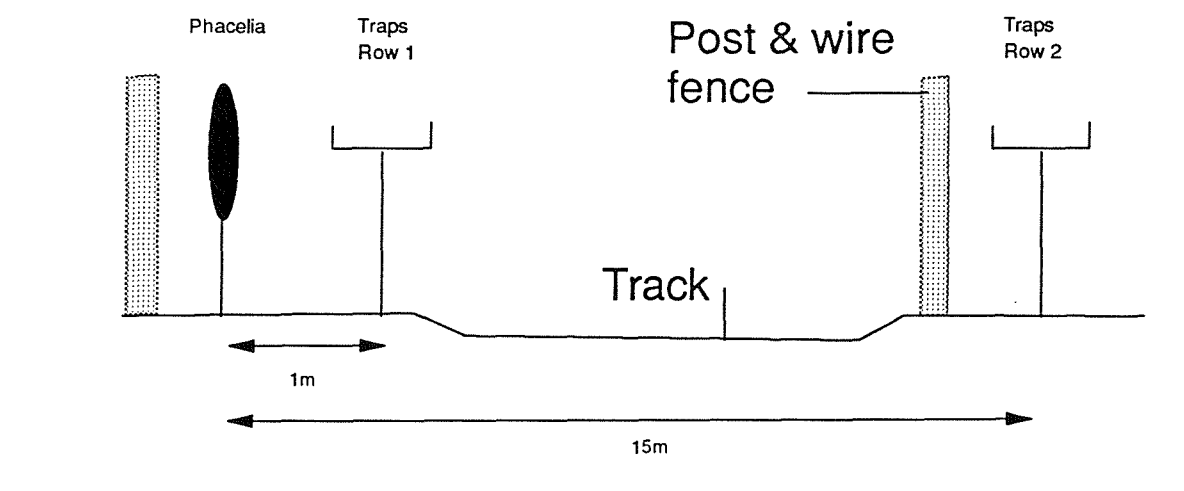
iii) Wheat



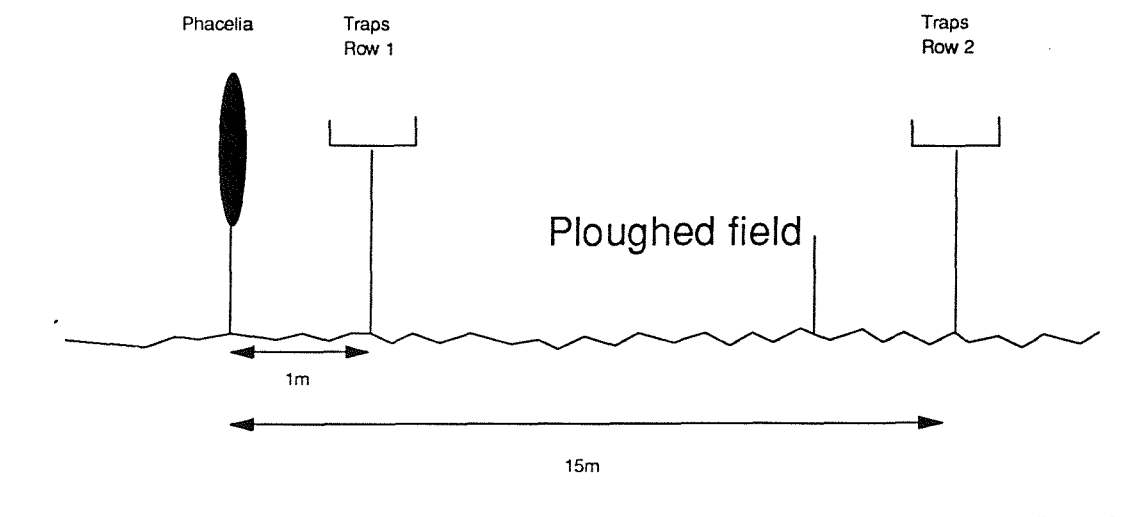
iv) Road



v) Track



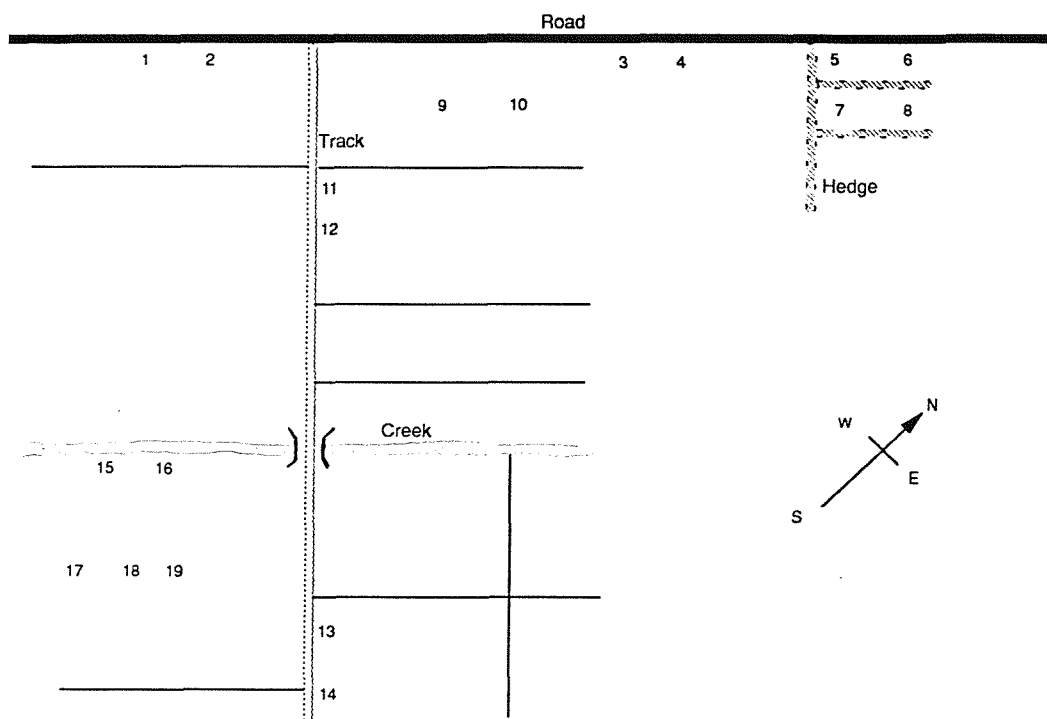
vi) Ploughed field



the track, the second row of traps were either in the wheat field (replicates 1 and 2) or pasture (replicates 3 and 4) (Fig 6.1 v).

Fig 6.2 shows the relative position of sites to each other and the relative position of replicates within each site.

Fig 6.2 Map showing the position of trap sites at linear feature types amongst fields at Flock House.



Key:

Trap site number	Type of linear feature
1,2,3,4	Asphalt road
5,6,7,8	Tall hedge
9,10	Ploughed field
11,12,13,14	Farm track, post and wire fence
15,16	Freshwater creek and short hedge
17,18,19	Wheat field control

#### Artificial strips of *P. tanacetifolia*

*Phacelia tanacetifolia* at replicates 1 and 2 of the tall hedge and both replicates of the freshwater creek failed to germinate. Since these were the linear features that provided the greatest physical obstruction to movement, and there was no time to resow the strips and wait for the *P.tanacetifolia* to grow and flower, an alternative method to provide pollen from *P.tanacetifolia* was used. Bunches of flowering *P.tanacetifolia* sown as part of a separate study were taken from a field on the Flock House estate and carried in buckets of water to the sites where the *P.tanacetifolia* had not grown. Ten glass bottles (0.57 l) were sunk into the ground at each replicate so that the lips of the bottles were just above the soil ground level. The bottles were then filled with fresh water and bunches of cut *P.tanacetifolia* placed into the glass bottles. The bunches were replaced with freshly cut *P.tanacetifolia* twice a week during the period of the study. Chandler (1968c) had previously used such a technique to manipulate the distribution of Syrphidae in plots of Brussels sprouts, but instead of using glass bottles sunk into the ground, he simply used buckets with water in them to hold *Senecio jacobaea*.

#### Emptying water traps

A weak solution of detergent was used in the yellow water-traps to collect syrphids. Traps were emptied on 12 dates between 20 January and 2 March. The *P.tanacetifolia* strips did not come into flower all at the same time at each linear feature and flowering lasted for different lengths of time; consequently not all replicates were examined on the same dates (Table 6.1).

On each date of emptying, individual trap contents were poured into a funnel lined with a nappy liner and an appropriate label. The nappy liner collected the entire contents of the trap but allowed the detergent solution to drain into a plastic beaker placed under the funnel. The nappy liner and contents were then tied shut with an elastic band and placed in a strong plastic bag. The water traps were then filled with a fresh solution of detergent. The nappy liners containing insects were stored in 70% alcohol until examined. The contents of each nappy liner were examined under a binocular microscope, any syrphids present were identified to species and sexed then placed in a labelled glass specimen tube.

Table 6.1: Dates of trap emptying and the replicates that were emptied at linear features and control sites. (n= no. of replicates)

Date	Ploughed Field (n=2)	Tall Hedge (n=4)	Creek (n=2)	Farm Track (n=4)	Road (n=4)	Wheat Field (n=3)
Jan 20	1,2	1,2, - -	1,2	- - - -	- - - -	- - -
Jan 26	1,2	1,2, - -	1,2	1,2,3,4	- - - -	- - -
Jan 29	1,2	1,2, - -	1,2	1,2,3,4	- - 3,4	- - -
Feb 2	1,2	1,2, - -	1,2	1,2,3,4	- - 3,4	1,2,3
Feb 5	1,2	1,2, - -	1,2	1,2,3,4	- - 3,4	1,2,3
Feb 9	1,2	*	1,2	1,2,3,4	- - 3,4	1,2,3
Feb 12	1,2	1,2,3,4	1,2	1,2,3,4	- - 3,4	1,2,3
Feb 16	1,2	1,2,3,4	1,2	1,2,3,4	- - 3,4	1,2,3
Feb 19	1,2	1,2,3,4	1,2	1,2,3,4	- - 3,4	1,2,3
Feb 23	- -	- - - -	1,2	1,2,3,4	1,2,3,4	1,2,3
Feb 26	- -	- - - -	1,2	1,2,3,4	1,2,3,4	1,2,3
Mar 2	- -	- - - -	1,2	1,2,3,4	1,2,3,4	1,2,3

Key: - - = *P.tanacetifolia* not in flower, \* = traps knocked over by sheep.

### Dissecting Syrphidae

Syrphidae were taken individually from labelled tubes and placed to one side of a glass microscope slide (76mm x 26mm). Viewed with a x10 binocular microscope, the thorax and abdomen were separated by teasing apart with size 4 watchmaker's forceps. The pregenital segments were then removed from the tip of the abdomen, using forceps to leave segments 1 to 4. The sternites were peeled away from the tergites to reveal the internal abdominal organs. The hind gut was removed from the abdomen and moved a few cm along the slide, away from the remains of the rest of the syrphid. Two drops of 70% alcohol were dropped onto the gut of the syrphid with a Pasteur pipette. Two drops of 5% safranin were then added to stain the pollen (Goot & Gerbandt, 1970) using another Pasteur pipette. The gut, alcohol and stain were mixed with a mounted needle. A size 4 cover slip (22mm x 22mm) was then placed on the slide and the slide was viewed under a x40 binocular microscope. The slide was scanned to detect any pollen grains. Once pollen had been found, it was viewed under x100 magnification to identify whether it was

*P.tanacetifolia* pollen. Each slide was scanned 20 times across the region of the slide where pollen was most concentrated while looking for *P.tanacetifolia* pollen, or until *P.tanacetifolia* pollen had been identified, if that was before 20 scans had been completed. Once *P.tanacetifolia* pollen had been identified, the slide was disposed of and instruments rinsed in alcohol before another syrphid was dissected.

The presence or absence of eggs was noted when female *M.fasciatum* were dissected.

## RESULTS

Three syrphid species (2637 individuals) were caught in yellow traps between 18 January and 2 March. The most abundant species caught was *Melanostoma fasciatum* (2483 individuals; 775 male; 1708 female) which comprised 94.2% of all individual Syrphidae. *Eristalis tenax* comprised 3.8% of individual syrphids and was the next most abundant syrphid species caught (100 individuals; 49 male; 51 female). *Melangyna novaezealandiae* was the least common species recorded comprising 2.0% of all individual syrphids (54 individuals; 25 male; 29 female).

All species were caught on both sides of each linear feature, and at both distances (1m and 15m) in the ploughed and wheat field sites.

Of 56 *E.tenax* caught in traps at 1m, none of them contained any *P.tanacetifolia* pollen, although other unidentified pollen grains were observed in the dissected guts. It was concluded that none of the trapped *E.tenax* had fed on *P.tanacetifolia* pollen, or that *P.tanacetifolia* pollen which had been fed upon passed through the guts of *E.tenax* too quickly to be of any experimental use. The remaining *E.tenax* from traps at 15m were not dissected. No further analysis was carried out on this species. Similarly none of the 20 *M.novaezealandiae* which were dissected contained any *P.tanacetifolia* pollen. Again other pollens were recorded but were not identified. No analysis was carried out on *M.novaezealandiae*.

*Melanostoma fasciatum* had been observed feeding on pollen from *P.tanacetifolia* plants at all sites including the sites where the *P.tanacetifolia* had to be put out in glass bottles. Of 775 males dissected, 260 (33.5%) were found to contain *P.tanacetifolia* pollen. There was a higher degree of *P.tanacetifolia* pollen feeding in females, with 804 of 1708 females (47.1%) dissected, containing *P.tanacetifolia* pollen. There was a highly significant association between sex and

having fed on *P.tanacetifolia* pollen, with females more likely to have fed upon pollen ( $G_{adj} = 4388.67$ ,  $DF=1$ ,  $P < 0.001$ ).

#### Differences in trap types

Two different trap types were used to collect syrphids at the tall hedge, creek and ploughed field sites. Before any analysis could be carried out, any significant differences in the catch efficiency of the two trap types had to be established. There was less than 2% difference in the trapping area of each type of trap (area of 19cm diameter trap  $\approx 284\text{cm}^2$ ; area of plastic tub  $\approx 289\text{cm}^2$ ).  $G_{adj}$  tests (Sokal & Rohlf, 1981) were carried out on pooled data from the tall hedge and creek sites. There were no significant differences in the distribution of total male and female *M.fasciatum* caught in either yellow trap types at the tall hedge (males  $G_{adj} = 1.75$ ,  $DF = 1$ , NS; females  $G_{adj} = 0.00$ ,  $DF = 1$ , NS) or at the creek (males  $G_{adj} = 1.37$ ,  $DF = 1$ , NS; females  $G_{adj} = 1.35$ ,  $DF = 1$ , NS). Only 10 *M.fasciatum* were caught in traps at the ploughed field site during the study, none of which contained *P.tanacetifolia* pollen. No analysis was carried out on data from this site.

#### Numbers of *M.fasciatum* caught at each feature

There was considerable variation in numbers of male and female *M.fasciatum* caught during the study period, at each feature type on each date that traps were emptied. The total number of each sex of *M.fasciatum* caught at each feature type was divided by the number of replicates examined on each date at that site, to give a mean number per replicate for each date. Fig 6.3 shows such data for males. Fig 6.4 shows the equivalent data for females. During the study, significantly more female than male *M.fasciatum* were caught (comparison of total numbers of males and females caught on each date, paired t-test,  $t = 2.49$ ,  $DF=22$ ,  $P < 0.05$ ). When traps in replicates at all features were emptied on the same dates, (Feb 2, 5, 12, 16 and 19), there were some significant differences between the mean numbers of male and female *M.fasciatum* caught in traps at the feature types (two-way ANOVA of numbers caught per replicate, with feature type and date as factors; males  $F_{5,20} = 5.23$ ,  $P < 0.01$ ; females  $F_{5,20} = 8.73$ ,  $P < 0.01$ ) Table 6.2 shows which sites were significantly different.



Fig 6.3 Mean number of male *Melanostoma fasciatum*, caught in yellow traps at each feature throughout the study period (mean no. per replicate at each feature).

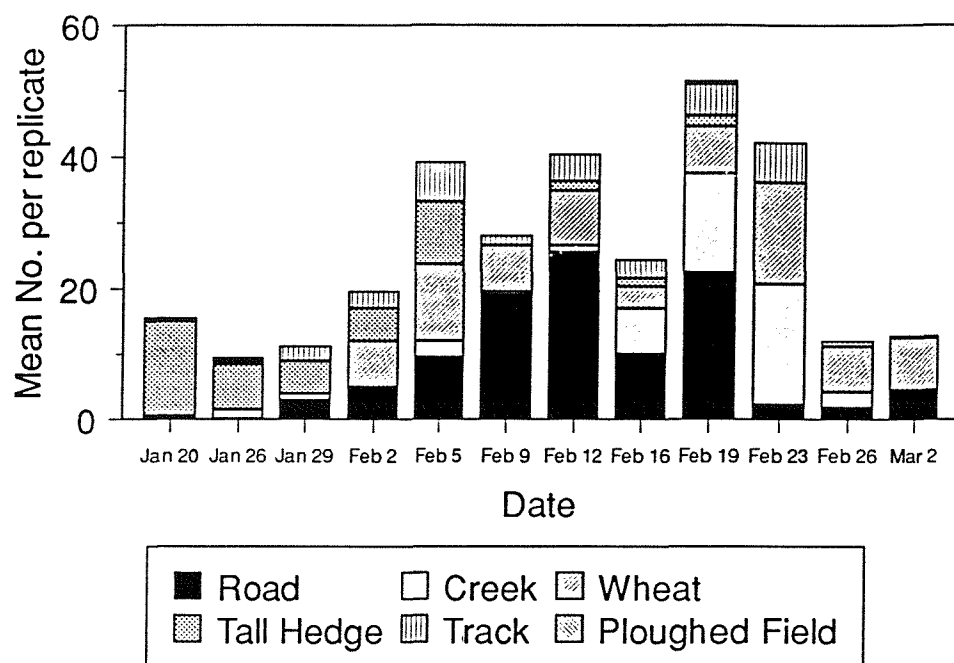


Fig 6.4 Mean number of female *Melanostoma fasciatum*, caught in yellow traps at each feature throughout the study period (mean no. per replicate at each feature).

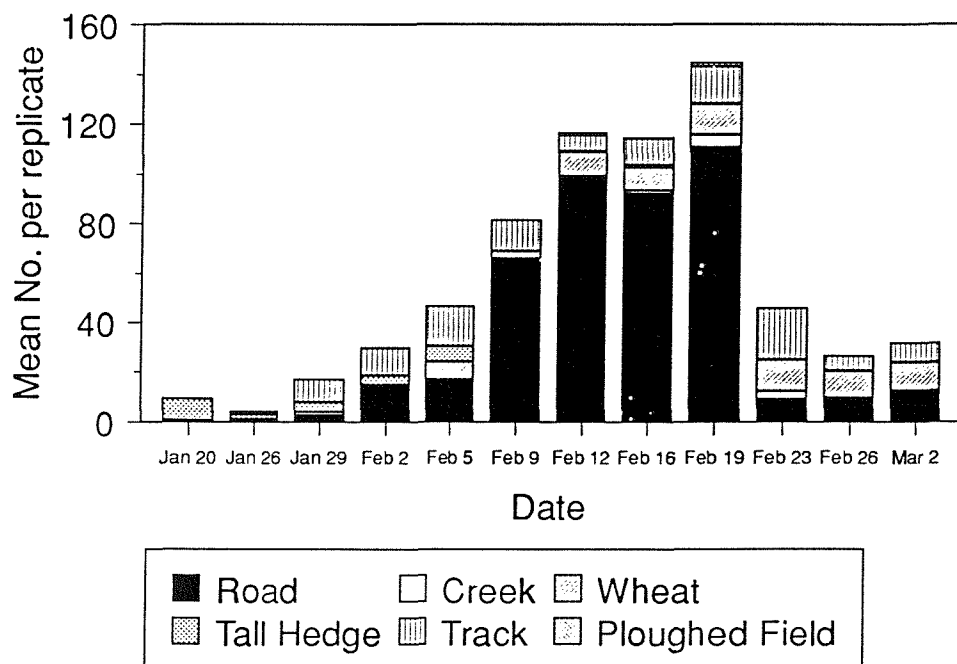


Table 6.2 Mean number of *M.fasciatum* caught at each type of feature, per replicate, on 5 dates in February. Features within a column sharing the same letter do not significantly differ ( $P > 0.05$ , two-way ANOVA followed by Tukey's (1949) test).

