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THE FORAGING ECOLOGY OF HOVERFLIES (DIPTERA: SYRPHIDAE) AND THE POTENTIAL FOR MANIPULATING THEIR DISTRIBUTION ON FARMLAND

by

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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THE FORAGING ECOLOGY OF HOVERFLIES AND THE POTENTIAL FOR MANIPULATING THEIR DISTRIBUTION ON FARMLAND.

by Susan E. Cowgill

Observations of the foraging behaviour of commonly occurring syrphid species were recorded in two floristically different field margin types. Individual syrphid species did not visit flowers according to their abundance in the habitat. The study has identified the arable weeds and hedgerow plants which are used selectively by syrphids. The growth of several selected plant species is encouraged via the implementation of the Game Conservancy Trust's "conservation headlands" technique. Comparison of the numbers of syrphid adults in fully sprayed and conservation headland plots showed that when there were significant differences in floral area (the number of flowers) between the two treatments there were also significant differences in the proportion of the total number of flies in the two treatments; the provision of selected adult food sources resulted in a local redistribution of flies with higher numbers of several syrphid species being recorded in the conservation headland plots. Flies were retained in these plots as a result of their foraging behaviour. Diurnal activity patterns for individual species are discussed in relation to microclimatic factors.

Syrphid eggs collected from the two treatments were identified to genus using the characteristic surface patterning of the eggs. *Pipizella*, *Episyrphus* and *Metasyrphus* were numerically the most important genera. Comparison of the number of eggs per aphid in fully sprayed and conservation headland plots showed that on several dates higher numbers of eggs per aphid were recorded from the conservation headland plots. This was in part due to the fact that the non-crop plants within the crop acted as oviposition sites for syrphids belonging to the genus *Melanostoma*. Females belonging to this group did not respond to aphid density when ovipositing; however, there was a significant positive relationship between the number of *Episyrphus* and *Metasyrphus* eggs and aphid density. Analysis of the distribution of unidentified syrphid eggs within a single field showed that the flies displayed a positive reproductive numerical response to aphid density.

The study has shown the importance of field margin composition in determining the distribution and species composition of syrphids; beneficial manipulation of field margin composition has the potential to enhance biocontrol potential of this important group of aphid predators.

CHAPTER ONE
GENERAL INTRODUCTION

Biology of syrphids

Occurrence

Syrphidae (hoverflies, flowerflies) are characterised by highly active adult insects which are often brightly coloured and have an aptitude for hovering flight. They can be distinguished from most other Dipterans by the presence of a "false vein" (*vena spuria*) between the radius and the media (Coe, 1953). Syrphids can be observed on the wing from early spring to late autumn; the greatest number of species occur during late July and August.

According to Thompson (1980) there are more than 5300 known species of syrphid world-wide; the British syrphid fauna comprising more than 250 species. Bankowska (1980) provided a comprehensive survey of the habitat associations of Polish syrphids, many of which are also present in Britain; syrphids are particularly characteristic of woodland glades and edges although they have also been recorded from open areas, including arable land (Claussen, 1980; Dean, 1982). Wright (1989) recorded more than 130 species of syrphid within a five mile radius of Coventry city centre, over a five year period.

Classification

There are three sub-families in the family Syrphidae: Syrphinae, Milesiinae and Microdontinae. The Milesiinae contains about two thirds of the British hoverfly fauna and Stubbs and Falk (1983) described ten constituent tribes within the subfamily. There are three tribes within the Syrphinae: Paragini, Bacchini and Syrphini, the latter two containing genera with aphidophagous larvae. The tribe Pipizini was also originally placed in the Syrphinae because the larvae are aphidophagous (Hartley, 1961) but it has since been transferred to the Milesiinae on the basis of the morphology of the adults (Thomson, 1972). However, recent taxonomic analysis of predacious syrphid larvae supports the original placement of this tribe in the sub-family Syrphinae (Rotheray and Gilbert, 1989).