Feature	Male	Female
	Mean number	Mean number
Ploughed Field	0.1 a	0.6 a
Tall Hedge	3.8 a	1.4 a
Track	4.0 a	2.4 a
Creek	5.1 ab	7.8 a
Wheat	7.5 ab	11.7 a
Road	14.5 b	66.4 b

Fig 6.5 shows the mean number of male *M.fasciatum* caught on either side of each feature, in traps at 1m and 15m, and of those caught, the mean number that were found to contain *P.tanacetifolia* pollen in their guts (pollen +ve). Fig 6.6 shows the equivalent data for female *M.fasciatum*. Figs 6.5 and 6.6 show that, regardless of pollen content, the mean number of individuals caught at 1m is generally higher than the mean number of individuals caught at 15m at each type of linear feature except at the creek for males and the creek and ploughed field for females. The differences in mean numbers of each sex caught at 1m and 15m, regardless of pollen content, were not significantly different (paired t-tests of mean number of *M.fasciatum* in traps at each feature type, males  $t = 1.53$ ,  $DF = 5$ , NS; females  $t = 1.78$ ,  $DF = 5$ , NS). When only pollen positive individuals were considered, the mean numbers caught in traps at 1m was always higher than the mean numbers caught in traps at 15m for both sexes at all feature types. These differences were significantly different for males ( $t = 3.36$ ,  $DF = 4$ ,  $P < 0.05$ ) but not for females ( $t = 1.69$ ,  $DF = 4$ , NS).

Fig 6.5 Mean number of total male *Melanostoma fasciatum* caught on either side of features in an agricultural landscape (1m= pre-feature, 15m= post-feature) and mean numbers of *Phacelia* pollen marked male *M.fasciatum* (pollen +ve). Mean per replicate per trap emptying date.

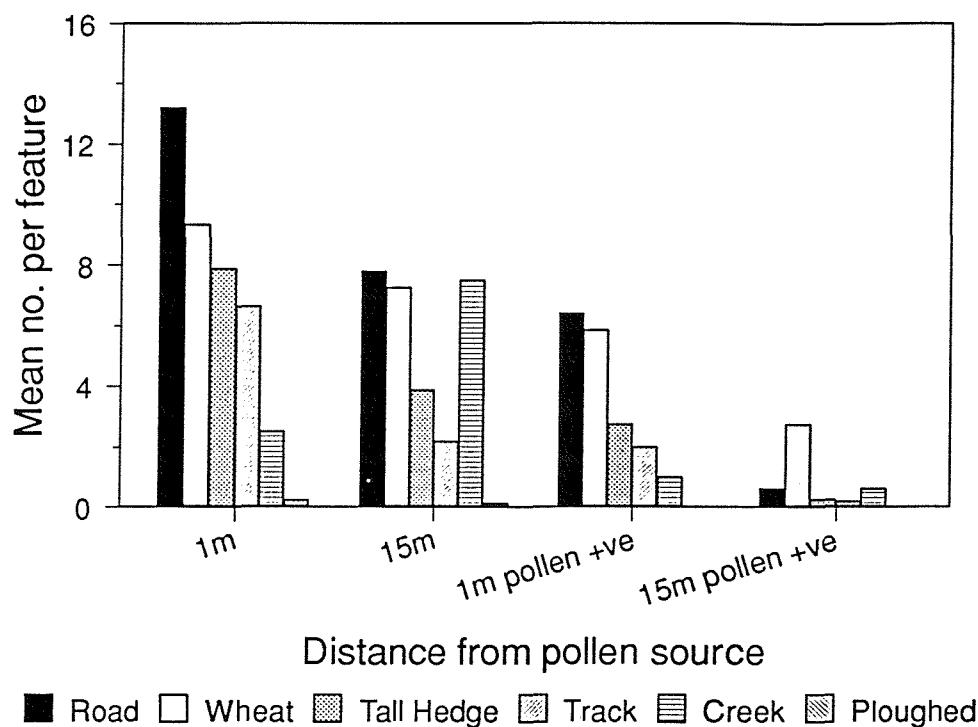
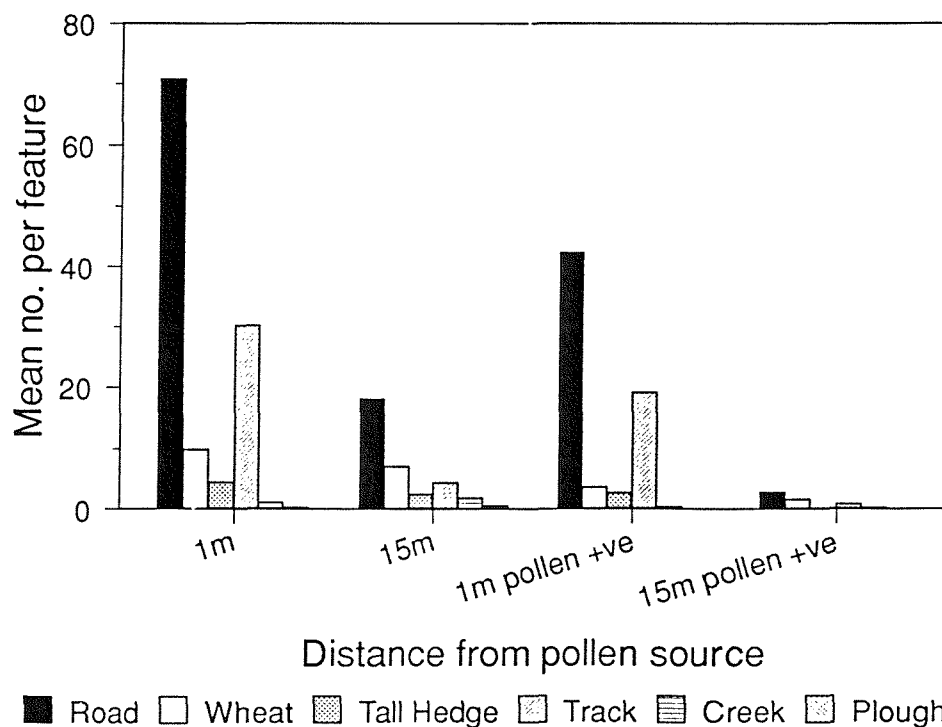


Fig 6.6 Mean number of total female *Melanostoma fasciatum*, caught on either side of features in an agricultural landscape and mean numbers of *Phacelia* pollen marked female *M.fasciatum* (pollen +ve). Mean per replicate per trap emptying date.



### Rationale for statistical methods used

No quantitative assessment of available *P.tanacetifolia* pollen was made at any of the sites, but there would have been differences in the amount of pollen resource available at each site. The amount of pollen available at the tall hedge site and creek site was probably less than at any other sites, because the number of *P.tanacetifolia* stems and flowers at these sites was less than at other sites since the *P.tanacetifolia* had to be provided in bunches in glass bottles. The wheat field strips of *P.tanacetifolia* were 13.5m long but strips of *P.tanacetifolia* at other sites were 5m long.

There was a significant difference in the mean percentage of male *M.fasciatum* containing *P.tanacetifolia* pollen, over all dates, between feature types, in traps at 1m ( $F_{4, 90}=7.41$ ,  $P<0.01$ ). However there were no significant differences in the mean percentage of female *M.fasciatum* containing *P.tanacetifolia* pollen, over all dates, between feature types, in traps at 1m. ( $F_{4, 102}=0.96$ , NS) (Table 6.3).

Table 6.3 Mean percentage of *M.fasciatum* containing *P.tanacetifolia* pollen in traps at 1m. Features sharing the same letter within a column do not significantly differ ( $P>0.05$ , two-way ANOVA followed by LSD range test) n= number of replicates with pollen +ve individuals examined.

Feature	Male		Female	
	Mean %	n	Mean %	n
Creek	17.5 a	7	37.5 a	8
Trees	22.6 a	14	39.2 a	15
Track	29.5 a	28	39.3 a	33
Road	39.7 a	20	47.2 a	26
Wheat	65.1 b	26	55.7 a	25

Since the mean numbers of both male and female *M.fasciatum* caught in traps at features significantly differed, the analysis of linear features causing impediment to syrphid movement was investigated by examining not the total number of syrphids containing *P.tanacetifolia* pollen, but the proportion of syrphids of a given sex containing *P.tanacetifolia* pollen, caught on either side of each feature i.e. in traps at

1m and 15m. Since proportions of Syrphidae containing *P.tanacetifolia* pollen on each side of a feature were not independent (proportions must sum to one) ANOVAs were carried out on the proportionate loss of Syrphidae containing *P.tanacetifolia* pollen caught at 15m compared to Syrphidae containing *P.tanacetifolia* pollen at 1m.

*Phacelia tanacetifolia* plants were not in flower at the same time at each site and consequently traps were not emptied on the same date at each site. Even when traps at different features were emptied on the same date, it was found that on some dates, no Syrphidae at a particular feature contained *P.tanacetifolia* pollen. Given such conditions, it was not possible to rigorously analyse the data to compare all features on all dates. However examination of the data revealed that wheat, road, track and tall hedge sites could be compared on February 2, 5 and 12 for both male and female *M.fasciatum*, since at these sites and on those dates, male and female *M.fasciatum* were found to contain *P.tanacetifolia* pollen at least in traps at 1m from the pollen source. In addition, data from sites at wheat, road, track and creek on February 16, 19 and 23, could be compared for male *M.fasciatum*.

#### Differences in ratios of *M.fasciatum* numbers on either side of linear features

The proportionate differences in the numbers of *M.fasciatum* containing *P.tanacetifolia* pollen in traps at 1m and 15m at each feature were transformed using the  $\sqrt{\text{arcsine}}$  transformation to stabilise the variance of the data. This transformation is appropriate for data which are expressed as proportions (Sokal & Rohlf, 1981). Two-way ANOVAs with feature type and date as factors were then carried out and summary results are given in Table 6.4.

Table 6.4 Results from two-way ANOVA of  $\sqrt{\text{arcsine}}$  transformed data - proportionate loss of Syrphidae containing *P.tanacetifolia* pollen on either side of features in an agricultural landscape (feature type and date as factors).

Dates	Sex	Factor	F-ratio	<i>P</i>
Feb 2, 5, 12	Female	Feature	$F_{3, 20} = 3.44$	<0.05
		Date	$F_{2, 20} = 2.98$	NS
Feb 2, 5, 12	Male	Feature	$F_{3, 15} = 1.29$	NS
		Date	$F_{2, 15} = 2.82$	NS
Feb 16, 19, 23	Male	Feature	$F_{3, 15} = 5.26$	<0.05
		Date	$F_{2, 15} = 0.81$	NS

The ANOVA results in Table 6.4 show that there were no significant differences in proportionate losses within each type of feature examined on different dates, but that there were significant differences in proportionate losses between feature types for females (Feb 2, 5 & 12) and males (Feb 16, 19 & 23). Mean losses for each sex over features and results from range tests, examining differences in the least significant means (Sokal & Rohlf, 1981) between each feature, to identify which features were significantly different are shown in Table 6.5.

Table 6.5 Mean proportionate losses of *M.fasciatum* containing *P.tanacetifolia* pollen over different linear features. n= number of replicates with pollen +ve individuals. (Losses sharing the same letter within a column do not significantly differ,  $P > 0.05$ , LSD)

Feature	Female (Feb 2, 5, 12)		Male (Feb 16,19, 23)	
	Mean	n	Mean	n
	proportionate loss		proportionate loss	
Wheat	0.72 a	9	0.50 a	8
Track	0.85 ab	6	0.88 b	4
Road	0.88 b	6	0.81 b	5
Tall Hedge	0.92 b	5	-	-
Creek	-	-	0.53 a	4

Table 6.5 shows that for female *M.fasciatum*, the tall hedge and road is more of a barrier to movement than the wheat or track; and that for male *M.fasciatum*, the track and road provide significantly more of a barrier to movement than wheat or the creek.

Data from all dates when traps were emptied have been pooled together for each feature type and the distribution of male and female *M.fasciatum* containing *P.tanacetifolia* pollen on either side of each feature is illustrated in Figs 6.7 and 6.8.

Fig 6.7 Distribution of *M.fasciatum* (male) containing *P.tanacetifolia* pollen on either side of features in an agricultural landscape (back transformation of  $\sqrt{\text{arcsine}}$  transformed proportions with 95% CI).

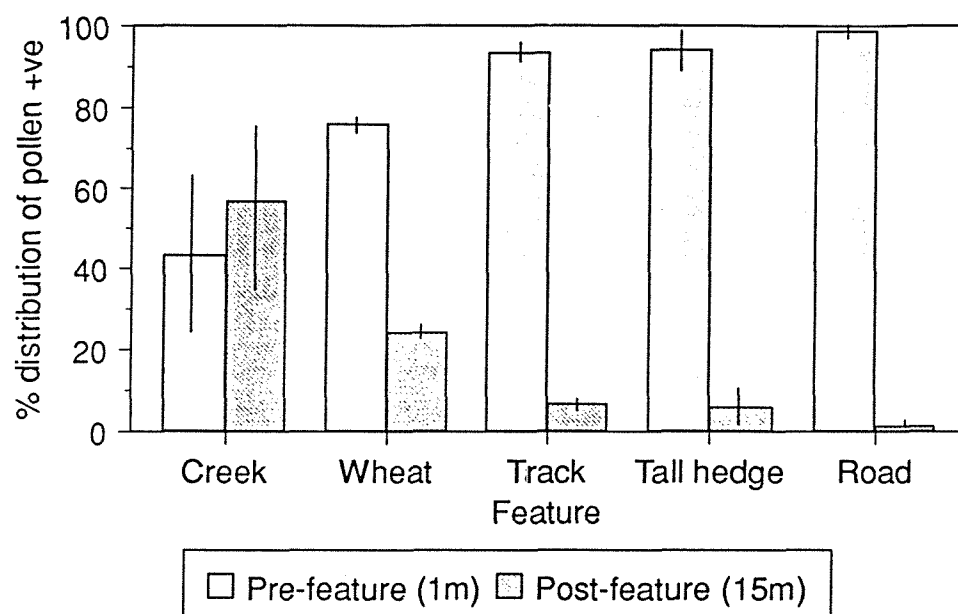
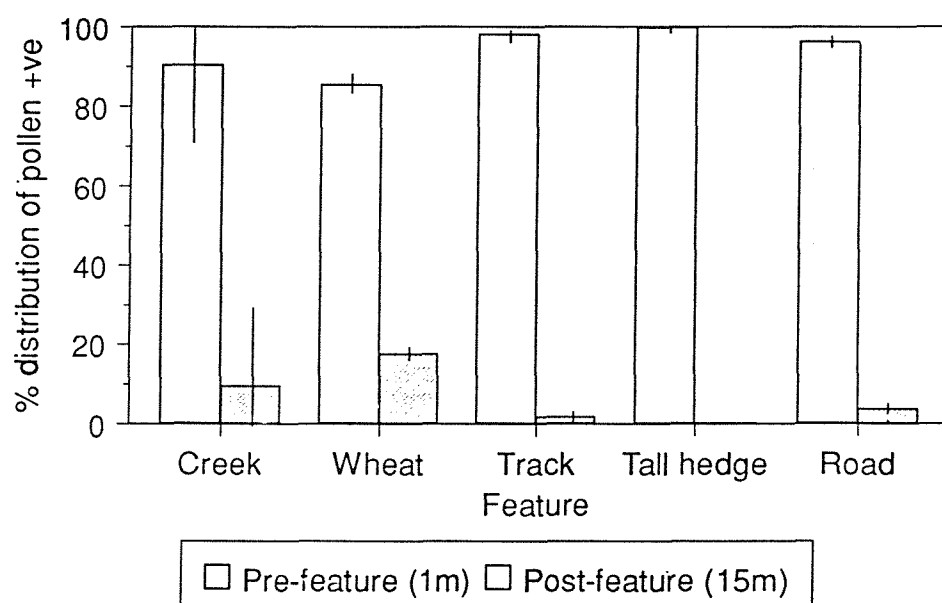


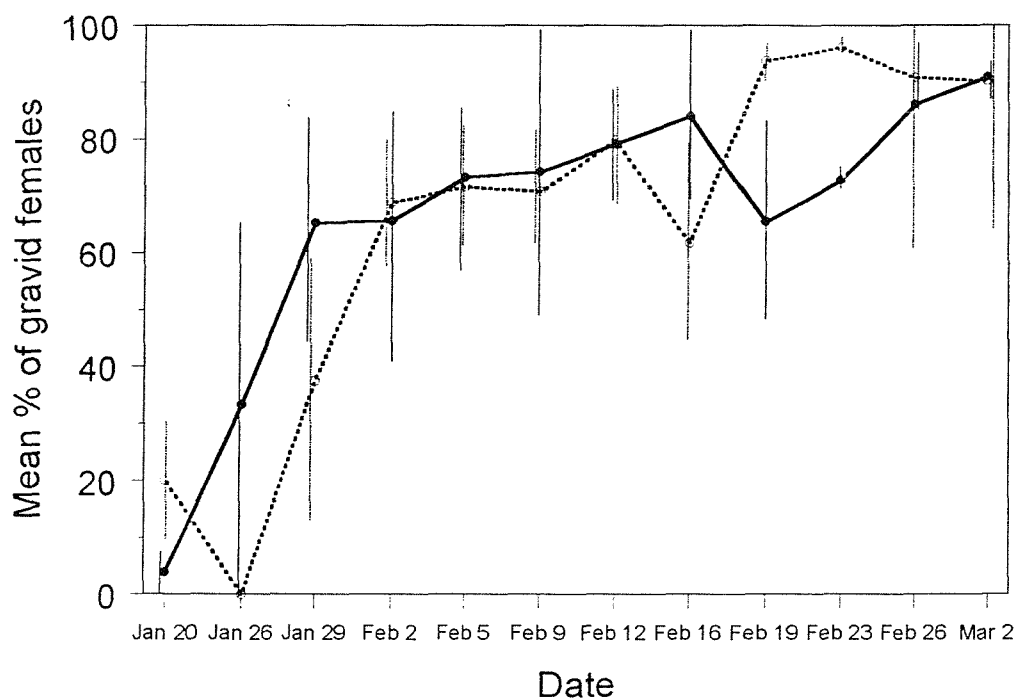
Fig 6.8 Distribution of *M.fasciatum* (female) containing *P.tanacetifolia* pollen on either side of features in an agricultural landscape (back transformation of  $\sqrt{\text{arcsine}}$  transformed proportions with 95% CI).



In all cases except for male *M.fasciatum* at the creek site, the greatest proportion of pollen +ve *M.fasciatum* were caught in traps at 1m.

1541 gravid *M.fasciatum* were caught during the study. The proportion of gravid individuals increased during the study period, with a trend of little difference between the mean percentage of gravid individuals caught at either 1m or 15m on any date (Fig 6.9).

Fig 6.9 Mean percentage of gravid *M.fasciatum* caught in traps at 1m (solid lines) and 15m (dotted lines) on each date of the study  $\pm$  1 SE.



Overall, 92.1% (1209) of females in traps at 1m were gravid, and 84.1% (332) were gravid in traps at 15m.

## DISCUSSION

Using *Phacelia tanacetifolia* pollen as a biological marker, the distribution, and by implication the movement, of male and female *M.fasciatum* over a variety of linear features, typical of a farming landscape, was shown to be inhibited by linear features such as tall hedges and roads.