The third section, the Microdontinae has sometimes been included in the Milesiinae (Kloet and Hinks, 1976) and sometimes been allocated a separate family, however; it is more usually accorded subfamilial status.

A full classification of the syrphids recorded during the present study is provided in Table 1; identification follows Stubbs and Falk (1983).

Adults

Adult syrphids feed on pollen and nectar, which most species obtain directly from flowers although members of the genus *Xylota* obtain pollen and other food items from leaf surfaces.

Female syrphids emerge with an undeveloped reproductive system and pollen feeding is necessary for full egg maturation and oviposition (Schneider, 1948; Stürken, 1964; Ruzicka, 1974; Maier, 1978; Heal,

Table 1. Classification of the syrphid species encountered in the present study; nomenclature follows Stubbs and Falk (1983).

Subfamily Syrphinae

Tribe Syrphini
Chrysotoxum cautum (Harris, 1776)
Episyrphus balteatus (Degeer, 1776)
Leucozona lucorum (Linnaeus, 1758)
Metasyrphus corollae (Fabricus, 1794)
Metasyrphus luniger (Meigen, 1822)
Meliscaeva auricollis (Meigen, 1822)
Scaeva pyrastri (Linnaeus, 1758)
Sphaerophoria scripta (Linnaeus, 1758)
Syrphus ribesii (Linnaeus, 1758)
Syrphus vitripennis (Meigen, 1822)

Tribe Bacchini
Melanostoma mellinum (Linnaeus, 1758)
Melanostoma scalare (Fabricius, 1794)
Platycheirus albimanus (Fabricius, 1781)
Platycheirus manicatus (Meigen, 1822)
Platycheirus peltatus (Meigen, 1822)
Platycheirus scutatus (Meigen, 1822)

Subfamily Milsiinae

Tribe Cheilosiini
Rhingia campestris Meigen, 1822

Tribe Eristalini
Eristalis (Eoseristalis) arbustorum (Linnaeus, 1758)
Eristalis (Eoseristalis) nemorum (Linnaeus, 1758)
Eristalis (Eoseristalis) pertinax (Scopoli, 1763)
Eristalis (Eristalis) tenax (Linnaeus, 1758)
Heliophilus pendulus (Linnaeus, 1758)

Tribe Pipizini
Pipizella varipes (Meigen, 1822)
Pipizella virens (Fabricius, 1805)

Tribe Volucellini
Volucella pellucens (Linnaeus, 1758)

Tribe Xylotini
Syritta pipiens (Linnaeus, 1758)

1979). Lyon (1965) reported that viable eggs could be obtained from female *Episyrphus balteatus* and *Metasyrphus corollae* when they were fed on sugar and honeydew but that the development was "feebler" and slower than in pollen fed females. Doucette and Eide (1955) demonstrated that a diet of pollen and water alone was inadequate for reproduction in *Merodon equestris*; the best diet for egg production consisted of a mixture of pollen and sucrose. Gilbert (1981) recorded that an increase in pollen feeding coincided with rapid expansion of the yolk deposits in females of several species.

Different pollen species appear to differ in their effectiveness in promoting egg maturation and oviposition: Saidov (in Way, 1966) is reported to have found that fecundity in *M. corollae* varies according to the type of pollen offered. Tanke (1976) reported that *E. balteatus* rejected coniferous pollen while Kurir (1963) recorded that *Narcissus* pollen was an inadequate diet for both *Pipizella festiva* and *Heringia heringii*. Stürken (1964) recorded a reduction in the number of eggs laid by *M. corollae* when any single amino-acid except cysteine was removed from artificial diets.

Mature sperm may be present on emergence in the males of some species; for example, Wilkening (1961) reported that male *M. corollae* were capable of fertilizing eggs immediately after emergence. In the majority of species a period of maturation feeding is probably necessary although the maintenance of sperm production probably requires comparatively few resources.

Patterns of emergence differ according to species and may vary for individual species between years according to geographical location. In some species, for example, *Eristalis tenax* and *E. balteatus*, a proportion of flies overwinter in the adult stage. Therefore, adults appearing in the first few days of spring are not recent emergents but overwintered flies. The majority of species overwinter as larvae although the pupa is the overwintering stage in several species (for example, *Cheilosia* species).

Eggs

All known syrphid eggs have a similar shape: an elongated ovoid with one end narrower than the other. They vary in size; generally larger species lay larger eggs although *Syritta* and *Xylota* species lay eggs which are much smaller than might be expected for flies of their size (Gilbert, 1986).

The egg membrane, or chorion, is secreted by follicular cells and consists of two layers which are perforated by a system of air conducting cavities. The chorion functions on the principle of tracheal gills allowing the egg to absorb oxygen from water and air (Kuznetsov, 1988); this is important during the periodic flooding of eggs under abundant dew.

The outer layer of the chorion, the exochorion, has a characteristic surface structure composed of individual structures which form a reticulate or longitudinal pattern of pits or ridges. Several authors (Klein-Krautheim, 1936; Kabos, 1943; Chandler, 1968) have demonstrated that the structure of the exochorion is species-specific and can be used to prepare keys for the identification of syrphid eggs. Early studies used light microscopy to examine the structure of the exochorion; more recently Kula (1988) and Kuznetsov (1988) have used scanning electron microscopy to characterise syrphid eggs.

The keys and descriptions prepared by the various authors have been used in an applied context.

Pollard (1971) examined the composition and distribution of syrphid eggs laid on Brussels sprouts plants in a range of habitats while Kan (1988) used the keys to examine the oviposition response of females of different species to the qualitative and quantitative value of aphid colonies.

Oviposition

Patterns of oviposition reflect the nutrition of the future larvae. Syrphids with larvae which feed on plant tissues generally lay eggs in small clusters, species with entomophagous larvae tend to lay single eggs while those whose larvae are scavengers lay large batches of eggs. The factors stimulating oviposition have been studied in entomophagous species and it has been suggested that there is a basic dichotomy in the stimuli required to effect oviposition (Chandler, 1968a,b). Several species (two *Melanostoma* species and probably all *Platycheirus* species except *P. scutatus*) are facultatively aphidophagous and lay several eggs on a plant whether or not there are aphids present; these species are termed phytozetic. The females of obligate entomophages (for example, *E. balteatus* and *M. corollae*) respond to aphid colonies and lay eggs singly; these are termed aphidozetic species.

Visual and mechanical cues have been shown to play a part in determining the choice of oviposition site; *M. corollae* females selected darker rather than lighter or striped areas and oviposited besides colonies on vertical rather than horizontal surfaces (Sanders, 1980; 1981).

Volk (1964) showed that a mixture of honeydew and exudate from the cornicles of aphids stimulated oviposition in *M. corollae.* Budenberg (1990) showed that honeydew was also an oviposition stimulant for *E. balteatus*; females laid more eggs as the concentration of honeydew increased; however, when honeydew was present at levels comparable to those encountered in the field, aphids rather than honeydew were the dominant cue for oviposition. The presence of syrphid eggs and larvae has not been shown to deter oviposition on suitable plants by *E. balteatus* (Budenberg, 1990), *M. corollae* and *Scaeva pyrastri* females (Chandler, 1968c).

The proximity of oviposition to aphid colonies varies between syrphid species (Chandler, 1968a,b; Dixon, 1959). *M. corollae* and *S. pyrastri* tend to lay eggs in very close proximity to aphid colonies whereas *Melanostoma* and *Platycheirus* species have been recorded ovipositing on uninfested plants. The mean distance between *M. corollae* eggs and the nearest aphid increased as the females aged (Chandler, 1968c).