Three syrphid species were caught during the study but only one was found to have fed on *P.tanacetifolia* pollen. Until recently, the only previous study of pollen feeding by New Zealand Syrphidae was by Holloway (1976) who concluded that *M.fasciatum* fed exclusively on anemophilous pollen (pollen from plants adapted for wind pollination), despite dissecting and microscopically examining only three specimens of *M.fasciatum* during her study. Of the 11 species of syrphid dissected (15 individuals) by Holloway (1976), *E.tenax* was found to have consumed the greatest variety of pollens, having fed on pollen from ten different plant families. However only two *E.tenax* was dissected by Holloway. In the present study, various pollens were observed in dissected specimens of *E.tenax* although none were identified as pollen from *P.tanacetifolia*. Syrphidae that feed on *P.tanacetifolia* pollen stand or hold onto the long stamen filaments of the *P.tanacetifolia* flower, which bend over with the weight of the syrphid. From the filament, a syrphid can reach the pollen on the anther. *Eristalis tenax* is larger than *M.fasciatum* (approximately double their size), and are probably too heavy, or too large, to hold onto the *P.tanacetifolia* filament and feed on the pollen. No *E.tenax* were observed feeding on *P.tanacetifolia* during the study.

More recently, White (unpublished) listed pollen from 13 plant families that have been found in the guts of dissected specimens of *M.fasciatum* and *Melanostoma noveazelandiae*. In the study by White, which was conducted on New Zealand's South Island, both *M.fasciatum* and *M.noveazelandiae* were found to have fed on *P.tanacetifolia* pollen. Over 120 *M.noveazelandiae* were caught during the study and approximately 40% had fed on *P.tanacetifolia*. In contrast, none of the *M.noveazelandiae* from the present study were found to contain *P.tanacetifolia* pollen. This could be due to the low number of *M.noveazelandiae*, which is much less common on the North Island than on the South Island (Miller, 1921), which were caught, and therefore lower number which were dissected.

Despite the assumed variability of quantity of pollen between feature types, there was little significant difference between the numbers of *M.fasciatum* caught at each feature type. Only at the road sites were there significantly more *M.fasciatum* captured. The traps at the road feature sites had the highest diversity of vegetation around them, and the high numbers of Syrphidae caught at these sites could have been due to the vegetational diversity. Bowden & Dean (1977), Molthan & Rupert (1988) and Molthan (1990) found higher numbers of Syrphidae at sites of greater

vegetational diversity than at sites with poorer vegetational diversity.

Of all the *M.fasciatum* caught in traps at 1m, at each type of feature, there was a significant difference in the proportion containing pollen only in males only at the wheat site. All other sites had homogenous proportions, with between approximately 1/3 and 1/2 of all individuals at 1m having fed on *P.tanacetifolia* pollen. It was noticeable that at each feature type, (except wheat) there was always a higher proportion of females containing pollen than males. This is probably due to the greater requirement that females have for pollen for the development of their ovaries (Schneider, 1948). Not surprisingly, given that *P.tanacetifolia* was provided in bottles at the creek and tall hedge sites, these sites had the lowest proportions of *P.tanacetifolia* +ve individuals at 1m than at other sites, although not by a significant amount. It had been anticipated that Syrphidae caught in traps at 1m at the features which provided a barrier to syrphid movement may contain a higher proportion of *P.tanacetifolia* +ve individuals, since dispersing Syrphidae would be prevented from crossing the barrier and would instead "bounce back" from the barrier and be more likely to get caught in the traps. This was not found to be the case however, and those features which provided the least physical barrier (wheat field) were found to have the highest percentage of pollen +ve individuals at 1m. Probably as a result of the longer strips of *P.tanacetifolia* in the wheat field site and consequently higher availability of pollen resource. The wheat field site also had the lowest proportionate loss of *P.tanacetifolia* pollen containing individuals between 1m and 15m. This is not surprising since there was no physical barrier between traps at 1m and 15m. Adult *E.balteatus* and *M.corollae* have been recorded in cereal fields, in yellow traps at distances of up to 200m from floral margins and their eggs have also been found on infested wheat plants at the same distance (Cowgill, 1991). Cowgill found no relationship between distribution of eggs or adults with distance from the field boundary, showing that at least two species of European syrphid are not restricted to the field margin and can disperse easily across cereal fields.

For female *M.fasciatum*, the tall hedge provided the greatest impediment to movement. The hedge could have been anticipated as a considerable impediment to movement as it was a physical barrier, 8m tall and very dense. However, the road was also found to be a significant barrier to females. Rather than acting as an impenetrable object, the road may have acted as a barrier because it created a break in vegetative ground cover, which inhibited movement of *M.fasciatum*. This may also

be an explanation for the low numbers of Syrphidae caught in the yellow traps at the ploughed field site. The bare soil did not provide food, shelter, a site where a mate could be found or a possible site for oviposition. It is possible that hoverflies may avoid crossing open, bare fields, or habitats which cause a break in ground vegetation. Butterflies do not often cross open fields (Dover 1990;1994), even with a standing crop present if the crop does not provide a food source or oviposition opportunity. The reluctance of butterflies to cross inhospitable terrain (Ford, 1971) means that instead, butterflies fly around fields staying within the vicinity of the field margin where resources are available, or shelter is provided for weak flying species. It was not possible to analyse the movement of both sexes at the tall hedge since males and females were not caught in sufficient numbers for analysis.

Similarly at the creek, only males were found in sufficient numbers for analysis. Vegetation on the banks on both sides of the creek was dense and diverse. The water in the creek and hedge of *Phormium tenax* did not appear to cause any impediment to movement. More pollen +ve males were found in traps at 15m than at 1m. This is a surprising result given that the syrphids dispersed from the pollen source which was nearer to traps at 1m than traps at 15m. However only a small number of males were found to be pollen +ve at the creek site, consequently each individual represents a greater proportion of the total and subsequent analysis should be interpreted with caution. Had the *P.tanacetifolia* successfully grown in the 5m strips which were sown, instead of being provided in glass bottles, more hoverfly individuals may have been found to have been pollen +ve and different results may have been obtained. Alternatively, the pollen +ve males in traps at 15m may not have fed on the *P.tanacetifolia* pollen in the bottles at the creek site, but at the *P.tanacetifolia* at the track sites which were within a few hundred metres of the creek. Such "contamination" between sites could have resulted in more pollen +ve males being caught in traps at 15m at the creek site than would otherwise have been caught, had there been no *P.tanacetifolia* at the farm track.

The mechanisms causing impediments to movement and dispersal of Syrphidae can be summarised and include the following,

i) physical obstruction e.g. tall hedge; this provided a barrier which Syrphidae could not fly through and would not normally fly over since it was 8m tall. Most anthophilous insects fly at low altitude, typically less than 10m and mostly less than 4m (C. O'Toole, pers. comm., cited by Dafni & Kevan, in prep). Although any syrphid

could fly around the hedge, there would be a temporal delay in dispersal, and distribution of Syrphidae on either side of the hedge would be biased at the ends of the hedge.

ii) break in vegetation ground cover e.g. by ploughed field or asphalt road; as discussed previously.

iii) thermal barrier e.g. above a road surface where the air temperature above is sufficiently high to inhibit or prevent movement of Syrphidae over the feature. This hypothesis was not examined experimentally, but the air temperature in the open above a road would be increased on sunny days by radiation from the dark road surface. If the air temperature was sufficiently high, the radiation may possibly prevent dispersal of Syrphidae across the road. Syrphidae are sensitive to changes in the microclimate (Cowgill, 1991) and may avoid crossing roads where high air temperatures above the ground could cause hygrothermal stress. Maier & Waldbauer (1979) recorded Syrphidae moving into the shade of a woodland at midday, from open spaces, where they had previously been feeding. Movement coincided with an increase in hygrothermal stress at the open site. Other authors which have recorded Syrphidae becoming inactive and avoiding activity in the hottest part of the day include Bankowska (1964), Hurkmans (1985) and Cowgill (1991).

iv) Air turbulence Munguira & Thomas (1992) noted that air turbulence may reduce the number of butterflies that cross unsheltered features such as roads. In this study, the ploughed field was the most exposed feature because it had no windbreaks on any side of the field. The resulting exposure and air flow may have prevented Syrphidae from flying over this field and hence led to the low incidence of capture in yellow traps.

From recording the number of gravid females dissected, it can be seen that the majority of females contained mature eggs by February 2. Gravid females were caught in traps at 1m so were assumed to have remained at, or returned to feeding sites which provided pollen resources. *Phacelia tanacetifolia* was therefore not used exclusively to mature the ovaries, but as a general energy source. That female Syrphidae will return to pollen resources once gravid, and continue to feed corresponds with the hypothesis that Hymenoptera commute between areas providing food for adults and host-containing areas (Powell, 1986; Jervis *et al.*, 1993). However, van Emden (1963) showed that 92% of female *Mesochorus* spp. (Hymenoptera: Ichneumonidae) contained immature ovaries in a flowering grassland site, compared

with 28% with immature ovaries in an adjacent wheat field. The implication is that females with mature ovaries did not return to the flowery grassland site.

The present experiment was limited to investigating the linear features that occurred on the Flock House estate. There were only a few types of linear feature and there was no variation of orientation within feature types. Thus it was not possible to take account of a feature's orientation, which may cause a bias in syrphid movement e.g. due to a prevailing wind or exposure to sunlight, which may influence flight activity of Syrphidae (Cowgill, 1991).

The vegetation at each linear feature varied, with some traps being in wheat fields, others in grass pastures. This would probably have affected how *M.fasciatum*, especially gravid females, dispersed. Females may have been more likely to fly in and around cereal fields as they searched for suitable sites for oviposition amongst cereal aphids. However no measure of aphid numbers was made in either cereal fields, or grass paddocks.

The implications of where floral resources, which are provided or managed by man for the benefit of Syrphidae, should be situated in an arable landscape for maximum benefit to Syrphidae are considered in Chapter Seven.

## CHAPTER 7

### GENERAL DISCUSSION

The experiments reported in the previous chapters have shown that there were occasions when provision of plant resources that are utilised by beneficial arthropods can influence the spatial distribution of a range of beneficial arthropods in an arable environment in the winter and summer. Grasses sown on a bank within a cereal field (Chapter Two) provided overwintering habitat for beneficial predatory arthropods, with total predator densities in the grasses consistently higher than in the adjacent field boundary, despite marked fluctuations in species densities between winters. Provision of floral resources for Syrphidae in the form of coriander border strips during the summer of 1992 did not lead to higher densities of Syrphidae within a cereal field with coriander borders compared with a cereal field without such borders (Chapter Four). However when sites of contrasting floral diversity were established within a single field in the following summer, significant differences in distribution of common arable Syrphidae were detected. A mechanism which may have caused such differences in syrphid numbers between sites of contrasting floral richness was described in Chapter Five. Whether provision of such resources significantly increases the population of beneficial arthropods on a farm scale remains unknown. However for enhanced predation of aphids, which is an ultimate aim of this type of work, increasing the number of predators in the medium to long term is not as important as influencing the distribution and synchronisation of predators in relation to aphid population development i.e. influencing the predator:aphid ratio is more important than increasing the maximum number of predators (van Emden, 1988). Using techniques described in earlier chapters, such as creating grassy banks within fields or herbaceous strips around fields, the ratio of predators:aphids may be increased within fields, although this may remain a local (field-scale) effect.

Increasing the variety and complexity of a crop system, in the majority of examples, reduces the abundance of pests (Risch *et al.*, 1983) or promotes the survival and success of beneficial arthropods (Speight, 1983). Polyphagous Coleoptera and Araneae as well as aphid-specific Syrphidae have a role to play in the control of aphids in cereals in some years (Sunderland, *et al.* 1981). The extent of the influence that such "beneficials" exert may be less than expected due to the

lack of suitable resources at appropriate times of the year which may result in the reduction of populations of groups of beneficials, or a reduction in the contribution of their numerical responses (Solomon, 1949) to the densities of their prey. The reductions in numbers of beneficial arthropods in cereal fields have been revealed in long-term surveys (Potts & Vickerman, 1974, Aebischer, 1991). It is possible that changes in agricultural practices that encourage diversification of the arable ecosystem described in previous chapters may slow or even prevent the decline in the populations of groups of beneficials such as carabids, staphylinids or spiders.

Ecosystem diversification, to promote the local density of predatory beneficial arthropods, on its own will not realistically replace the farming technique which is currently used to control aphids in cereals, namely the application of pesticide. Biological control is often possible only in a system of integrated control (Wilson & Huffaker, 1976). Thus plans for ecosystem diversification should be incorporated into a system of integrated pest management, that is the selective use of two or more pest control measures (Carver, 1989) such as combining the careful use of appropriate chemicals and doses (Poehling, 1989; Turner, 1995), encouragement of natural enemies (Wratten & van Emden, 1995) and/or development of plant resistance (Auclair, 1989).

The technique of using within-field grassy banks has recently been implemented by some farmers, throughout the UK, and has been used in attempts to increase the number and quality of suitable habitats for overwintering beneficial arthropods and to increase habitat diversity in fields, while attempting to genuinely reduce farm costs. Banks are relatively cheap to establish (Wratten, 1988). A single bank in a 20ha field can save money if it helps to prevent a single application of an aphicide to the field, or prevents a 5% loss in yield due to aphid attack (Wratten, 1988). The value of grassy banks will be affected by variables such as grain yields, quality and quantity. In years of high quality and quantity, the income lost from land taken out of production by a bank will be higher than in years with poor quality grain. However if a bank is able to prevent a loss in quality of the grain due to aphid infestation, then the value of a bank increases in years when grain is of high quality and quantity.

Although a strategy for the management of grassy banks has not been developed, and aphid control in fields containing grassy banks is not guaranteed, such banks, like hedgerows, have other uses and may reduce soil erosion by

preventing surface run-off (Forman & Baudry, 1984) or reduce the quantity of pollutants reaching water courses (Schloser & Karr, 1981).

A method of diversification which does not take land out of production, as is required when establishing a grassy bank, is the use of conservation headlands which can provide resources in field margins which increases the populations of both polyphagous epigeal arthropods (Chiverton & Sotherton, 1991) and aphid specific Syrphidae (Cowgill, *et al.*, 1993a). Since the most common Syrphidae of arable land can feed on pollen and/or nectar from a variety of arable weeds (Cowgill, 1991; Cowgill *et al.*, 1993a) as well as from exotic garden plants (A. MacLeod, pers. obs.) and are therefore considered as generalist flower feeders, (Gilbert, 1981) provision of floral resources for beneficial Syrphidae, known to be rich in easily accessible pollen and nectar, is an attractive option when attempting to manipulate the distribution of beneficial Syrphidae on a field scale. Providing such resources around cereal fields in what would otherwise be sterile strips, allows sensible use of land which has already been taken out of production. It was found in Chapter Three that *Lobularia maritima* was selectively foraged upon by both males and females from a range of beneficial species of Syrphidae, but did not grow well in an arable environment. Other plants that would grow well when sown in an arable environment were investigated and led to the utilisation of alternative crops as plants to provide resources for Syrphidae.

Use of potential alternative crops to encourage Syrphidae (Chapter Four) or other beneficial predators into areas of possible aphid infestation could be considered as a "trap cropping" technique. Traditionally, trap cropping is the use of plants that are grown to attract crop pests into selected areas, to prevent pest attack of a more valuable crop. Trap crops should prevent pests from reaching the main crop (Speight, 1983). However trap crops can also function as attractants for natural enemies, concentrating predators to enhance biological control (Hokkanen, 1991). For Syrphidae to be effective at controlling aphids, the hatching of syrphid eggs and development of larvae should coincide, in time and space with the initial growth phase of a population of aphids (Schneider, 1969; Wratten, 1987). Most adult Syrphidae caught during the 1992 and 1993 field experiments were caught after aphid populations had begun to decline. The adults caught in yellow traps may have been larvae in the fields in which they were caught as adults, or could have emerged from nearby fields, or could have been immigrants which pupated much further away.



Provision of flowering resources for the late summer generation of adult Syrphidae then, would not contribute to significant biological control of aphids in cereals. However if provision of plentiful resources contributed to significantly greater numbers of eggs being developed by the late summer generation, then the next generation of Syrphidae may be significantly larger and long-term enhancement of syrphid populations may result. It is possible that the number of eggs developed by a female and/or timing of oviposition is related to the quality and quantity of pollen in field margins from which the female has fed (Cowgill, 1991). Working on the life cycle of *Metasyrphus* sp. in India, Verma & Makhmoor (1989) concluded that egg survival and pupal parasitism were key factors in determining the proportionate survival of adults. If the same factors are involved in the UK, then any increase in the number of eggs that are laid, by providing abundant floral resources, may lead to more eggs surviving and consequently higher adult numbers, assuming that floral resources are a limiting factor in egg production.

Having shown that *E.balteatus* can be attracted preferentially into the vicinity of floral resources, and that while in the area of the resources, *E.balteatus* remains there for longer (Chapter Five), a number of questions need addressing in terms of how such patches can be used in a programme of IPM. The siting of floral patches must be carefully considered. It remains unknown what the optimal length or shape of a floral patch is, or whether two patches covering the same area would act in the same way i.e. does a strip of suitable food plants 100m x 1m attract as many syrphids from the same area as a block of the same food plants 10m x 10m? Another important question that is raised is over what range do the floral attractants work. This will depend upon the flower species in a patch and responses to flowers will probably vary between syrphid species.

Despite the high mobility of Syrphidae, certain features in the arable landscape were shown to provide significant impediments to the even distribution of Syrphidae and presumably to the movement that preceded and resulted in their actual distribution (Chapter Six). Mader *et al.* (1990) found that when Carabidae encountered a linear feature which acted as a barrier, the resultant movement and distribution of Carabidae was parallel to the feature. With more information about such features in the UK, it may be possible to identify the localities on a farm where floral strips could be situated and which would be able to attract beneficial arthropods, including syrphids, from a wide area and allow them to disperse easily to surrounding

crops providing the maximum opportunity for beneficials to influence the development of aphid populations.

Broad-spectrum insecticides used in attempts to control aphids can be toxic to non-target beneficial organisms (e.g. Powell, Dean & Bardner, 1985; Cole, Everett, Wilkinson & Brown, 1986; Wiles & Jepson, 1992). Mathematical simulation models have been developed which illustrate the impact that applications of pesticides have on non-target organisms (Thacker, 1991). Such models should consider the patterns of resurgence of aphids, or re-invasion of beneficials which occur after such perturbations (Duffield & Aebischer, 1994). Some of the models have taken into account the influence that field boundaries can have on the rate of movement of epigeal arthropods into insecticide treated areas, from adjacent untreated areas (Sherratt & Jepson, 1993). The rate of re-invasion can be related to the permeability of field boundaries (Mauremootoo & Wratten, 1994; Jepson, 1994; Frampton *et al.*, 1995). With more information about the toxicity of pesticides to Syrphidae (Moyle, 1994) and the permeability of various linear feature types to Syrphidae (Chapter Six), the range of taxa covered by such models can be increased to include Syrphidae, so that pesticide side effects can be predicted with greater accuracy.

The summer field experiments described in Chapters 4, 5 & 6 relied on the use of yellow water pan-traps. Interpretation of any data collected should take into account the sampling technique used to gather the data. Pitfall traps, extensively used in the study of epigeal arthropods, supposedly reflect the activity and abundance of populations from which individuals are sampled. Use of pitfall traps has been criticized e.g. Topping & Sunderland (1992). Yellow water pan traps may also be liable to some of the same types of criticism directed at pitfall traps e.g. between species, between sex and between individuals with differences in hunger levels, affecting likelihood of capture. However no other convenient means of sampling could be used to get sufficient data when trying to examine differences between control and experimental fields or control and experimental strips when studying Syrphidae and interpretation of results did take into consideration intrinsic faults that the sampling technique may be susceptible to.