The relationship between oviposition and prey density has been studied by several authors: Sanders (1979) recorded that female syrphids remained longer in areas of higher aphid density (aggregative numerical response) and that females laid larger numbers of eggs at higher aphid density (reproductive numerical response). Chandler (1968b) observed that larger numbers of eggs were laid on Brussels sprouts infested with progressively higher aphid densities up to a maximum above which oviposition was apparently inhibited. Ito and Iwao (1977) recorded that although *E. balteatus* laid more eggs at higher aphid densities the number of eggs per aphid progressively decreased. Similarly, although Entwistle and Dixon (1990) recorded a significant positive relationship between the number of syrphid eggs and aphid density there was no evidence of density-dependent oviposition.

The majority of studies of the relationship between prey density and oviposition have paid little attention to the age structure of the aphid colonies to which the flies were responding. Kan (1988, 1989) studied the selection of oviposition sites by females of several syrphid species, including *E. balteatus*. Female flies assessed the qualitative and quantitative value of aphid colonies for securing successful development of their larvae; they oviposited in small young colonies, ensuring that newly hatched larvae would be able to find at least one young aphid nymph to successfully start its larval development (Kan, 1989). Females which oviposited at the older, larger colonies risked their newly emerged larvae starving because of a lack of young nymphs and/or by the dispersal of fourth instar nymphs and adults. *E. balteatus* females were able to discriminate between winged and wingless-aphid models and Kan (1986) suggested that aphid wings may be a repellent factor in ovipositional selection by females of this species.

Non-entomophagous syrphids usually lay their eggs on, or in close proximity to the larval food source. For example eggs of *R. campestris* have been found on vegetation overhanging the cow pat larval food sites (Coe, 1942).

The number of eggs produced by a female over her lifetime is influenced by several factors. Cornelius and Barlow (1980) showed that the reproductive output of *M. corollae* was affected by the nutritional status of the larvae. Lal and Haque (1955) reported that temperature and relative humidity, as well as adult nutrition affected reproductive output in *Sphaerophoria scutellaris*. Retention and resorption of eggs in the response to a lack of suitable oviposition stimuli has been recorded in syrphids (Dixon, 1959; Lyon, 1965, 1968).

Development of syrphid eggs is rapid in aphidophagous species: 4.8 days for *E. balteatus* at 15°C (Ankersmit *et al.*, 1986) and 2.7 days for *M. corollae* eggs at 21°C (Chambers, 1986). However, eggs of some of the members of the sub-family Milesiinae appear to develop more slowly; between 6 and 15 days has been reported for eggs of *Merodon equestris* (Doucette *et al.*, 1942).

Larvae

Syrphid larvae show a variety of feeding habits; larval food includes dung (*Rhingia*), rotting vegetation (*Xylota, Neocasia*), aphids (*Metasyrphus, Syrphus, Platycheirus, Episyrphus, Sphaerophoria, Melanostoma*) and the dead grubs and faeces from the nests of social insects (*Volucella* spp.). There are three larval instars in all syrphid species (Doucette *et al.*, 1942; Benestad, 1970) although the length of the larval stage varies considerably between species. The majority of species overwinter as larvae; development is retarded during the winter and the final larval instar may last several months. Polyvoltine predatory species normally have short larval lives, depending on temperature and food type, for example, 12.5 days for *M. corollae* reared on an excess of *Sitobion avenae*(Fabricius) at 15°C and 86% R.H. (Adams, 1984). At low prey densities larval development is longer and pupation occurs at lower larval weights (Ruzicka and Cairo, 1976; Cornelius and Barlow, 1980; Scweizer, Zebitz and Poehling, 1988).