#### Future Work

##### i) Grassy banks

Future work on within-field grassy banks should investigate the effect that polyphagous predators have on field populations of aphids. It has been shown

elsewhere (Thomas *et al.*, 1991) that polyphagous Coleoptera emigrate in the spring and early summer from overwintering sites on grassy banks within cereal fields. Artificial baits at various distances from the banks were fed upon by emigrating beetles (Thomas, 1991) but no effect on aphid populations in the open field has been shown. However, Mauremootoo, Wratten & Worner (in prep) have recently carried out a preliminary investigation on predation of aphids by polyphagous predators from a bank within a cereal field. Emigrating predators were however prevented from dispersing more than 5m from the bank by polythene barriers which surrounded parts of the bank and standing crop to a distance of 5m from the bank. This ensured a high density of predators in enclosed plots and a substantial predation pressure on aphids within the enclosed plots. Future work should compare fields with and without grassy banks. Sampling polyphagous predators and aphids throughout the year would allow comparison of polyphagous predators and aphid populations between fields, and would be of great value in assessing the impact that such grassy banks and predators have in the cereal ecosystem.

#### ii) Additional floral resources for Syrphidae

Existing wild flowers can provide suitable resources which allow the development of eggs in female Syrphidae, but a more active management strategy for field boundaries would be to drill plants, known to be fed upon by beneficial Syrphidae, into field boundaries. Current work at Southampton University is investigating this technique with native and non-native flora. In collaboration with Willmot Industries, mixtures of native herbs have been sown in field boundaries to encourage beneficial arthropods into such sites. Managed sites with a high diversity of vegetation also have conservation value for butterflies and small mammals. In contrast to using mixtures of native plants, a single sown non-native plant (*Phacelia tanacetifolia*) is currently being investigated for its potential to be used to manipulate beneficial Syrphidae on a field scale. The development of alternative crops in the future could result in crop plants which have added value as providers of nutrients to beneficial Syrphidae.

Measurement of syrphid utilisation of potentially alternative crops could result in a ranking of crops to determine which are most suitable to be used to manipulate Syrphidae on a field or farm scale. The timing and duration of flowering should also be considered, as should the nutritive value of pollen or nectar. Alternative crops could also be examined for their potential to harbour non-pest aphids which could act

as alternative resources early in the season, before cereal aphid populations rise. However alternative crops are still being investigated for use in the UK and much work remains to be carried out to determine which candidate crops will grow best in the UK climate. Optimal sowing dates and rates are still to be determined, as are the responses to herbicides of potential alternative crops (P. Burton pers. comm.). Harvesting techniques and commercial viability of alternative crops are also being investigated. It is possible however, that if a candidate crop is successfully developed for large scale use in the UK, and that it is also foraged upon by Syrphidae, that the crop may be grown in wide strips around or even within cereal fields, especially if pressure to reduce cereal production continues.

### iii) Manipulating syrphid oviposition

Differences in the distribution of Syrphidae at sites of contrasting floral richness, has been attributed to syrphids attraction to the resources and the additional time that is spent foraging at the resources. However few investigations which provided additional floral resources for Syrphidae have resulted in enhanced oviposition. The scale at which such investigations have been carried out has been too small, and future work should be conducted on a much larger scale, possibly with farms as replicates. This would reduce the effect that results from the high mobility of Syrphidae.

A useful approach to investigate any spatial relationship between feeding sites and oviposition sites would be to provide a food source which contained a marker which would be passed to any subsequent eggs which developed. Parker & Pinnel (1972) reported that lepidoteran eggs could be stained pink by feeding a red dye to females. Sucrose solutions containing an orange dye, fed to female Syrphidae, have resulted in the females' laying orange eggs (J. Hickman, pers. comm.) Development of this technique to allow its use in the field, could provide important information about the spatial dynamics of syrphid movement between feeding and ovipositional sites.

In summary, the work in this thesis has developed the potential for enhancing local syrphid populations and activity in the agroecosystem. It remains to be seen whether this approach, along with other IPM strategies will assume a significant role in the sustainable production of cereals in Western Europe. Socio-economic factors, as always, will influence this.

## APPENDIX I

Tabulated representation of the linear randomised block design of the raised grassy bank as it was established in Spring 1987. A.s. = *Agrostis stolonifera*, D.g. = *Dactylis glomerata*, H.I. = *Holcus lanatus*, L.p. = *Lolium perenne*, 25% = mix of all of the four grass species, 33% = mix of D.g., H.I. & L.p., B.G. = bare ground, F.P. = flowering herabaceous plants. F.P. plots were not sampled during the study.

Block	Plot	Treatment	Block	Plot	Treatment
A	1	A.s.	D	1	D.g.
A	2	D.g.	D	2	L.p.
A	3	25%	D	3	33%
A	4	B.G.	D	4	A.s.
A	5	33%	D	5	F.P.
A	6	F.P.	D	6	H.I.
A	7	L.p.	D	7	25%
A	8	H.I.	D	8	B.G.
B	1	F.P.	E	1	B.G.
B	2	H.I.	E	2	H.I.
B	3	A.s.	E	3	L.p.
B	4	B.G.	E	4	33%
B	5	L.p.	E	5	25%
B	6	D.g.	E	6	D.g.
B	7	33%	E	7	A.s.
B	8	25%	E	8	F.P.
C	1	B.G.	F	1	L.p.
C	2	H.I.	F	2	H.I.
C	3	25%	F	3	33%
C	4	L.p.	F	4	D.g.
C	5	A.s.	F	5	A.s.
C	6	F.P.	F	6	F.P.
C	7	D.g.	F	7	B.G.
C	8	33%	F	8	25%

B.G. plots were resown with *Arrhenatherum elatius* and F.P. plots were resown with *Festuca rubra* during Autumn 1991.

## APPENDIX II

Hartley's (1950)  $F_{\max}$ -test for homoscedasticity and ANOVA F ratio results for Carabidae within years between grasses

Winter	$F_{\max}$ \ F ratio	<i>Agonum dorsale</i>	<i>Amara</i> spp.	<i>Bembidion obtusum</i>	<i>Bembidion lampros</i>	<i>Demetrias atricapillus</i>	<i>Notiophilus biguttatus</i>	<i>Trechus</i> spp.	other Carabidae	TOTAL Carabidae
1	$F_{\max(0.05)}$	2.47 *	-	1.18 ns	1.76 ns	9.69 *	3.36 *	3.13 *	-	1.43 ns
	F	(0.21 ns)	-	1.98 ns	0.06 ns	(2.26 ns)	(0.60 ns)	(0.87 ns)	-	1.36 ns
2	$F_{\max(0.05)}$	-	2.43 ns	3.86 ns	2.69 ns	6.29 *	-	1.25 ns	-	3.31 ns
	F	-	0.67 ns	3.28 *	4.96 **	(49.29**)	-	0.60 ns	-	25.67 **
3	$F_{\max(0.05)}$	-	1.65 ns	1.94 ns	10.08 *	29.47**	1.32 ns	1.83 ns	-	3.11 *
	F	-	0.22 ns	1.88 ns	(1.70 ns)	(23.90**)	0.03 ns	2.82 *	-	(25.38 **)
4	$F_{\max(0.05)}$	-	-	4.08 ns	-	4.43 *	-	1.80 ns	7.49 *	3.12 ns
	F	-	-	1.81 ns	-	(67.42 **)	-	1.81 ns	(2.74 ns)	22.45 **
5	$F_{\max(0.05)}$	2.70 ns	5.33 *	2.43 ns	1.39 ns	16.83 *	-	-	5.53 *	4.16 ns
	F	0.18 ns	(1.83 ns)	2.00 ns	0.03 ns	(23.72 **)	-	-	(3.15 *)	15.04 **
6	$F_{\max(0.05)}$	12.26 *	2.43 ns	-	4.08 ns	33.21 *	-	-	2.78 ns	5.36 ns
	F	(2.15 ns)	0.75 ns	-	0.03 ns	(28.85 **)	-	-	3.63 *	21.47 **
7	$F_{\max(0.05)}$	6.04 *	1.80 ns	5.39 ns	3.47 ns	4.98 ns	-	4.10 ns	5.00 ns	4.72 ns
	F	(0.72 ns)	0.88 ns	1.68 ns	0.54 ns	30.08 **	-	2.83 *	10.65 **	2.88 *

**Key:** - = density too low for analysis, ns = not significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , numbers in brackets indicate F ratio results from heteroscedastic data.

### APPENDIX III

Hartley's (1950)  $F_{\max}$ -test for homoscedasticity and ANOVA F ratio results for Carabidae between years , within grasses

Grass	$F_{\max}$ \ F ratio	<i>Agonum dorsale</i>	<i>Amara</i> spp.	<i>Bembidion obtusum</i>	<i>Bembidion lampros</i>	<i>Demetrias atricapillus</i>	<i>Notiophilus biguttatus</i>	<i>Trechus</i> spp.	other Carabidae	TOTAL Carabidae
As	$F_{\max(0.05)}$	2.07 ns	5.36 ns	5050 ns	3.11 ns	4.56 ns	-	4.42 ns	4.99 ns	1.93 ns
	F	0.10 ns	0.73 ns	8.14 **	6.07 **	0.97 ns	-	4.99 **	2.30 ns	11.68 **
Dg	$F_{\max(0.05)}$	17.39 *	1.00 ns	13.05 *	6.75 *	2.23 ns	-	1.93 ns	1.47 ns	4.14 ns
	F	(0.55 ns)	1.00 ns	(22.26 **)	(14.21 **)	11.50 **	-	2.38 ns	0.74 ns	11.29 **
Hl	$F_{\max(0.05)}$	36.05 *	2.45 ns	22.59 *	6.46 *	4.30 ns	-	4.15 ns	4.10 ns	9.89 *
	F	(1.04 ns)	0.50 ns	(5.70 **)	(3.98 **)	21.49 **	-	4.07 *	0.95 ns	21.74 **
Lp	$F_{\max(0.05)}$	7.88 *	2.70 ns	3.22 ns	2.98 ns	4.33 ns	-	7.55 *	1.35 ns	1.20 ns
	F	(0.37 ns)	0.01 ns	2.66 ns	1.75 ns	12.20 **	-	2.07 ns	1.00 ns	10.94 **
Ae	$F_{\max(0.05)}$	-	-	-	2.65 ns	2.51 ns	-	-	1.76 ns	2.16 ns
	F	-	-	-	3.00 ns	0.99 ns	-	-	0.30 ns	0.87 ns
Fr	$F_{\max(0.05)}$	-	-	-	1.19 ns	1.01 ns	-	-	-	1.36 ns
	F	-	-	-	0.14 ns	0.01 ns	-	-	-	1.78 ns

**Key:** - = density too low for analysis, ns = not significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$  , numbers in brackets indicate F ratio results from heteroscedastic data.

#### APPENDIX IV

Carabidae recorded in the grassy bank (F21) during sampling over seven winters.

Carabid	Winter	Winter						
	habit	1	2	3	4	5	6	7
<i>Amara</i> spp.	-	*	*	*				
<i>Trechus</i> spp.	-	*	*	*				
<i>Notiophilus biguttatus</i>	O	*	*	*	*		*	
<i>Bembidion obtusum</i>	O	*	*	*	*	*		*
<i>Agonum dorsale</i>	B	*			*	*	*	*
<i>Bembidion lampros</i>	B	*	*	*	*	*	*	*
<i>Demetrias atricapillus</i>	B	*	*	*	*	*	*	*
<i>Bradycellus verbasci</i>	-				*	*	*	*
<i>Dromius linearis</i>	-				*	*	*	*
<i>Trechus secalis</i>	B				*			
<i>Badister bipustulatus</i>	-				*	*		
<i>Pterostichus madidus</i>	O				*	*		
<i>Harpalus affinis</i>	O				*	*		
<i>Calathus melanocephalus</i>	-				*		*	
<i>Trechus quadrisriatus</i>	B				*			*
<i>Amara apricaria</i>	-				*	*		*
<i>Pterostichus melanarius</i>	O					*		
<i>Amara plebeja</i>	B					*	*	*
<i>Stomis pumicatus</i>	-						*	
<i>Amara similata</i>	-						*	
<i>Panageaus bipustulatus</i>	B						*	
<i>Harpalus rufipes</i>	-						*	
<i>Patrobus atrorufus</i>	-						*	*
<i>Asaphidion flavipes</i>	B						*	*
<i>Bembidion quadrimaculatum</i>	B							*
<i>Loricera pilicornis</i>	-							*
Number of Genera		6	5	5	12	9	13	11

B= Boundary type Carabidae; O= Open-field type Carabidae; -= Unknown overwintering strategy; \*= species present on the bank.



# APPENDIX V

Hartley's (1950)  $F_{\max}$ -test for homoscedasticity and ANOVA  $F$  ratio results for Staphylinidae within winters between grasses

Winter	$F_{\max}$ \ $F$ ratio	<i>Tachyporus hypnorum</i>	other <i>Tachyporus</i> spp.	<i>Stenus</i> spp.	Aleocharinae	Paederinae	Staphylininae	other Staphylinidae	TOTAL Staphylinidae
1	$F_{\max(0.05)}$	12.37 *	5.44 *	1.00 ns	-	-	3.48 ns	1.83 ns	3.84 *
	$F$	(4.33 **)	(3.13 ns)	0.00 ns	-	-	1.96 ns	0.72 ns	(5.18 **)
2	$F_{\max(0.05)}$	2.18 ns	2.02 ns	1.87 ns	1.45 ns	-	-	-	6.04 *
	$F$	8.20 **	0.90 ns	7.23 **	5.03 **	-	-	-	(7.85 **)
3	$F_{\max(0.05)}$	2.55 ns	1.40 ns	2.06 ns	-	-	1.99 ns	2.22 ns	1.71 ns
	$F$	5.99 **	0.81 ns	0.79 ns	-	-	3.61 *	1.24 ns	2.85 *
4	$F_{\max(0.05)}$	2.28 ns	1.82 ns	1.35 ns	1.90 ns	2.50 ns	1.58 ns	-	3.00 ns
	$F$	3.68 *	3.11 *	0.33 ns	0.19 ns	0.70 ns	1.18 ns	-	4.83 **
5	$F_{\max(0.05)}$	1.52 ns	4.52 ns	3.38 ns	1.64 ns	-	1.52 ns	-	1.94 ns
	$F$	1.05 ns	2.00 ns	0.28 ns	0.28 ns	-	0.73 ns	-	1.40 ns
6	$F_{\max(0.05)}$	8.39 *	1.98 ns	8.70 *	2.41 ns	2.38 ns	2.80 ns	-	2.55 ns
	$F$	(31.90 **)	14.95 **	(5.31 **)	6.78 ns	4.48 **	5.96 **	-	110.26 **
7	$F_{\max(0.05)}$	2.50 ns	3.30 ns	24.92 *	3.12 ns	2.06 ns	2.17 ns	-	4.25 ns
	$F$	3.90 **	2.26 *	0.26 ns	20.99 **	1.76 ns	3.28 *	-	63.97 **

Key: - = density too low for analysis, ns = not significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , numbers in brackets indicate  $F$  ratio results from heteroscedastic data.

# APPENDIX VI

Hartley's (1950)  $F_{\max}$ -test for homoscedasticity and ANOVA F ratio results for Staphylinidae between winters within grasses

Winter	$F_{\max}$ \ F ratio	<i>Tachyporus hypnorum</i>	other <i>Tachyporus</i> spp.	<i>Stenus</i> spp.	Aleocharinae	Paederinae	Staphylininae	other Staphylinidae	TOTAL Staphylinidae
As	$F_{\max(0.05)}$	2.01 ns	2.04 ns	7.30*	1.56 ns	6.71 *	6.95 *	-	3.33 ns
	F	14.48 **	2.83 *	(2.96 *)	2.18 ns	(10.44 **)	(5.66 **)	-	6.72 **
Dg	$F_{\max(0.05)}$	5.87 ns	2.61 ns	28.11 *	1.26 ns	1.38 ns	4.26 ns	-	3.57 ns
	F	9.47 **	3.91 **	(3.57 *)	7.04 **	1.63 ns	7.31 **	-	10.20 **
HI	$F_{\max(0.05)}$	1.65 ns	4.52 ns	6.40 *	3.41 ns	4.21 ns	6.50 *	-	5.29 ns
	F	13.27 **	4.17 **	(12.48**)	1.58 ns	34.68 **	(4.03 **)	-	8.43 **
Lp	$F_{\max(0.05)}$	2.16 ns	2.37 ns	11.59 *	2.01 ns	-	7.70 *	-	2.43 ns
	F	36.28 **	11.27 **	(8.85 **)	1.50 ns	-	(50.72 **)	-	7.90 **
Ae	$F_{\max(0.05)}$	2.72 ns	1.11 ns	1.38 ns	1.82 ns	1.48 ns	3.13 ns	-	1.32 ns
	F	4.83 *	0.20 ns	1.70 ns	3.95 ns	0.38 ns	0.33 ns	-	0.07 ns
Fr	$F_{\max(0.05)}$	1.38 ns	1.48 ns	1.13 ns	1.13 ns	1.40 ns	1.17 ns	-	2.03 ns
	F	0.03 ns	6.21 *	10.47 **	0.53 ns	0.94 ns	0.21 ns	-	0.68 ns

Key: - = density too low for analysis, ns = not significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$  Numbers in brackets indicate F ratio results from heteroscedastic data.

## APPENDIX VII

Hartley's (1950)  $F_{\max}$ -test for homoscedasticity and ANOVA F ratio results for Araneae within winters between grasses.

Winter		Linyphidae	Lycosidae	other Araneae
1	$F_{\max (0.05)}$	2.90 ns	2.48 ns	-
	F ratio	25.14 **	1.44 ns	-
2	$F_{\max (0.05)}$	2.84 ns	2.73 ns	-
	F ratio	10.61 **	0.48 ns	-
3	$F_{\max (0.05)}$	2.14 ns	2.46 ns	-
	F ratio	5.65 **	5.67 **	-
4	$F_{\max (0.05)}$	3.30 ns	2.92 ns	-
	F ratio	2.89 ns	24.65 **	-
5	$F_{\max (0.05)}$	9.32 *	2.66 ns	5.63 ns
	F ratio	(0.53 ns)	0.60 ns	2.74 ns
6	$F_{\max (0.05)}$	2.59 ns	8.49 *	7.25 *
	F ratio	13.77 **	(17.59 **)	(138.75 **)
7	$F_{\max (0.05)}$	3.47 ns	1.77 ns	6.87 *
	F ratio	5.00 **	9.45 **	(210.41 **)

## APPENDIX VIII

Hartley's (1950)  $F_{\max}$ -test for homoscedasticity and ANOVA F ratio results for Araneae between winters within grasses.

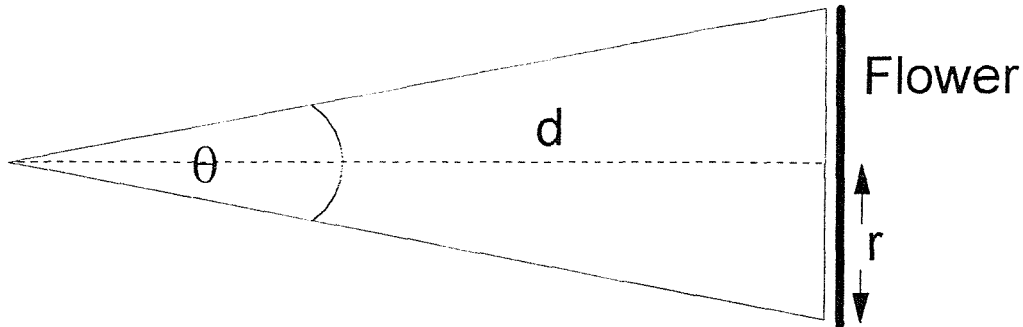
Grass		Linyphidae	Lycosidae	other Araneae
A.s.	$F_{\max (0.05)}$	5.32 ns	4.99 ns	-
	F ratio	3.11 **	7.49 **	-
D.g.	$F_{\max (0.05)}$	3.03 ns	5.53 ns	4.20 ns
	F ratio	3.25 *	11.38 **	1.43 ns
H.l.	$F_{\max (0.05)}$	2.28 ns	4.27 ns	6.45 *
	F ratio	15.74 **	5.43 **	( 1.30 ns)
L.p.	$F_{\max (0.05)}$	6.91 *	1.66 ns	-
	F ratio	(15.48 **)	6.92 **	-
A.e.	$F_{\max (0.05)}$	1.33 ns	1.75 ns	-
	F ratio	20.68 **	1.62 ns	-
F.r.	$F_{\max (0.05)}$	2.56 ns	4.59 *	-
	F ratio	0.05 ns	(10.35 **)	-

**Key :** ns = not significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , numbers in brackets indicate F ratio results from heteroscedastic data.