Aphidophagous syrphid larvae have been the most extensively studied as a result of their potential as biological control agents. Laboratory studies have shown the larvae to be voracious predators: *E. balteatus* consumed between 137 and 190 third instar *S. avenae* (Ankersmit *et al.*, 1986) and an average of 416 *Aphis pomi* (Wnuk, 1977) during the larval stage. *Scaeva pyrastri* larvae consumed 550 *Brevicoryne brassicae* during development while the smaller larvae of the tribe Melanostomini consumed fewer aphids: 135 and 150 *Acrythosiphon pisum* respectively for *Platycheirus clypeatus* and *Melanostoma mellinum* (Bankowska, Mikloajczyk, Palmowska and Trojan, 1978).

Syrphid larvae have no perception of prey at a distance and prey are located by "casting": the anterior of the larva is raised off the substrate and extended forwards and from side-to-side without forward progression of the posterior portion of the body (Chandler, 1969). In larvae of *Syrphus ribesii* and *Melanostoma scalare* the rate of casting increased after capture of a prey and then gradually decreased when no further prey were encountered (Rotheray, 1983). Larvae which caught and then lost contact with an aphid moved forward more slowly and were observed casting more frequently (Chandler, 1969). Larvae starved for 48 hours covered a greater distance compared with larvae starved for 24 hours (Rotheray and Martinat, 1984) therefore dispersing over a wider area.

Larvae hold onto plants by the use of meniscus forces created by coating the undersurface of the body with saliva (Roberts, 1971). Many species have locomotory prominences on their undersurface, the structure of which varies between species according to the substrate on which the larvae normally occur.

Holmes (1984) observed the occurrence of syrphid larvae in wheat crops; he recorded that younger syrphid instars tended to rest on wheat ears in the gaps between the spikelets after feeding, while older instars tended to leave the ear after feeding.

The efficiency with which syrphid larvae capture their prey and the time they spend handling prey varies with the relative sizes of predator and prey. First instar *Myzus persicae* were captured with 88% success and consumed in less than two minutes by large larvae of *S. ribesii*, while adults were caught with 98% success and discarded after 3.5 minutes. In contrast, first-instar larvae caught adult prey with 56% success; small *M. corollae* were unable to capture adult *M. persicae* (Hagvar, 1974). Hagvar (1972, 1973) recorded high mortality of *M. corollae* larvae in competition with *S. ribesii* larvae due to predation by *S. ribesii* on the smaller *M. corollae* larvae. Starved *S. ribesii* and *M. scalare* larvae had higher capture efficiencies and longer handling times, presumably due to the more complete removal of food from each aphid (Rotheray, 1983).

Cereal aphids

Aphidophagous syrphid larvae have been identified as having the potential to limit cereal aphid population growth (Chambers and Adams, 1986). Cereal aphids have been considered as pests in western Europe since the wide-spread outbreaks during the 1960's. The three most common cereal aphids in Britain are *S. avenae, Metopolophium dirhodum* (Wlk.) and *Rhopalosiphum padi* (L.). The biology and pest status of these species has been extensively reviewed (Vickerman and Wratten, 1979; Carter *et al.*, 1980; Dixon, 1987; Burn 1987). *R. padi* is the principal vector of Barley Yellow Dwarf Virus in the U.K., and causes damage to autumn sown wheat and barley. *M. dirhodum* may reach economically damaging levels during summer, but does so only rarely; *S. avenae* has reached outbreak levels on at least nine occasions since 1968 (N. Carter pers. comm.). Damage by *S. avenae* is caused by direct feeding and by honeydew production (Vereijken, 1979; Rabbinge and Carter, 1984) which causes yield loss by reduction in grain weight and quality changes, the latter involving a range of protein and enzyme components of the grain (Lee *et al.*, 1979).

Natural enemies of cereal aphids

The natural enemies of cereal aphids can be divided into four groups; parasitoids, pathogens, polyphagous predators and aphid-specific predators, which includes syrphid larvae.