## APPENDIX IX

### Calculations used to estimate the distance at which a syrphid will identify a flower

1) M.Land (Pers. Comm.)



$\theta$  = ommatidial acceptance angle

$d$  = distance to flower

$r$  = radius of flower head

Then,  $\tan \theta/2 \cdot d = r$

1) Consider a flower, with a diameter of 1cm, then  $r = 0.5\text{cm}$ .

and if  $\theta = 1^\circ$  (as suggested by Land), and  $r = 0.5\text{cm}$ ,

then  $d = r / (\tan \theta/2)$

$$= 0.5 / (\tan 0.5^\circ) \approx 0.5 / 0.0087$$

$$\approx \underline{57.29\text{cm}}$$

2) Consider a flower with a diameter of 10cm,  $r = 5\text{cm}$ .

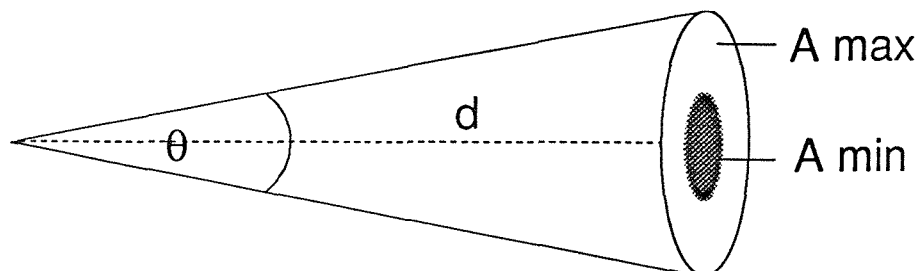
$$\text{then } d = 5 / (\tan 0.5^\circ) \approx 5 / 0.0087$$

$$\approx \underline{5.73\text{m}}$$

## APPENDIX X

Calculations used to estimate the distance at which a syrphid will identify a flower

2) Dafni & Kevan (In Prep.)



$\theta$  = ommatidial acceptance angle

$d$  = distance to flower

$A_{\max}$  = Area covered by the complete field of vision of a single ommatidium.

$A_{\min}$  = Minimum area of an object to be resolved by a single ommatidium

Assume a contrast sensitivity ( $C$ ) of 23% (Wolf, 1933)

$$\text{Now, } A_{\max} = \pi r_{\max}^2 = \pi (\tan \theta/2)^2 (d)^2$$

$$A_{\min} = \pi r_{\min}^2$$

$$\text{To distinguish } A_{\min}, d^2 = A_{\min} / C \pi (\tan \theta/2)^2$$

$$\text{and } d = \sqrt{A_{\min}} / \sqrt{C \pi (\tan \theta/2)^2}$$

For  $C$  of 23%, and  $\theta$  of  $1^\circ$ ,

$$d = \sqrt{A_{\min}} / \sqrt{0.23 \cdot \pi \cdot 0.0087^2}$$

1) Consider a flower of diameter 1cm, then  $r_{\min} = 0.5\text{cm}$ , and  $A_{\min} = 0.7854\text{cm}^2$

$$d = \sqrt{0.7854} / 0.0074$$

$$= 119.87\text{cm}$$

$$\approx \underline{120\text{cm}}$$

2) Consider a flower with 10cm diameter, then  $r_{\min} = 5\text{cm}$ , and  $A_{\min} = 78.54\text{cm}^2$

$$d = \sqrt{78.54} / 0.0074$$

$$= 11.99\text{m}$$

$$\approx \underline{12.0\text{m}}$$

## APPENDIX XI

### A mathematical model to describe the number of Syrphidae at two different floral resources

The purpose of this model is to find the equilibrium ratio of the number of syrphids at a control versus enhanced site based solely on differential retention rates of each site.

Consider two sites of different floral resources.

One site (the control) is poor in terms of floral resources available to Syrphidae

Number of Syrphidae at control, at time  $t = N_{ct}$  . . . . .  $N_{ct}$

Number of Syrphidae at control, at time 0 =  $N_{c0}$  . . . . .  $N_{c0}$

The second site (flowers) is rich in available resources.

Number of Syrphidae at flower site, at time  $t = N_{ft}$  . . . . .  $N_{ft}$

Number of Syrphidae at flower site, at time 0 =  $N_{f0}$  . . . . .  $N_{f0}$

#### Assumptions

i) Syrphidae move randomly and come across either site with equal chance, the rate of immigration into both sites is therefore the same.

Rate of immigration to both sites =  $\mu$  . . . . .  $\mu$

ii) Syrphidae emigrate from the sites at different but constant rates e.g. due to differences in time spent feeding.

Rate of emigration from Control site =  $\lambda_c$  . . . . .  $\lambda_c$

Rate of emigration from Flower site =  $\lambda_f$  . . . . .  $\lambda_f$

The rate of change of numbers of Syrphidae at each site can be expressed mathematically e.g. for the control site,

$$dN_{ct}/dt = \mu - \lambda_c N_{ct}$$

$$\int_{N_{c0}}^{N_{cT}} \frac{1}{(\mu - \lambda_c N_{ct})} dN_{ct} = \int_0^T dt$$

Solving the above expression gives the following equation,

$$T = \left[ (-1/\lambda_c) \log e (-\lambda_c N_{ct} + \mu) \right]_{N_{c0}}^{N_{cT}}$$

i.e. 
$$T = -1/\lambda_c \left[ \log e^{(-\lambda_c N_{ct} + \mu) / (-\lambda_c N_{c0} + \mu)} \right]$$

expanding the log,

$$(\mu - \lambda_c N_{c0} / \mu - \lambda_c N_{ct}) = e^{\lambda_c T}$$

rearranged,

$$\mu - \lambda_c N_{c0} = e^{\lambda_c T} \mu - \lambda_c N_{ct} e^{\lambda_c T}$$

rearranged,

$$\lambda_c N_{ct} e^{\lambda_c T} = e^{\lambda_c T} \mu + \lambda_c N_{c0} - \mu$$

rearranged,

$$N_{ct} = (\mu e^{\lambda_c T} + \lambda_c N_{c0} - \mu) / \lambda_c e^{\lambda_c T}$$

The same equation (substituting  $N_{t0}$  and  $N_{ct}$  for  $N_{c0}$  and  $N_{ct}$ ) also describes the number of Syrphidae at the flower site.

Thus the ratio of numbers of Syrphidae at the flower site to the numbers of Syrphidae at the control site ( $N_t / N_{ct}$ ) can be expressed as shown below,

$$N_t / N_{ct} = \left[ (\mu e^{\lambda_t T} + \lambda_t N_{t0} - \mu) / \lambda_t e^{\lambda_t T} \right] / \left[ (\mu e^{\lambda_c T} + \lambda_c N_{c0} - \mu) / \lambda_c e^{\lambda_c T} \right]$$

At time zero assume there are no Syrphidae at either site, hence  $\lambda_t N_{t0} = 0$  and  $\lambda_c N_{c0} = 0$

thus,

$$N_t / N_{ct} = \left[ (\mu e^{\lambda_t T} - \mu) / \lambda_t e^{\lambda_t T} \right] / \left[ (\mu e^{\lambda_c T} - \mu) / \lambda_c e^{\lambda_c T} \right]$$

take  $\mu$  outside the brackets,

$$N_t / N_{ct} = \left[ \mu (e^{\lambda_t T} - 1) / \lambda_t e^{\lambda_t T} \right] / \left[ \mu (e^{\lambda_c T} - 1) / \lambda_c e^{\lambda_c T} \right]$$

$\mu$ 's cancel on both sides,

$$N_t / N_{ct} = \left[ (e^{\lambda_t T} - 1) / \lambda_t e^{\lambda_t T} \right] / \left[ (e^{\lambda_c T} - 1) / \lambda_c e^{\lambda_c T} \right]$$

cross multiplying,

$$N_t / N_{ct} = \left[ (e^{\lambda_t T} - 1) \lambda_c e^{\lambda_c T} \right] / \left[ (e^{\lambda_c T} - 1) \lambda_t e^{\lambda_t T} \right]$$

therefore,

$$N_{ft} / N_{ct} = \left[ k (\lambda_c / \lambda_f) \right]$$

$$\text{where } k = \left[ (e^{\lambda_{ft}} - 1) e^{\lambda_{ct}} \right] / \left[ (e^{\lambda_{ct}} - 1) e^{\lambda_{ft}} \right]$$

We seek a limit for k,

Conditions for  $k < 1$  are as follows,

$$e^{\lambda_{ft}} e^{\lambda_{ct}} - e^{\lambda_{ct}} < e^{\lambda_{ct}} e^{\lambda_{ft}} - e^{\lambda_{ft}}$$

cancelling on both sides,

$$- e^{\lambda_{ct}} < - e^{\lambda_{ft}}$$

since we expect  $\lambda_c \geq \lambda_f$  we know that this condition is always satisfied.

Hence,

$$N_{ft} / N_{ct} \leq \lambda_{ct} / \lambda_{ft}$$

If immigration rates are the same, and emigration rate from the control is higher than from the flower site, then  $N_{ft} / N_{ct}$  should be equal to or no more than  $\lambda_{ct} / \lambda_{ft}$ .

If however  $N_{ft} / N_{ct}$  is greater than  $\lambda_{ct} / \lambda_{ft}$ , then immigration rates to the sites are not equal, and immigration rate to the flower site is higher than the immigration rate to the control site. A higher immigration rate to the flower site could be as a result of being attracted to the visual stimuli of flowers, from an unknown distance.



## REFERENCES

- Adams, T.H.L. (1984)** The effectiveness of aphid-specific predators in preventing outbreaks of cereal aphids. PhD Thesis, University of East Anglia.
- Aebischer, N.J. (1991)** Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. In: The Ecology of Temperate Cereal Fields. Eds. L.G. Firbanks, N. Carter, J.F. Darbyshire & G.R. Potts. Blackwell, London.
- Allen, R.T. (1979)** The occurrence and importance of ground beetles in agriculture and surrounding habitats. In: Carabid Beetles, Their Evolution, Natural History and Classification. Eds. T.L. Edwin, G.E. Ball & D.R. Whitehead. W.Junks, The Hague.
- Altieri, M.A. & Letourneau, D.K. (1982)** Vegetation management and biological control in agroecosystems. Crop Protection, **1**, 405-430.
- Ankersmit, G.W. (1989)** Integrated control of cereal aphids. In: Aphids, Their Biology, Natural Enemies and Control Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- Ankersmit, G.W., Dijkman, H., Keuning, N.J., Mertens, H., Sins, A. & Tacoma, H.M. (1986)** *Episyrphus balteatus* as a predator of the cereal aphid *Sitobion avenae* on winter wheat. Entomologia Experimentalis et Applicata, **42**, 271-277.
- Andow, D. (1983)** Effect of agricultural diversity on insect populations. In: Environmentally Sound Agriculture Ed. W.Lockeretz, Praeger, New York.
- Anon. (1977)** Standard Names for Common Insects of New Zealand The Entomological Society of New Zealand, Auckland.
- Anon. (1984)** Ministry of Agriculture, Fisheries and Food ADAS Identification Cards (IC) No.91, Grain aphid; No. 92 Rose-grain aphid & No.95. Bird-cherry aphid. HMSO, London.
- Anon. (1988)** Grain aphid control. ADAS Divisional Bulletin No.144, June 1988.
- Anon. (1990)** Set-aside:MAFF leaflet SA1 (revision 2) and SA6. Ministry of Agriculture, Fisheries and Food, London.
- Anon. (1992)** 1992 Harvest: Provisional estimates of cereal production - England and Wales Ministry of Agriculture, Fisheries and Food, Statistics 189/92.
- Asselin, A. & Baudry, J. (1989)** Les araneids dans un espace agricole en mutation. Acta Oecologica Oecologia Applicata, **10**, 143-156.
- Auclair, J.L. (1989)** Host Plant Resistance. In: Aphids, Their Biology, Natural Enemies and Control, Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- Baker, H.G. & Baker, I. (1979)** Starch in angiosperm pollen grains and its evolutionary significance. American Journal of Botany, **66**, 591-600.
- Banaszak, J. (1984)** The occurrence and numbers of bees (Apoidea) on some cultivated crop plants in the Wiekopolska region (West Poland). Bulletin Entomologique De Pologne,

- Bankowska, R. (1964) Studies on the palearctic species of the genus *Sphaerophoria*. Annotates Zoologici, **22**, 285-353.
- Bardner, R. & Fletcher, K.E. (1974) Insect infestations and their effects on the growth and yield of field crops: a review. Bulletin of Entomological Research, **64**, 141-160.
- Barr, C., Howard, D., Bunce, B., Gillespie, M. & Hallam, C. (1991) Changes in the hedgerows in Britain between 1984 and 1990. NERC contract report to Dept. of Environment, Institute of Terrestrial Ecology, Grange-Over-Sands.
- Basedow, T. (1982) The effects of *Coccinella septempunctata* on the population dynamics of the cereal aphids in Northern Germany. In: Aphid Antagonists, Ed. R. Cavalloro. AA Balkema, Rotterdam.
- Basedow, T., Leidtke, W. Rzehak, H. (1990) Population density of cereal aphids and of their antagonists in cereal fields grown at different intensities in Schleswig-Holstein. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie, **7**, 600-607.
- Baswana, K.S. (1984) Role of insect-pollinators on seed production in coriander and fennel. South Indian Horticulture, **32**, 117-118.
- Ben Saad, A.A. & Bishop, G.W. (1976) Effect of artificial honeydew on insect communities in potato fields. Environmental Entomology, **5**, 453-457.
- Bhati, D.S. (1988) Effect of nitrogen application and row spacing on coriander (*Coriandrum sativum*) production under irrigated conditions in semi-arid Rajasthan. Indian Journal of Agricultural Sciences, **58**, 568-569.
- Boatman, N.D. (1989) Selective weed control in field margins. Proceedings 1989 Brighton Crop Protection Conference - Weeds, **2**, 785-794.
- Boatman, N.D. (1992) Improvement of field margin habitat by selective control of annual weeds. Aspects of Applied Biology, **29**, 431-436.
- 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.
- Bode, E. (1980) Aphids in winter wheat: abundance and limiting factors from 1976 - 1979. IOBC Bulletin WPRS, **3**, 49-57.
- Bossenbroek, P.H., Kessler, A., Liem, A.S.N. & Viljm, L. (1977) The significance of plant growth-forms as "shelter" for terrestrial animals. Journal of Zoology, **182**, 1-6.
- Bowden, J., & Dean, G.J.W. (1977) The distribution of flying insects in and near a tall hedgerow. Journal of Applied Ecology, **14**, 343-354.
- Brenner, R.J. (1984) An *in vivo* fluorescent marker for spermatozoa of the screwworm (Diptera: Caliphoridae): a first report. Proceedings of the Entomological Society.

Washington, 86, 714-719.

- 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 aphid prey. Ecological Entomology, 9, 251-259.
- Bugg, R.L. (1993)** Habitat manipulation to enhance the effectiveness of aphidophagous hoverflies (Diptera: Syrphidae). Sustainable Agriculture Technical Reviews, 5, 12-15.
- Bugg, R.L., Dutcher, J.D. & McNeill, P.J. (1991)** Cool-season cover crops in the Pecan orchard understory: Effects on Coccinellidae (Coleoptera) and Pecan aphids (Homoptera: Aphididae). Biological Control, 1, 8-15.
- Bugg, R.L., Sarrantonio, M., Dutcher, J.D., & Phatak, S.C. (1991)** Understory cover crops in pecan orchards: possible management systems. American Journal of Alternative Agriculture, 6, 50-62.
- Bultman, T.L. & Uetz, G.W. (1982)** Abundance and community structure of forest floor spiders following litter manipulation. Oecologia, 55, 34-41.
- Bunce R.G.H & Heal O.W. (1984)** Landscape evaluation and the impact of changing land use on the rural environment: the problem and an approach. In : Planning and Ecology Eds. R.D. Roberts & T.M. Roberts, Chapman & Hall, London.
- Burel, F. (1989)** Landscape structure effects on carabid beetles spatial patterns in western France. Landscape Ecology, 2, 215-226.
- Burel, F. & Baudry, J. (1990)** Structural dynamics of hedgerow network landscapes in Brittany, France. Landscape Ecology, 4, 197-210.
- Burn, A.J., Coaker, T.H. & Jepson, P.C. (1987)** Integrated Pest Management. Academic Press, London.
- Campbell, C.G. (1987)** Registration of CM221 semidwarf buckwheat germplasm. Crop Science, 27, 151.
- Carter, N., McLean, I.F.G., Watt, A.D. & Dixon, A.F.G., (1980)** Cereal aphids: a case study and review. Applied Biology, 5, 271- 348.
- Carter, N. & Sotherton, N.W. (1983)** The role of polyphagous predators in the control of cereal aphids. Tenth International Congress of Plant Protection 1983, 778.
- Carver, M. (1989)** Biological control of aphids. In: Aphids, Their Biology, Natural Enemies and Control. Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- Cavalloro, R. (1982)** In: Aphid Antagonists Ed. R.Cavalloro. A.A. Balkema, Rotterdam.
- Chambers, R.J. (1986)** Preliminary experiments on the potential of hoverflies (Dipt:Syrphidae) for the control of aphids under glass. Entomophaga, 31, 197-204.
- Chambers, R.J. (1988)** Syrphidae. In: Aphids, Their Biology, Natural Enemies and Control Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- 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. (1982)** The abundance of natural enemies of cereal aphids on two farms in Southern England. In: Aphid Antagonists. Ed. R.Cavalloro, A.A. Balkema, Rotterdam.
- Chambers, R.J., Sunderland, K.D., Stacey, D.L., & Wyatt, I.J. (1982)** A survey of cereal aphids and their natural enemies in winter wheat in 1980. Annals of Applied Biology, **101**, 175- 178.
- Chambers, R.J., Sunderland, K.D., Stacey, D.L., & Wyatt, I.J. (1986)** Control of cereal aphids in winter wheat by natural enemies: aphid specific predators, parasitoids and pathogenic fungi. Annals of Applied Biology, **108**, 219-231.
- 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. (1967)** Oviposition responses by aphidophagous Syrphidae (Diptera). Nature, **213**, 736
- Chandler, A.E.F. (1968a)** The relationship between aphid infestations and oviposition by aphidophagous Syrphidae (Diptera). Annals of Applied Biology, **61**, 425-434.
- Chandler, A.E.F. (1968b)** Some host-plant factors affecting oviposition by aphidophagous Syrphidae (Diptera). Annals of Applied Biology, **61**, 415-423.
- Chandler, A.E.F. (1968c)** Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). Annals of Applied Biology, **61**, 435-446.
- Chaney, W.E. (1990)** Biological control of aphids in lettuce using in-field insectaries I. First Year Progress Report, University of California Cooperative Ext. Salinas.
- Chapman, R.F. (1985)** The Insects. Structure and Function 3rd Edition, Hodder & Stoughton, London.
- Charles, A.H. (1964)** Differential survival of plant types in swards. Journal of the British Grassland Society, **19**, 198-204.
- Chesson, J. (1978)** Measuring preference in selective predation. Ecology, **59**, 211-215.
- Chiverton, P.A. (1986)** Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Homoptera: Aphididae) in spring barley. Annals of Applied Biology, **109**, 49-60.
- Chiverton, P.A. (1987)** Predation of *Rhopalosiphum padi* (Homoptera: Aphididae) by polyphagous predatory arthropods during the aphids pre-peak period in spring barley. Annals of Applied Biology, **111**, 257-269.
- Chiverton, P.A. (1989)** The creation of within-field overwintering sites for natural enemies of cereal aphids. Proceedings 1989 Brighton Crop Protection Conference - Weeds, **3**,

1093-1096.

- Chiverton, P.A. & Sotherton, N.W. (1991) The effects on beneficial arthropods of the exclusion of herbicides from cereal crop edges. Journal of Applied Ecology, **28**, 1027-1039.
- Çilgi, T. (1994) Selecting arthropod "indicator species" for environmental impact assessment of pesticides in field studies. Aspects of Applied Biology, **37**, 131-140.
- Çilgi, T., Wratten, S.D., Frampton, G.K., & Holland, J.M. (1993) The long-term effects of pesticides on beneficial invertebrates-lessons from the Boxworth project. Pesticide Outlook, **4**, 30-35.
- Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1962) Flora of the British Isles, 2nd Edition, Cambridge University Press, Cambridge.
- Clements, F.E. & Long, F.L. (1923) Experimental Pollination. Carnegie Institution Publ. No. 336, Washington.
- de Clercq, R. & Pietraszko, R. (1982) Epigeal arthropods in relation to predation of cereal aphids. In: Aphid Antagonists. Ed. R. Cavalloro, A.A. Balkema. Rotterdam.
- Cole, J.F.H., Everett, C.J., Wilkinson, W. & Brown, R.A. (1986) Cereal arthropods and broad spectrum insecticides. Proceedings of the 1986 Brighton Crop Protection Conference, Pests and Diseases, **1**, 181-188.
- Collett, T. & King, A.J. (1975) Vision during flight. In: The Compound Eye and Vision of Insects Ed. G.A. Horridge, Clarendon, Oxford.
- Collett, T.S. & Land, M.F. (1975) Visual control of flight behavior in the hoverfly *Syritta pipiens* (L.). Journal of Comparative Physiology, **99**, 1-66.
- Collocot, T.C. (1971) Dictionary of Science and Technology. W. & R. Chambers, London.
- Constance, L. & Chuang, T.I. (1982) S.E.M. survey of pollen morphology and classification in Hydrophyllaceae (Waterleaf family). American Journal of Botany, **69**, 40 - 53.
- Coombes, D.S. (1987) Factors limiting the effectiveness of *Demetrias atricapillus* as a predator of cereal aphids. PhD Thesis, University of Southampton.
- Coombes, D.S. & Sotherton, N.W. (1986) The dispersal and distribution of polyphagous predatory Coleoptera in cereals. Annals of Applied Biology, **108**, 461-474.
- Corbet, S.A. (1978) Bee visits and the nectar of *Echium vulgare* L. and *Sinapis alba* L. . Ecological Entomology, **3**, 25-37.
- Corbet, S.A., Unwin, D.M. & Prys-Jones, O.E. (1979) Humidity, nectar and insect visits to flowers, with special reference to *Crataegus*, *Tilia* and *Echium*. Ecological Entomology, **4**, 9-22.
- Cowgill, S.E. (1991) The foraging ecology of hoverflies (Diptera: Syrphidae) and the potential for manipulating their distribution on farmland. PhD Thesis, University Of Southampton.
- 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. Annals 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**, 491-515.
- Crawshaw, A. (1994) Learn to paint : Acrylics. Harper Collins, London.
- Cripps, C. & Rust, C.W. (1989) Pollen foraging in a community of *Osmia* bees (Hymenoptera: Megachilidae). Environmental Entomology, **18**, 582-589.
- Dafni, A. (1994) Note on side advertisement in flowers. Functional Ecology, **8**, 136-138.
- Dafni, A. & Kevan, P.G. (In Prep) Quantification of floral inflorescence and patch sizes for the attraction of pollinators: Implications in pollination ecology
- Daumann, E. (1932) Über die "Scheinnektarien" von *Parnissa palustris* und anderer Blütenasten Jahrbuch der Wissenschaften Botanischer, **77**, 104-149.
- Daumann, E. (1935) Über die Bestäubungsökologie der *Parnissa* II. Jahrbuch der Wissenschaften Botanischer, **81**, 707-717.
- Davies, D.H.K. & Carnegie, H.M. (1994) Vegetation patterns and changes in field boundaries and conservation headlands in Scottish arable fields. In: Field Margins: Integrating Farming and Conservation, Ed. N. Boatman, BCPC Monograph, **58**, 173-178.
- Davies, E.T. & Dunford, W.J. (1962). Some physical and economic considerations of field enlargement. University of Exeter, Dept. of Agricultural Economics Publication No. 133.
- Davies, J.B. (1965) Three techniques for labelling *Culcoides* with radioactive tracers both in the laboratory and in the field. Mosquito News, **25**, 419-422.
- Dean, G.J.W. (1973) Bionomics of aphids reared on cereals and some Graminae. Annals of Applied Biology, **73**, 127-135.
- Dean, G.J. (1974) Effects of parasites and predators on the cereal aphids *Metopolophium dirhodum* and *Macrosiphum avenae* (Hemiptera: Aphididae). Bulletin of Entomological Research, **63**, 411-422.
- Dean, G.J. (1982) Phenology of aphidophagous predators. Annals of Applied Biology, **101**, 182- 184.
- Dean, G.J. (1983) Survival of some aphid (Hemiptera: Aphidae) predators with special reference to their parasites in England. Bulletin of Entomological Research, **73**, 469-480.
- Dean, G.J.W. & Wilding, N. (1971) *Entomophthora* infecting the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae*. Journal of Invertebrate Pathology, **18**, 169-176.
- Dean, G.J.W. & Wilding, N. (1973) Infection of cereal aphids by the fungus *Entomophthora*. Annals of Applied Biology, **74**, 133-138.
- De Bach, P. (1964) Biological Control of Insect Pests and Weeds. Chapman & Hall, London.

- De Bach, P. (1974) Biological Control by Natural Enemies. Cambridge University Press. London.
- Dempster, J.P. & Coaker, T.H. (1974) Diversification of crop ecosystems as a means of controlling pests. In: Biology in Pest and Disease Control. Eds. D. Price-Jones & M.E. Solomon, Blackwell, London.
- Den Boer, P.J. (1977) Dispersal power and survival. Carabids in a cultivated countryside. Miscellaneous papers, Landouwhogeschool; Wageningen, **14**, 1-190.
- Den Boer, P.J. (1981) On the survival of populations in a heterogeneous and variable environment. Oecologia, **50**, 39-53.
- Dennis, P. (1989) The predatory potential of staphylinid beetles in cereals. PhD Thesis, University of Southampton.
- Dennis, P. & Wratten, S.D. (1991) Field manipulations of individual staphylinid species in cereals and their impact on aphid populations. Ecological Entomology, **16**, 17-24.
- Dennis, P., Wratten, S.D. & Sotherton, N.W. (1990) Feeding behaviour of the staphylinid beetle *Tachyporus hypnorum* in relation to its potential for reducing aphid numbers in wheat. Annals of Applied Biology, **117**, 267-176.
- Dennis, R.L.H. (1986) Motorways and cross-movements: an insects "mental map" of the M56 in Cheshire. Bulletin of the Amateur Entomologists Society, **45**, 228-243.
- Dent, D. (1990) Insect pest management. CAB international, Wallingford.
- Desender, K. (1982) Ecological and faunal studies on Coleoptera in agricultural land. II Hibernation of Carabidae in agro-ecosystems. Pedobiologia, **23**, 295-303.
- Desender, K. & D' Hulster, M. (1982) Ecological and faunal studies on Coleoptera in agricultural land. III Seasonal abundance and hibernation of Staphylinidae in the grassy edge of a pasture. Pedobiologia, **23**, 403-414.
- Dethier, V.G. & Chadwick, L.E. (1948) Chemoreception in insects. Physiological Reviews, **28**, 220- 254.
- Dewar, A.M. (1984) Factors affecting cereal aphids in fields monitored by RISCAMS in 1983. Proceedings 1984 Brighton Crop Protection Conference - Pests and Diseases, **1**, 25 - 30.
- D' Hulster, M. & Desender, K. (1983) Ecological and faunal studies on Coleoptera in agricultural land III. Hibernation of the Staphylinidae in agro-ecosystems. Pedobiologia, **26**, 65-73.
- Dietrick, E.J. (1961) An improved back-pack motor fan for suction sampling of insect populations. Journal of Economic Entomology, **54**, 394-395.
- Dixon, T.J. (1959) Studies on oviposition behaviour of Syrphidae (Diptera). Transactions of the Royal Entomological Society of London, **111**, 57-80.
- Dixon, A.F.G. (1987) Cereal aphids as an applied problem. Agricultural Zoology Reviews, **2**,

- Dobson, H.E.M. (1987)** Role of flower and pollen aromas in host-plant recognition by solitary bees. Oecologia, **72**, 618-623.
- Doodson, J.K. (1967)** A survey of barley yellow dwarf virus in S.24 perennial rye grass in England and Wales 1966. Plant Pathology, **16**, 42-45.
- Doodson, J.K. & Saunders, P.J.W. (1970)** Evaluation of the reaction of spring and winter cereal cultivars to BYDV: A summary of methods and results 1965-1970. Journal of the National Institute of Agricultural Botanists, **12**, 100-111.
- Dover, J.W. (1989)** The use of flowers by butterflies foraging - cereal field margins. Entomologist's Monthly Gazette, **40**, 283-291.
- Dover, J.W. (1990)** Butterflies and wildlife corridors. The Game Conservancy Review of 1989, **21**, 62-64.
- Dover, J.W. (1994)** Arable field margins: factors affecting butterfly distribution and abundance. In: Field Margins: Integrating Agriculture and Conservation. Ed. N. Boatman, BCPC Monograph No. 58.
- Duelli, P., Studer, M., Marchand, I. & Jakobs, S. (1990)** Population movement of arthropods between natural and cultivated areas. Biological Conservation, **54**, 193-207.
- Duffey, E. (1956)** Aerial dispersal in a known spider population. Journal of Animal Ecology, **25**, 85-111.
- 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.
- Edgar, W. & Loenen, M. (1974)** Aspects of the habitat of the overwintering wolf spider *Pardosa lugubris*. Journal of the Zoological Society of London, **172**, 383-388.
- Edwards, A.J. (1970)** Field size and machinery efficiency. In: Hedges and Hedgerows Trees. Eds. M.D. Hooper & M.W. Holdgate. Monks Wood Symposium No.4, The Nature Conservancy.
- von Eirdanz, H. & Hirsinger, F. (1990)** New raw materials for oleochemical reactions. Fett-Wissenschaft Technologie, **92**, 463-467.
- Ekbom, B.S. & Wikteliuss, S. (1985)** Polyphagous arthropod predators in cereal crops in central Sweden, 1979-1982. Zeitschrift fur angewandte Entomologie, **99**, 433-442.
- Ellis, P.R. (1992)** The influence of weed vegetation on populations of aphids and their natural enemies. Phytoparasitica, **20** (supplement), 71-75.
- van Emden, H.F. (1963)** Observations on the effect of flowers on the activity of parasitic Hymenoptera. Entomologists Monthly Magazine, **98**, 265-270.
- van Emden, H.F. (1965)** The effect of uncultivated land on the distribution of the cabbage aphid (*Brevicoryne brassicae*) on an adjacent crop. Journal of Applied Ecology, **2**,



- van Emden, H.F. (1988) Potential for managing indigenous natural enemies of aphids in cereal crops. Philosophical Transactions of the Royal Society of London B, **318**, 183-201.
- van Emden, H.F. & Hagen, K.S. (1976) Olfactory reactions of the green lacewing *Chrysopa carnea*, to tryptophan and certain breakdown products. Environmental Entomology, **5**, 460- 473.
- Entwistle, J.C. & Dixon, A.F.G. (1990) The effect of augmenting grain aphid *Sitobion avenae* numbers in a field of winter wheat in spring on the aphid's abundance in summer and its relevance to the forecasting of outbreaks. Annals of Applied Biology, **114**, 397-408.
- Faegri, K. & van der Pijl, L. (1979) The Principles of Pollination Ecology, 3rd Edition, Pergamon Press, Oxford.
- Feinsinger, P., Spears, E.E. & Poole, R.W. (1981) A simple measure of niche breadth. Ecology, **62**, 27-32.
- Finch, S. (1977) Monitoring insect pests on cruciferous crops. Proceedings 9th British Insecticide and Fungicide Conference, **1**, 219-226.
- Fletcher, K.E. & Bardner, R. (1969) Cereal aphids on wheat. In: Report of the Rothamsted Experimental station, 1968, 200-201.
- Ford, E.B (1971) Ecological Genetics, 3rd Edition, Chapman & Hall, London.
- Forman, R.T.T., & Baudry, J. (1984) Hedgerows and hedgerow networks in landscape ecology. Environmental Management, **8**, 495-510.
- Frampton, G.K., Cilgi, 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 (In press)
- Fraser, A.M. (1982) The role of spiders in determining cereal aphid numbers. Ph.D Thesis, University of East Anglia.
- Frazer, B.D. (1972) A simple and efficient method of rearing aphidophagous hoverflies (Diptera: Syrphidae) Journal of the Entomological Society of British Columbia, **69**, 23-24.
- Frazer, B.D. (1988) Predators, In: Aphids, Their Biology, Natural Enemies and Control. Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- Freer, B. (1990) The story on your novel crops. Crops, **7**, 8-9.
- Fry, G.L.A. & Robson, W.J. (1994) The effect of field margins on butterfly movement. In: Field Margins: Integrating Agriculture and Conservation. Ed. N. Boatman. BCPC Monograph No. 58
- Fuller, J. (1975) The aggregativeness of various materials on Carabidae. Masters Thesis University of Arkansas.

- George, K.S. (1957) Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). Bulletin of Entomological Research, 619-629.
- George, K.S. & Gair, R. (1979) Crop loss assessment on winter wheat attacked by the grain aphid *Sitobion avenae* F. 1974-1977. Plant Pathology, 28, 143-149.
- Gibson, C.W.D., Hambler, C. & Brown, V.K. (1992) Changes in the spider (Araneae) assemblages in relation to succession and grazing management. Journal of Applied Ecology, 29, 132-142.
- Gilbert, F.S. (1980) Flower visiting by hoverflies (Syrphidae). Journal of Biological Education, 14, 70-74.
- Gilbert, F.S. (1981) The foraging ecology of hoverflies (Diptera, Syrphidae): Morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecological Entomology, 6, 245-262.
- Gilbert, F.S. (1985) Ecomorphological relationships in hoverflies (Diptera, Syrphidae). Proceedings of the Royal Society of London B, 224, 91-105.
- Gilbert, F.S. (1986) Naturalists' Handbook 5 - Hoverflies. Eds. S.A. Corbet & R.H.L. Disney, Cambridge University Press, London.
- Gillies, M.T. (1961) Studies on the dispersal and survival of *Anopheles gambiae* in East Africa, by means of marking and release experiments. Bulletin of Entomological Research, 52, 99-127.
- van der Goot, V.S., Grabandt, R.A.J. (1970) Some species of the genera *Melanostoma*, *Platycheirus* and *Pyrophaena* (Diptera: Syrphidae) and their relationship to flowers. Entomologische Berichten, 30, 135-143.
- Greaves, M.P. & Marshall, E.J.P. (1987) Field Margins: Definitions and statistics. In: Field Margins Eds. J.M. Way & P.W. Greig-Smith. BCPC No. Monograph 35.
- Greenstone, M.H. (1984) Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. Oecologia, 62, 299-304.
- Greig-Smith, P.W., Frampton, G.K. & Hardy, A.R. (1992) Pesticides, Cereal Farming and the Environment :The Boxworth Project, HMSO, London.
- Griffiths, E. Wratten, S.D. & Vickerman, G.P. (1985) Foraging by the carabid *Agonum dorsale* in the field. Ecological Entomology, 10, 181-189.
- Grime, J.P. (1987) Dominant and subordinate components of plant communities: Implications for succession, stability and diversity. In: Colonisation, Succession and Stability Eds. A.J. Gray, M.J. Crawley & P.J. Edwards. Blackwell, London.
- Gross, H.R. (1987) Conservation and enhancement of entomophagous insects - a perspective. Journal of Entomological Science, 22, 97-105.
- Grubb, P.J. (1982) Control of relative abundance in roadside *Arrhenatherum*: results of a long-term garden experiment. Journal of Ecology, 70, 845-861.

- Hagvar, E.B. (1974) Effectiveness of larvae of *Syrphus ribesii* and *S.corollae* as predators of *Myzus persicae*. Entomophaga, 19, 123-134.
- Hamakawa, H. (1986) Feeding behaviour of honeybees (*Apis cerana* and *Apis mellifera*) and *Vespa flavipes* visiting the flowers of buckwheat *Fagopyrum esculentum* Moench. Honeybee Science, 7, 53-56.
- Hartley, H.O. (1950) The maximum F-ratio as a short cut test for the heterogeneity of variances. Biometrika, 37, 308-312.
- Harwood, R.W.J., Wratten, S.D. & Nowakowski, M. (1992) The effect of managed field margins on hoverfly (Diptera: Syrphidae) distribution and within-field abundance. Proceedings Brighton Crop Protection Conference 1992 - Pests and Diseases, 3, 1033-1037.
- Haslett, J.R. (1982) Feeding ecology and behaviour of some adult hoverflies (Diptera: Syrphidae) DPhil Thesis, University of Oxford.
- Haslett, J.R. (1989a) Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris*. Oecologia, 81, 361-363.
- Haslett, J.R. (1989b) Interpreting patterns of resource utilisation. Oecologia, 78, 433-442.
- Hassell, M.P., Latto, J & May, R.M. (1989) Seeing the wood for the trees: detecting density dependence from existing life-table studies. Journal of Animal Ecology, 58, 883-892.
- Heitzmann, A. Lys, J. & Nentwig, W. (1992) Augmentation of beneficial insects at field edges - or: The advantages of weeds. Landwirtschaft Schweiz Band, 5, 26-36.
- Hejkal, J. (1985) The development of a carabid fauna (Coleoptera: Carabidae) on spoil banks under conditions of primary succession. Acta Entomologica Bohemoslovaca, 82, 321-346.
- Helenius, J. (1995) Enhancement of predation through within-field diversification. In: Enhancing Natural Control of Arthropod Pests Through Habitat Management Eds. C.H. Pickett & R.L. Bugg.
- Hemptinne, J.L. Dixon, A.F.G., Doucet, J.L. & Petersen, J.E. (1993) Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms. European Journal of Entomology, 90, 451-455.
- Hickman, J.M. & Wratten, S.D. (1994) Use of *Phacelia tanacetifolia* (Hydrophyllaceae) as a pollen resource to enhance hoverfly (Diptera: Syrphidae) populations in sweetcorn fields. IOBC Bulletin WPRS, 17, 156-167.
- Hickman, J.M. & Wratten, S.D. (In prep) Use of *Phacelia tanacetifolia* (Hydrophyllaceae) as a pollen resource to enhance hoverfly (Diptera: Syrphidae) populations in cereal fields. (In prep)
- Hirsinger, F. (1989) New Oil Crops In: Oil Crops Of The World Their Breeding And Utilization, Eds. G. Robbelen, R.K. Downey, & A. Ashri, McGraw Hill, New York.