Aphid parasitoids belong to two families of Hymenoptera: the Aphelinidae and the Aphidiidae, the later being most common in the U.K. (Carter *et al.*, 1980). The most common species are *Aphidius ervi*, *Aphidius picipes*, *Aphidius rhapalosiphi* and *Praon volucre.*

Parasitoids need to be active in the crop early in the year if they are to play a significant role in the control of summer cereal aphid populations (Powell, 1983; Vorley, 1986; Fougeroux *et al.* 1988). A high parasitoid : aphid ratio early in the season will slow down the initial growth rate of the aphid population; this reduces potential peak population levels and increases the likelihood that other natural enemies will be able to keep aphids below economic damage levels later in the season (Wratten and Powell, 1991).

Chambers *et al.* (1986) concluded that in the second of two study years, parasitoids in conjunction with fungal pathogens and aphid-specific predators played an important role in limiting aphid populations on the study farms in West Sussex. Simulation studies of the role parasitoids in the population development of *S. avenae* demonstrated that parasitoids could reduce the rate of aphid population growth (Carter *et al.*, 1982) and that aphid populations could be as much as seven times higher at flowering in the absence of parasitism (Vorley and Wratten, 1985)

Three species of fungal pathogen have been recorded attacking *S. avenae* in the U.K. (Dean and Wilding, 1971; 1973). Their importance varies from year to year; diseased aphids normally appear late on in the season although when conditions are humid they may appear earlier which may result in lower aphid populations (Latteur, 1973). Attempts to introduce aphid-pathogenic fungi into populations of cereal aphids to limit population growth have proved unsuccessful (Remaudiere, 1981; Latteur and Godefroid, 1982; Wilding *et al.* 1990).

Polyphagous predators in cereals comprise members of the Carabidae, Staphylinidae and Araneae; Sunderland *et al.* (1985) recorded more than 390 species of polyphagous predators in UK cereals, of which 100 may be common during the summer months. Manipulative experiments using exclusion barriers showed that aphid populations could be as much as seven times higher than in control plots when polyphagous predators were excluded (Edwards *et al.* 1979; Chiverton, 1986). Simulation studies of the role of polyphagous predators in the population development of *S. avenae* demonstrated that some species, particulary the staphylinids *Tachyporus* species, are of importance early in the season, but that other mortality, possibly imposed by other natural enemies was necessary to prevent aphid outbreaks from occurring (Winder, 1990).

Aphid specific predators include members of the families Coccinellidae, Syrphidae and Chrysopidae although the latter are sometimes considered as polyphagous (Carter, 1983). Coccinellid adults and larvae and syrphid larvae have been recorded as predators of cereal aphids. The commonest coccinellids in UK cereals are *Coccinella 7-punctata*, *Adalia 2-punctata* and *Propylea 14-punctata* (Dean, 1982). Rataupää (1976) recorded a positive relationship between peak aphid density and the ratio of aphids to coccinellid adults at the start of the season indicating that coccinellids could be controlling cereal aphid numbers. Carter, Dixon and Rabbinge (1982) and Carter, Gardner, Fraser and Adams (1982) used simulation modelling to show that coccinellids could theoretically prevent cereal aphid outbreaks from occurring, although the results were very sensitive to small changes in predator densities.

Syrphids commonly found in cereals as larvae include representatives of the genera *Syrphus, Platycheirus, Melanostoma, Scaeva, Sphaerophoria* and *Episyrphus* (Dean, 1974; Laska and Stary, 1980; Adams, 1984; Honek, 1983; Chambers *et al.*, 1986). Species composition varies with time and according to geographical location. However, *E. balteatus* and *M. corollae* are the most commonly recorded species on arable land in Great Britain (Dean, 1982; Chambers *et al.*, 1986); *E. balteatus* has been recorded as the predominant syrphid species in winter wheat in Germany (Poehling, 1988; Tenhumberg and Poehling, 1991).