- Hodek, I. (1970) Coccinelids and modern pest management. Bioscience, 20, 543-552.
- Hodgson, D.J. & Lövei, G.L. (1993) Novel crops in cereal fields: Habitat refuges for arthropod natural enemies. Proceedings of 46th New Zealand Plant Protection Conference 1993, 329-333.
- Hokkanen, H.M.T. (1991) Trap cropping in pest management. Annual Review of Entomology, 36, 119-138.
- Holland, J.M., Frampton, G.K., Wratten, S.D. & Cilgi, T. (1994) Arable acronyms analysed - a review of integrated arable farming systems research in Western Europe. Annals of Applied Biology (In press)
- Holloway, B. (1976) Pollen-feeding in hoverflies (Diptera: Syrphidae). New Zealand Journal of Zoology, 3, 339-350.
- Holloway, G.J. & McCaffery, A.R. (1990) Habitat utilisation and dispersion in *Eristalis pertinax*. The Entomologist, 109, 116-124.
- Holmes, P.R. (1984) A field study of the predators of the grain aphid, *Sitobion avenae* (F.) (Hemiptera: Aphidae), in winter wheat in Britain. Bulletin of Entomological Research, 74, 623-631.
- Holtz, F. (1988) Occurrence of aphids on wild plants in crop edges and boundary strips. In: Effects of Crop Edges; Proceedings of the Symposium "Crop Edges - positive effects for agriculture ?"
- Hopper, K.R. & Woolson, E.A. (1990) Labeling a parasitic wasp, *Microplitis crocipes* (Hymenoptera: Braconidae), with trace elements for mark-recapture studies. Annals of the Entomological Society of America, 84, 255-262.
- Horion, A. (1963) Faunistik der Mitteleuropaischenkafer. IX; Staphylinidae I. Micropeplinae bis Euaesthetinae, Feyel, Überlingen - Bodensee.
- Horridge, G.A., Mimura, K. & Tsukahara, Y. (1975) Fly photoreceptors II. Spectral and polarised light sensitivity in the drone fly *Eristalis* Proceedings of the Royal Society of London B, 190, 225-237.
- Huhta, V. (1971) Succession in spider communities of the forest floor after clear-cutting and prescribed burning. Annales Zoologici Fennici, 8, 483-542.
- Hurkmans, W.E.G. (1985) Territorial behaviour of two *Merodon* species (Diptera: Syrphidae). Entomologische Berichten, 45, 69-70.
- Hurlbert, S.H. (1978) The measurement of niche overlap and some relatives. Ecology, 59, 67-77.
- Ilse, D. (1949) Colour discrimination in the dronefly *Eristalis tenax*. Nature, 163, 255.
- Jepson, P.C. (1994) Field Margins as habitats, refuges and barriers of variable permeability to Carabidae In: Field Margins: Integrating Agriculture and Conservation. Ed. N. Boatman, BCPC Monograph No. 58.

- Jervis, M.A., Kidd, N.A.C., Fitton, M.G., Huddleston, T. & Dawah, H.A. (1993) Flower visiting by hymenopteran parasitoids. Journal of Natural History, **27**, 67-105.
- Johnson, C.G. (1969) Migration and dispersal of insects by flight. Methuen, London.
- Johnson, C.G. (1980) Syrphid (Diptera) migration on the Norfolk coast in August. Entomologists Monthly Magazine, **96**, 196-197.
- Joly, N. (1842) Notice sur les ravages que la *Liparis dispar* (*Bombyx dispar* Latr.) a exercés aux environs de Toulouse, suite de quelques reflexions sur un nouveau moyen de détruire certains insects nuisibles. Rev. Zoo. Soc. Cuvierienne, 115-119.
- Jones, D. (1987) Sunflowers Crops, **4**, 12-16.
- Jones, M.G. (1972) Cereal aphids, their parasites and predators caught in cages over oat and winter wheat crops. Annals of Applied Biology, **72**, 13-25.
- Jones, M.G. (1979) The abundance and reproductive activity of common carabidae in a winter wheat crop. Ecological Entomology, **4**, 31-43.
- Jones-Walters, L.M. (1989) Keys to the families of British Spiders. Field Studies, **9**, 365-443.
- Joy, N.H. (1932) Practical Handbook of British Beetles, Volume I and II, H.F. & G. Witherby, London.
- Kamla-Singh, A., Ram, P. Singh, V., Singh, A.K. & Singh, K. (1987) Response of Bulgarian coriander (*Coriandrum sativum* L.) to seed rates and fungicide at various planting dates. Annals of Agricultural Research, **8**, 231-236.
- Kan, E. (1988a) Assessment of aphid colonies by hoverflies I. Maple aphids and *Episyrphus balteatus* (de Geer) (Diptera: Syrphidae). Journal of Ethology, **6**, 39-48.
- Kan, E. (1988b) Assessment of aphid colonies by hoverflies II. Pea aphids and three syrphid species; *Betasyrphus serarius* (Walker) *Betasyrphus serarius* (Matsumura) and *Syrphus vitripennis* (Neigen). Journal of Ethology, **6**, 135-142.
- Kan, E. (1989) Assessment of aphid colonies by hoverflies III. Pea aphids and *Episyrphus balteatus* (de Geer) (Diptera: Syrphidae). Journal of Ethology, **7**, 1-6.
- Kay, Q.O.N. (1976) Preferential pollination of yellow flowered morphs of *Raphanus raphanistrum* by *Pieris* and *Eristalis* spp. Nature, **261**, 230-232.
- Kennedy, J.S., Booth, C.O., & Kershaw, W.J.S. (1959) Host finding by aphids in the field I. Gynoparae of *Myzus persicae* (Sulz.) Annals of Applied Biology, **47**, 410-423.
- Kenny, G.J. & Chapman, R.B. (1988) Effects of an intercrop on the insect pests, yield, and quality of cabbage. New Zealand Journal of Experimental Agriculture, **16**, 67-72.
- Kevan, P.G. (1978) Floral colouration, its colorimetric analysis and significance in anthecology. In: The Pollination of Flowers by Insects Ed. A.J. Richards, Academic Press, London.
- Kirby, W. & Spence, W. (1815) An Introduction to Entomology. Longman, Brown, Green & Longmans, London.
- Klinger, K. (1987) Effects of margin strips along a winter wheat field on the predatory

- arthropod fauna and cereal aphid infestation. Journal of Applied Entomology, **104**, 47-58.
- Koblev, S.Y. (1986) Breeding buckwheat for resistance to lodging. All Union Scientific Research Institute of Cereal and Legume Cultures: Scientific and Technical Bulletin, **35**, 55-57.
- Kolbe, W. & Linke, W. (1974) Studies of cereal aphids; their occurrence, effect on yield in relation to density levels and their control. Annals of Applied Biology, **77**, 85-87.
- Kowalski, R. (1986) Biology of *Tachyporus* spp. (Coleoptera: Staphylinidae) in relation to their role as predators of cereal aphids. In Feeding Behaviour and Accessibility of Food for Carabid Beetles. Eds. P.J. den Boer, L.Grüm & J. Szyszko. Warsaw Agricultural Press, Warsaw.
- Kugler, H. (1943) Hummeln als Blütenbesucher. Ergebnisse der Biologie, **19**, 143-323.
- Kumar, A., Kapoor, V.C. & Mahal, M.S. (1988) Population build-up and dispersion of immature stages of aphidophagous syrphids (Syrphidae: Diptera) on raya (*Brassica juncea*). Journal of Insect Science, **1**, 39-48.
- Lack, D. & Lack, L. (1951) Migration of insects and birds through a Pyrenean Pass. Journal of Animal Ecology, **70**, 773-790.
- Lagerlof, J. & Wallin, H. (1993) The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. Agriculture, Ecosystems and Environment, **43**, 141-154.
- Land, M.F. (1990) The design of the compound eye. In: Vision, Coding and Efficiency, Ed. C.Blackmore, Cambridge University Press, Cambridge.
- Lapchin, L. Ferran, A., Iperiti, G., Rabasse, J.M. & Lyon, J.P. (1987) Coccinellids (Coleoptera: Coccinellidae) and syrphids (Diptera: Syrphidae) as predators of aphids in cereal crops: A comparison of sampling methods. Canadian Entomologist, **119**, 815-822.
- Latteur, G. & Godefroid, J. (1982) Trial of field treatments against cereal aphids with mycelium of *Erynia neoaphidis* (Entomophthorale) produced *in vitro*. In: Aphid Antagonists Ed. R.Cavalloro, A.A. Balkema, Rotterdam.
- Laughlin, S.B. & Horridge, G.A. (1971) Angular sensitivity of retinula cells of dark-adapted worker bees. Journal of Comparative Physiology, **74**, 329-335.
- Lee, G., Stevens, D.J., Stokes, S. & Wratten, S.D. (1982) Duration of cereal aphid (*Sitobion avenae*) populations and the effects on wheat yields and bread making quality. Annals of Applied Biology, **98**, 169-178.
- Lee, J.A., Harmer, R. & Ignaciuk, R. (1983) Nitrogen as a limiting factor in plant communities. In: Nitrogen as an Ecological Factor Eds. J.A.Lee, S.McNeil, & I.H. Rorison, Blackwell, London.
- Leius, K. (1967a) Food sources and preferences of adults of a parasite *Scambus buolinae*

- (Hym: Ichn) and their consequences. Canadian Entomologist, **99**, 865-871.
- Leius, K. (1967b)** Influence of wild flowers on parasitism of tent caterpillar and codling moth. Canadian Entomologist, **99**, 444-446.
- Letourneau, D.K. & Altieri, M. A. (1983)** Abundance patterns of a predator, *Orius tristicolor* (Hemiptera: Anthocoridae), and its prey, *Frankliniella occidentalis* (Thysanoptera: Thripidae): habitat attraction in polycultures versus monocultures. Environmental Entomology, **12**, 1464-1469.
- Lewis, T. (1965)** The effects of an artificial windbreak on the aerial distribution of flying insects. Annals of Applied Biology, **55**, 503-512.
- Lewis, T. (1966)** An analysis of components of wind affecting the accumulation of flying insects near artificial windbreaks. Annals of Applied Biology, **58**, 365-370.
- Lewis, T. (1969)** The distribution of flying insects near a low hedgerow. Journal of Applied Ecology, **6**, 443-452.
- Lewis, T. & Dibley, G.C. (1970)** Air movements near windbreaks and a hypothesis of the mechanism of accumulation of airborne insects. Annals of Applied Biology, **66**, 477-484.
- Lewis, T. & Stephenson, J.W. (1966)** The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. Annals of Applied Biology, **58**, 355-364.
- Lindroth, C.H. (1974)** Handbook for the Identification of British Insects, 4 (2) Coleoptera: Carabidae, Royal Entomological Society, London.
- Lipkow, V.E. (1966)** Biologische-okologische untersuchungen uber *Tachyporus* -Arten und *Tachinus rufipes* (Staphylinidae: Col.). Pedobiologia, **6**, 140-177.
- Lövei, G.L., McDougal, D., Bramley, G., Hodgson, D.J. & Wratten, S.D. (1992)** Floral resources for natural enemies: the effect of *Phacelia tanacetifolia* (Hydrophyllaceae) on within-field distribution of hoverflies (Diptera: Syrphidae) Proceedings of the 45th New Zealand Plant Protection Conference, Wellington, 60-61.
- Long, E. (1990)** A new look at plant properties. Grower, March 8th, 1990, 21-23.
- Long, E. (1991)** Sunrise for sunflowers. Crops, **8**, 46-47.
- Luff, M.L. (1965)** The morphology and microclimate of *Dactylis glomerata* tussocks. Journal of Ecology, **53**, 771-787.
- Luff, M.L. (1974)** Adult and larval feeding habits of *Pterostichus madidus* (F.) (Coleoptera: Carabidae). Journal of Natural History, **8**, 403-409.
- Luff, M.L. (1982)** Population dynamics of Carabidae. Annals of Applied Biology, **101**, 164-170.
- Luff, M.L. (1987)** Biology of polyphagous ground beetles in agriculture. Agricultural Zoology Reviews, **2**, 237-278.
- Lutman, P.J. & Tucker, G.G. (1987)** Standard descriptions of growth stages of annual

- dicotyledenous weeds. Annals of Applied Biology, **110**, 683-687.
- Lyons, J.P. (1965) Influence de quelque facteurs sur l'expression du potentiel de multiplication des syrphides aphidiphages. Annales des Epiphyties (Paris), **16**, 397-398.
- McClea, I., Carter, N. & Watt, A. (1977) Pests out of control. New Scientist, **76**, 74-75.
- McCook, H. (1882) Ants as beneficial insecticides. Proceedings of the Academy of Natural Sciences of Philadelphia - 1882, 263-271.
- MacLeod, A., Harwood, R.J.W., & Wratten, S.D. (1994) The efficiency of a new lightweight suction sampler for sampling aphids and their predators in arable land. Annals of Applied Biology, **124**, 11-17.
- MacLeod, J. & Donnelly (1957) Individual and group marking methods for fly population studies. Bulletin of Entomological Research, **48**, 585-592.
- Mader, H.J. (1984) Animal habitat isolation by roads and agricultural fields. Biological Conservation, **29**, 81-96.
- Mader, H.J. (1988) Effects of increased spatial heterogeneity on the biomass in rural landscapes. Ecological Bulletins, **39**, 169-179.
- Mader, H.J., Schell, C. & Kornacker, P. (1990) Linear barriers to arthropod movements in the landscape. Biological Conservation, **54**, 209-222.
- Maier, C.T. & Waldbauer, G.P. (1979) Diurnal activity patterns of flower flies in an Illinois sand area. Annals of the Entomological Society of America, **72**, 237-245.
- Manly, B.F.J., Miller, P., Cook, L.M. (1972) Analysis of a selective predation experiment. American Naturalist, **106**, 719-736.
- Mansour, F. & Heimbach, U. (1993) Evaluation of Lycosid, Micryphantid and Linyphiid spiders as predators of *Rhopalosiphum padi* (Hom: Apdididae) and their functional response to prey density -laboratory experiments. Entomophaga, **38**, 79-87.
- 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. (1990) Interference between sown grasses and the growth of rhizome of *Elymus repens* (couch grass). Agriculture, Ecosystems & Environment, **33**, 11-22.
- Marshall, E.J.P. & Nowakowski, M. (1992) The use of herbicides in the creation of a herb-rich field margin. Proceedings Brighton Crop protection Conference 1992 - Weeds, **2**, 655-660.
- Mauremootoo, J.R., Joyce, K. & Jepson., P.C. (In prep) Manipulative studies on within-field refugia.
- Mauremootoo, J.R. & Wratten, S.D. (1994) Permeability of field boundaries to predatory carabid beetles. IOBC Bulletin WPRS, **17**, 188-200.
- Mauremootoo, J.R. & Wratten, S.D. & Worner S.P. (In Prep) Permeability of hedgerows to predatory carabid beetles. (In prep)



- Mazokhin-Porshnyakov, G.A. (1969), Insect Vision, Plenum Press, New York.
- Meier-zu-Beerentrup, H. & Robbelen, G. (1987) *Calendula* and *Coriandrum* - new potential for oil crops for industrial uses. Fett-Wissenschaft - Technologie, **89**, 227-230.
- Miller, D. (1918) The economic bearing of hoverflies. New Zealand Journal of Agriculture, **17**, 129- 135.
- Miller, D. (1921) Material for a monograph on the Diptera fauna of New Zealand. Marcus F. Marks Pubs., Wellington.
- Miller, D. & Watt, W.N. (1915) Contributions to the study of New Zealand Entomology from an economic and biological standpoint: No. 6 *Syrphus ropalus* Walk. (Diptera) Transactions of the New Zealand Institute, **47**, 274-284.
- Minks, A.K. & Harrewijn, P. (1988) Eds. Aphids. Their Biology, Natural Enemies and Control. Elsevier, Oxford.
- Mitchell, B. (1963a) Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schränk) I. Life cycles and feeding behaviour. Journal of Animal Ecology, **32**, 289-299.
- Mitchell, B. (1963b) Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schränk) II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. Journal of Animal Ecology, **32**, 377-392.
- Molthan, J. (1990) Composition, community structure and seasonal abundance of hoverflies (Dipt: Syrphidae) on field margin biotopes in the Hessian Ried. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie, **7**, 368-379.
- Molthan, J. & Ruppert, V. (1988) Significance of flowering wild herbs in boundary strips and fields for flower-visiting beneficial insects; Effects of crop edges. In: Proceedings "Crop Edges -Positive effects for agriculture ?", 85-99, Berlin.
- Morris, R.F. (1959) Single-factor analysis in population dynamics. Ecology, **40**, 580-588.
- Morse, D. (1981) Interactions among syrphid flies and bumblebees on flowers. Ecology, **62**, 81-88.
- Moyle, J.L. (1994) The lethal and sub-lethal effects of lambda-cyhalothrin to the syrphid *Episyrphus balteatus* (Degeer) (Diptera: Syrphidae). PhD Thesis University of Southampton.
- Munguira, M.L. & Thomas, J.A. (1992) Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and modality. Journal of Applied Ecology, **29**, 316- 329.
- Murdoch, W.W. (1969) Switching in general predators: Experiments on predator specificity and stability of prey populations Ecological Monographs, **39**, 335-354.
- Namai, H. (1986) Pollination biology and seed multiplication method of buckwheat genetic resources. In: Proceedings of 3rd International Symposium on Buckwheat, 7-12th July

- 1986, Palawy, Poland, Institute of Soil Science and Plant Cultivation, Warsaw.
- Nentwig, W. (1988) Augmentation of beneficial arthropods by strip management. I. Succession of predacious arthropods and long-term change in the ratio of phytophagous and predacious arthropods in a meadow. Oecologia, **76**, 597-606.
- Nentwig, W. (1992) The importance of weeds for the augmentation of beneficial arthropods. In: Enhancing natural control of insect pests through habitat management. Eds :C.H. Pickett, & R.L. Bugg. AgAccess and John Wiley Sons. London.
- New, T.R. (1988) Neuroptera In: Aphids. Their Biology, Natural Enemies and Control, Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- Nielsen, T. (1969) Population studies of *Heliophilus hydribus* and *Sericomyia silentis* (Diptera: Syrphidae) on Jaeren. Norsk Entomologisk Tidsskrift, **19**, 91-98.
- Nix, J. (1993) Farm Management Pocketbook 1993 23rd Edition, Wye College, University of London.
- Ohara, K. (1985) Observations on the prey-predator relationship between *Pseudoregma bambucicola* (Homoptera, Pemphigidae) and *Metasyrphus confrater* (Diptera, Syrphidae) with special reference to the behaviour of the aphid soldiers. Esakia, **23**, 107-110.
- Owen, D. (1977) Are aphids really pests ? New Scientist, **76**, 76-77.
- Owen, D.F. (1956) A migration of Insects at Spurn Point, Yorkshire. Entomologists Monthly Magazine, **92**, 43-44.
- Parker, F.D. & Pinnell, R.E. (1972) Further studies of the biological control of *Pieris rapae* using supplemental host and parasite releases. Environmental Entomology, **1**, 150-157.
- Percival, M.S. (1956) The presentation of pollen in certain angiosperms and its collection by *Apis mellifera*. New Phytologist, **54**, 353-368.
- Pickering, J. Dutcher, J.D. & Ekbom, B.S. (1989) An epizootic caused by *Erynia neoaphidis* and *E. radicans* (Zygomycetes, Entomophthoraceae) on *Acyrtosiphum pisum* (Hom. Aphididae) on legumes under irrigation. Journal of Applied Entomology, **107**, 331-333.
- Poehling, H.M. (1989) Selective application strategies for insecticides in agricultural crops. In: Pesticides and Non-target Invertebrates, Ed. PC. Jepson, Intercept, Wimborne
- Poehling, H.M., Tenhumberg, B. & Groeger, U. (1991) Different patterns of cereal aphid population dynamics in northern and southern areas of West Germany. IOBC Bulletin WPRS, **14**, 1- 12.
- Pollard, E. (1971) Hedges VI: Habitat diversity and crop pests: a study of *Brevicoryne brassicae* and its syrphid predators. Journal of Applied Ecology, **8**, 751-780.
- Potts, G.R. & Vickerman, G.P. (1974) Studies in the cereal ecosystem. Advances in Ecological Research, **8**, 107-197.

- Powell, W. (1982) The identification of hymenopterous parasitoids attacking cereal aphids in Britain. Systematic Entomology, **7**, 465-473.
- Powell, W. (1986) Enhancing parasitoid activity in crops. In: Insect Parasitoids Eds. J.K. Waage & D.J. Greathead, Academic Press, London.
- Powell, W., the late Dean, G.S. & Bardner, R. (1985) Effects of pirimicarb, dimethoate and benomyl on natural enemies of cereal aphids in winter wheat. Annals of Applied Biology, **106**, 235-242.
- Powell, W., the late Dean, G.J. & Dewar, A. (1985) The influence of weeds on polyphagous arthropod predators in winter wheat. Crop Protection, **4**, 298-312.
- Powell, W., Dewar, A.M., Wilding, N. & Dean, G.J. (1983) Manipulation of cereal aphid natural enemies. Proceedings Brighton Crop Protection Conference 1983 - Plant Protection for Human Welfare, **2**, 780
- Rabbinge, R., Ankersmit, G.W. & Pak, G.A. (1979) Epidemiology and simulation of population development of *Sitobion avenae* in winter wheat. Netherlands Journal of Plant Pathology, **85**, 197-200.
- Rands, M.R.W. & Sotherton, N.W.S. (1987) The management of field margins for the conservation of game-birds. In: Field Margins, BCPC Monograph No. 35.
- Real, L.A. (1983) Pollination Biology, Academic Press, New York.
- Rideout, C.L., Price, K.R., Pont, M.S. du, Parker, M.L., & Fenwick, G.R. (1991) Quinoa saponins - analysis and preliminary investigations into the effects of reduction by processing. Journal of the Science of Food and Agriculture, **54**, 165-176.
- Ridley, H.N. (1912) Spices Macmillan & Co.Ltd., London.
- Riedel, W. (1989) Some natural enemies of cereal aphids. Grøn Viden. Landbrug, **37**.
- Risch, S.J., Andow, D. & Altieri, M.A. (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environmental Entomology, **12**, 625- 629.
- Röbbelen, G., Downey, R.K. & Ashri (1989) Oil Crops of The World. Their Breeding And Utilization. McGraw-Hill, New York.
- Robinson, J.V. (1981) The effect of architectural variation in habitat on a spider community: an experimental field study. Ecology, **62**, 73-80.
- Root, R.B. (1973) Organisation of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs, **43**, 95-124.
- Rotheray, G.E. (1986) Colour, shape and defence in aphidophagous syrphid larvae (Diptera). Zoological Journal of the Linnean Society, **88**, 201-216.
- Rotheray, G.E. (1987) Larval morphology and searching efficiency in aphidophagous syrphid larvae. Entomologia Experimentalis et Applicata, **43**, 49-54.
- Rotheray, G.E. (1989) Naturalists' Handbook 11 - Aphid predators. Eds. S.A. Corbet & R.H.L.

- Disney, Richmond Publishing Co. Ltd. Slough.
- de Rougemont, G.M. (1989) A field guide to the crops of Britain and Europe, Collins, London.
- Ruppert, V. & Klingauf, F. (1988) Attraktivität ausgewählter Blütenpflanzen für Nutzinsekten am Beispiel der Syrphinae (Diptera: Syrphidae) Mitteilung Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie, **6**, 255-261.
- Ruppert, V. & Molthan, J. (1991) Augmentation of aphid antagonists by field margins rich in flowering plants. Aphidophaga, **4**, Proceedings of Symposium, Godollo, Hungary.
- Russell, E.P. (1989) Enemies hypothesis: A review of the effects of vegetational diversity on predatory insects and parasitoids. Environmental Entomology, **18**, 590-599.
- Schaefer, M. (1977) Winter ecology of spiders (Araneida). Zeitschrift für Angewandte Entomologie, **83**, 113-134.
- Schlosser, E.J. & Karr, J.R. (1981) Water quality in agricultural watersheds: impact of riparian vegetation during base flow. Water Research Bulletin, **17**, 233-240.
- Schneider, F. (1948) Beitrag zur Kenntnis der Generationsverhältnisse und Diapause räuberischer Schwebfliegen. Mitteilungen der Schweizerischen Entomologischen Gesellschaft, **21**, 249- 285.
- Schneider, F. (1958) Künstliche Blumen zum Nachweis von Winterquastieren, Futterpflanzen und Tageswanderern von *Lasiopticus pyrastris* und anderen Schwebfliegen. Mitteilungen der Schweizerischen Entomologischen Gesellschaft, **31**, 1-24.
- Schneider, F. (1969) Bionomics and physiology of aphidophagous Syrphidae. Annual Review of Entomology, **14**, 103-124.
- Schnitter, P.H. (1994) The development of carabid communities from uncultivated fields and meadows in the first five years of a succession. In: Carabid Beetles: Ecology and Evolution Eds. K. Desender, M. Dufrene, M. Loreau, M. Luff & J.-P. Maelfait, Kluwer Academic Pubs., Dordrecht.
- Scott, R.R. (1984) New Zealand pest and beneficial insects, Lincoln University Press, Canterbury.
- Sengonca, C. & Frings, B. (1988) The influence of *Phacelia tanacetifolia* to pests and beneficial insects in sugar beet plots. Pedobiologia, **32**, 311-316.
- Sergeeva, D.S. & Sil'chenko, V.M. (1984) Resistance of coriander to low temperatures. Physiology and Biochemistry of Cultivated Plants, **16**, 52-55.
- Shahjahan, M. (1974) Erigon flowers as a food and attractive odor source for *Peristenus pseudopallipes*, a braconid parasitoid of the tarnished plant bug. Environmental Entomology, **3**, 69-72.
- Sheehan, W. (1986) Response by specialist and generalist natural enemies to agro-ecosystem diversification: A selective review. Environmental Entomology, **15**, 456-461.
- Sherratt, T.N. & Jepson, P.C. (1993) A metapopulation approach to modelling the long-term

- impact of pesticides on invertebrates. Journal of Applied Ecology, **30**, 696-705.
- Sih, A. & Baltus, M.S. (1987) Patch size, pollinator behaviour and pollinator limitation in catnip. Ecology, **68**, 1679-1690.
- Smith, H.S. (1919) On some phases of insect control by the biological method. Journal of Economic Entomology, **12**, 288-292.
- Sokal, R.F. & Rohlf, F.J. (1981) Biometry, 2nd edition, W.H. Freeman & Co. New York.
- Solomon, M.E. (1949) The natural control of animal populations. Journal of Animal Ecology, **18**, 1-35.
- Sopp, P.I. & Chiverton, P. (1987) Autumn predation of cereal aphids by polyphagous predators in Southern England: A "first-look" using ELISA. IOBC Bulletin WPRS, **10**, 103-108.
- Sotherton, N.W. (1984) The distribution and abundance of predatory arthropods overwintering on farmland. Annals 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.
- Speight, M.R. (1983) The potential of ecosystem management for pest control. Agricultural Ecosystems and Management, **10**, 183-199.
- Speight, M.R. & Lawton, J.H. (1976) The influence of weed-cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia, **23**, 211-223.
- Stanley, R.G. & Liskens, H.F. (1974) Pollen: Biology, Biochemistry, Management, Springer, Berlin.
- Starvenga, D.G. (1979) Visual pigment processes and prolonged pupillary responses in insect photoreceptor cells. Biophysics, Structure and Mechanisms, **5**, 175-185.
- Storck-Weyhermuller, S. (1989) Application of reduced dosages of insecticides as a possibility to the integrated control of cereal aphids. Gesunde Pflanzen, **41**, 285-289.
- Stubbs, A.E. & Falk, S.J. (1983) British hoverflies: An Illustrated Identification Guide. British Entomological & Natural History Society, London.
- Sunderland, K.D. (1975) The diet of some predatory arthropods in cereal crops. Journal of Applied Ecology, **12**, 507-515.
- Sunderland, K.D. (1987) Spiders and cereal aphids in Europe. IOBC Bulletin WPRS, **10**, 82-102.
- Sunderland, K.D. (1988) Carabidae and other invertebrates. In: Aphids, Their Biology, Natural Enemies and Control, Eds. A.K. Minks & P. Harrewijn, Elsevier, Oxford.
- Sunderland, K.D. (1991) The ecology of spiders in cereals. Proceedings of 6th International Symposium on Pests and Diseases of small grain cereals and maize. Board Of Plant Protection, Halle, Halle/Saale, Germany.
- Sunderland, K.D., Chambers, R.J., Stacey, D.L. & Crook, N.E. (1985) Invertebrate polyphagous predators and cereal aphids. IOBC Bulletin WPRS, **8**, 105-114.

- 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.
- Sunderland, K.D., Fraser, A.M. & Dixon, A.F.G. (1986) Field and laboratory studies on money spiders (Linyphidae) as predators of cereal aphids. Journal of Applied Ecology, 23, 433- 447.
- Sunderland, K.D., Stacey, D.L. & Edwards C.A. (1981) The role of polyphagous predators in limiting the increase of cereal aphids in winter wheat. IOBC Cereal aphid ecology Sub-group meeting of the working group "Integrated Control in Cereals". Colmar, France 14th- 15th Nov. 1979.
- Sunderland, K.D. & Vickerman, G.P. (1980) Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. Journal of Applied Ecology, 17, 389-396.
- Sutton, S.L. (1969) A migration of syrphid flies at Spurn. Naturalist, 909, 51-53.
- Svenson, B. & Janzon, G.L.A. (1984) Why does the hoverfly *M.corollae* migrate? Ecological Entomology, 9, 329-335.
- Svenson, K.G. (1968) Plant susceptibility to virus infection by insect transmission. In: Viruses, Vectors & Vegetation. Ed. K. Maramorosch. Interscience, New York.
- Tahir, I. & Farooq, S. (1988) Review article on buckwheat. Eagopyrum, 8, 33-53.
- Tanasijtschuk, U.N., Remaudiere, G. & Leclant, F. (1977) Dipt:Chaemaemyidae, predateurs de pucerons et de cochenilles en France. Annales de la Societe Entomologique de France, 12, 691-698.
- Taylor, L.R. (1986) Synoptic dynamics, migration and the Rothamsted Insect Survey. Journal of Animal Ecology, 55, 1-38.
- Taylor, L.R. (1987) Objectives and experiment in long-term research. In: Long-term Studies in Ecology, Ed. G.E.Likens, Springer Verlag, NewYork.
- Tenhumberg, B. & Poehling, H.M. (1993) Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. Aphidophaga, 5,
- Tew, T.E., Todd, I.A. & MacDonald, D.W. (1994) Field Margins and small mammals. In: Field Margins: Intergrating agriculture and conservation. Ed. N.Boatman. BCPC Monograph No. 58
- Tew, T.E. (1994) Farmland hedgerows:habitat, corridors or irrelevant ? A small mammal's perspective. In: Hedgerow management and nature conservation, Ed. T.A. Watt, Wye College Press, Kent.
- Thacker, J.R.M. (1991) The spatial and temporal dynamics of pesticide side effects on non-target invertebrates in UK cereal crops. PhD Thesis, University of Southampton.
- Theile, H.U. (1977) Carabid Beetles in Their Environments. Spring-Verlag, Berlin.

- Thiele, H.U. (1979)** Relationships between annual and daily rhythms, climatic demands and habitat selection in carabid beetles. In: Carabid Beetles. Their Evolution, Natural History and Classification. Proceedings of the first International Symposium of Carabidology, Washington D.C. Aug 21-25 1976. Eds. T.L. Erwin, G.E. Ball & D.R. Whitehead. W.Junk Pubs. The Hague.
- Thomas, C.F.G. (1992)** The spatial dynamics of spiders in farmland. PhD Thesis, University of Southampton.
- Thomas, M.B. (1989)** The creation of island habitats to enhance populations of beneficial insects. Proceedings 1989 Brighton Crop Protection Conference - Weeds, **3**, 1097-1102.
- Thomas, M.B. (1991)** Manipulation of overwintering habitats for invertebrate predators on farmland. PhD Thesis, University of Southampton.
- Thomas, M.B., Mitchell, H. & Wratten, S.D. (1992a)** Abiotic and biotic factors influencing the winter distribution of predatory insects. Oecologia, **89**, 78-84.
- Thomas, M.B. & Wratten, S.D. (1990)** Ecosystem diversification to encourage natural enemies of cereal aphids. Proceedings 1990 Brighton Crop Protection Conference - Pests and Diseases, **2**, 691-696.
- 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, M.B., Wratten, S.D. & Sotherton, N.W. (1992b)** Creation of island habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. Journal of Applied Ecology, **29**, 524-531.
- Thomas, W.P. (1977)** Biological control of the blue-green lucerne aphid. The Canterbury situation. Proceedings of the 30th New Zealand Weed and Pest Control Conference, 182-187.
- Thomson, J.D. (1981)** Spatial and temporal components of resource assessment by flower feeding insects. Journal of Animal Ecology, **50**, 49-60.
- Thórhallsdóttir, T.E. (1990)** The dynamics of five grasses and white clover in a simulated mosaic sward. Journal of Ecology, **78**, 909-923.
- Tilman, D. (1987)** Ecological experimentation: Strengths and conceptual problems. In: Long-term Studies in Ecology. Ed. G.E. Likens, Springer-Verlag, New York.
- du Toit, A.P. (1990)** The importance of certain insects as pollinators of sunflower (*Helianthus annuus* L.). South African Journal of Plant Science, **7**, 159-162.
- Topping, C. J. & Sunderland, K.D. (1992)** Limitations to the use of pitfall traps in ecological studies as exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology, **29**, 485-491.

- Tukey, J.W. (1949) One degree of freedom for non-additivity. Biometrics, **5**, 232-242.
- Turner, D.E. (1995) Environmental and economic consequences of reduced rate insecticide application in cereals. PhD Thesis, University of Southampton.
- Varley, G.C. & Gradwell, G.R. (1960) Key factors in population studies. Journal of Animal Ecology, **29**, 399-401.
- Verma, A.K. & Makhmoor, H.D. (1989) Development of life tables for *Metasyrphus confrater* (Wiedmann) Diptera: Syrphidae, a predator of the cabbage aphid (Homoptera, Aphididae) in cauliflower crop ecosystem. Entomon, **14**, 227-232.
- Vickerman, G.P. (1974) Some effects of grass weed control on the arthropod fauna of cereals. Proceedings of the 12th British Weed Control Conference 1974, 929-939, BCPC, Croydon.
- Vickerman, G.P. (1978) The arthropod fauna of undersown grass and cereal fields. Scientific Proceedings, Royal Dublin Society, Series A, **6**, 273-283.
- 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. & Wratten, S.D. (1979) The biology and pest status of cereal aphids in Europe: a review. Bulletin of Entomological Research, **69**, 1-32.
- Villa, A. (1845) Degli insetti carnivori adoperati a distruggere le specie dannose all'agricoltura. Sepettatore, **3**, 359.
- Vorley, W.T. (1986) The activity of parasitoids (Hymenoptera: Braconidae) of cereal aphids (Hemiptera: Aphididae) in winter and spring in Southern England. Bulletin of Entomological Research, **76**, 491-504.
- Vorley, W.T. & Wratten, S.D. (1985) A simulation model of the role of parasitoids in the population development of *Sitobion avenae*. Journal of Applied Ecology, **22**, 813-823.
- Wallin, H. (1985) Spatial and temporal distribution of some abundant carabid beetles (Coleoptera:Carabidae) in cereal fields and adjacent habitats. Pedobiologia, **28**, 19-34.
- Way, M.J., Hardie, G. & Galley, D.J. (1969) Experiments on integration of chemical and biological control of aphids on brussel sprouts. Annals of Applied Biology, **63**, 459-475.
- Weinreich, E. (1968) Über den klebfangapparat der imagines von *Stenus* Latr. (Coleopt. staphylinidae) mit einem Beitrag zur kenntnis der Jugendstadien dieser Gattung. Zeitschrift für Morphologie und Ökologie der Tiere, **62**, 162-210.
- White, A.J., Wratten, S.D., Berry, N.A. & Weigmann, U. (1994) Habitat manipulation to enhance biological control of brassica pests by hoverflies (Diptera: Syrphidae) Proceedings of 47th New Zealand Plant Protection Conference, Horticultural Crops, 128-134.
- White, A.J., Wratten, S.D., Weigmann, U., Bowie & Berry, N.A. (In prep) Phenology and



- ecology of New Zealand hoverflies (Diptera: Syrphidae). (In prep)
- Wilding, N. (1981) The effect of introducing aphid-pathogenic Entomophthoraceae into field populations of *Aphis fabae*. Annals of Applied Biology, **99**, 11-23.
- Wilding, N., Mardell, S., Brobyn, P.J., Wratten, S.D. & Lomas, J. (1990) The effect of introducing the aphid-pathogenic fungus *Erynia neoaphidis* into populations of cereal aphids. Annals of Applied Biology, **117**, 683-691.
- Wiles, J.A. & Jepson, P.C. (1992) The susceptibility of a cereal aphid pest and its natural enemies to deltamethrin. Pesticide Science, **36**, 263-272.
- Williams, W. (1978) New crops and agricultural systems Proceedings of the British Crop Protection Conference, **3**, 1005-1012.
- Wilson, F. & Huffaker, C.B. (1976) The philosophy, scope, and importance of biological control. In: Theory and Practice of Biological Control Eds. C.B Huffaker & P.S. Messenger, Academic Press, London.
- Wilson, K. (1992) A study on plant preference by hoverflies (Diptera: Syrphidae) and its application in biocontrol. Undergraduate BSc Honours Project, University of Southampton.
- Winder, L. (1990a) Modelling the effects of polyphagous predators on the population dynamics of the grain aphid *Sitobion avenae* (F.), PhD Thesis, University of Southampton.
- Winder, L.(1990b) Predation of the cereal aphid *Sitobion avenae* by polyphagous predators on the ground. Ecological Entomology, **15**, 105-110.
- Winder, L., Hirst, D.J., Carter, N., Wratten, S.D. & Sopp, P.I. (1994) Estimating predation of the grain aphid *Sitobion avenae* (F.) by polyphagous predators. Journal of Applied Ecology, **31**, 1-12.
- Wnuk, A. & Wojciechowicz-Zytko, E. (1991) The attractiveness of flowers of Cruciferae for the aphidophagous Syrphidae. Folia Horticulturae, **3**, 29-36.
- Woiwod, I.P. (1991) Long-term synoptic monitoring. In: The Ecology of Temperate Cereal Fields. Eds. L.G. Firbanks, N. Carter, J.F. Darbyshire, & G.R. Potts, Blackwell, London.
- Wolf, E. (1933) Die Verhalten der Bienen gegenüber flimmernden Feldern und bewegten Objekten. Zeitschrift Vergl. Physiologie, **20**, 151-161.
- Wratten, S.D. (1973) The effectiveness of the coccinellid beetle *Adalia bipunctata* (L.) as a predator of the lime aphid *Eucallipterus tilae* L. Journal of Animal Ecology, **42**, 785-802.
- Wratten, S.D. (1975) The nature of 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. (1987) The effectiveness of native natural enemies. In: Integrated Pest

- Management, Eds. A.J. Burn, T.H. Coaker & P.C. Jepson. Academic Press, London.
- Wratten, S.D. (1988)** The effectiveness of polyphagous predators as aphid natural enemies. In: Ecology and Effectiveness of Aphidophaga Eds. E. Niemczyk & A.F.G. Dixon, SPB Academic Publishing, The Hague.
- Wratten, S.D., Hickman, J.M., Bowie M.H. & Lovei, G.L. (In prep)** "Permeability" of field boundaries to hoverflies (Diptera Syrphidae).
- Wratten, S.D. & van Emden, H.F. (1995)** Habitat management for enhanced activity of natural enemies of insect pests. In: Enhancing Natural Control of Arthropd Pests Through Habitat Management, Eds. C.H.Pickett & R.L. Bugg (In press).
- Wratten, S.D. & Powell, W. (1991)** Cereal aphids and their natural enemies. In: The Ecology of Temperate Cereal Fields. Eds. L. Firbank, N. Carter & G.R. Potts. Blackwell, Oxford.
- Zadoks, J.C., Chang, T.T. & Konzak, C.F. (1974)** A decimal code for the growth stages of cereals. Weed Research, **14**, 415-421.
- Zimmerman, M., & Pleasants, J.M. (1982)** Competition among pollinators: quantification of available resources. Oikos, **38**, 381-383.