Indications that syrphid larvae play a role in limiting cereal aphid population growth have been provided by observations, manipulative techniques and by modelling. Several authors have recorded an association between the presence of syrphid larvae and the cessation of aphid population growth (Dean, 1974; Smith, 1981; Chambers, Sunderland, Wyatt and Vickerman, 1983; Holmes, 1984; Chambers, Sunderland, Stacey and Wyatt, 1986; Storck-Weyhermuller, 1987; Poehling 1988; Entwistle and Dixon, 1990; Poehling, Tenhumberg and Groger, 1991). The studies have included observations of unmanipulated field populations of aphids and larvae or the removal or exclusion of larvae from areas of crop using pesticides or cages. In one of the most detailed observational studies Holmes (1984) returned to marked tillers three times per day and recorded the destruction of *S. avenae* colonies; syrphid and *Tachyporus* larvae were identified as the main predators during the study with the majority of predation occurring between 19.00h and 07.00h.

Chambers *et al.* (1983) used field cages to exclude aphid specific predators, including syrphids, from plots of winter wheat; they then compared changes in the numbers of cereal aphids inside and outside the cages. Three phases of aphid population growth were distinguished: an initial rapid growth phase, a divergence phase and a decline phase. In each year the field and cage aphid populations increased at the same rate during the initial growth phase but during the divergence phase populations inside the cages continued to increase to a peak while populations in the open field increased at a lower rate or decreased. Although the possibility that the caging technique itself had some affect on these differences can not be excluded, the results suggested that aphid-specific predators had at least some effect on the aphid

Table 2 (modified from Gilbert, 1981). A summary of papers in which limitation of aphid population growth is attributed to syrphid larvae.

Aphid species	Crop	Reference
Several species	Apple	Holdsworth (1970)
Several species	Maize	Jasiolek *et al.* (1974)
Aphis fabae	Sugar beet	Hurej (1982)
Aphis gossypii	Cotton	Barbosa (1952)
Aphis pomi	Apple	Wnuk (1977)
Brachycaudus schwartzii	Plum, peach	Bartoszeck (1976)
Brevicoryne brassicae	Kale	Hughes (1963)
B. brassicae	Cabbage	Markkula (1953)
B. brassicae	Brussel sprouts	Pollard (1971)
B. brassicae	Brussel sprouts	Way *et al.* (1969)
Myzus persicae	*Eruca sativa*	Bakhetia and Sharma (1979)
M. persicae	Peach	Tamaki (1973, 1974)
M. persicae	Collard	Horn (1981)

population peak. Syrphid larvae were the most abundant predators during one of the three study years.

Chambers *et al* (1983) compared the consumption rate necessary to bring about the observed differences aphid density between the cages and open field with the values recorded for aphid-specific predators, particularly *Coccinella 7-punctata*, in the literature. The required values fell within recorded values indicating that aphid specific predators were the most likely cause of the differences in cage and field aphid populations. Using a similar approach Chambers and Adams (1986) calculated required kill necessary to account for the observed change in aphid density between sampling dates and compared it with the estimated kill attributable to syrphid larvae. These authors showed that syrphid larvae could have been responsible for the early decline in aphid populations which were recorded in four of the six populations which were analysed. Aphid numbers did not exceed the recommended spray threshold of five *S. avenae* at the start of flowering (George and Gair, 1979). Similar results were reported by Entwistle and Dixon (1990) who calculated that syrphid larvae were sufficiently numerous to cause the significant decline in aphid numbers observed in some plots during their study.

Rabbinge, Ankersmit and Pak (1979) incorporated a predator sub-model for syrphid larvae in their cereal aphid simulation model which resulted in the lowering of the aphid peak and the hastening of the decline, based on field results from 1976.

In addition to their role in cereals, syrphid larvae have also been recorded limiting aphid population growth on a range of other crops; Table 2 summarises some examples available from the literature.

The effect of field margin composition on the bio-control potential of syrphids in cereals

The observations that adult syrphids feed on pollen and that females need to feed on pollen to mature their reproductive system have implications for the effectiveness of syrphids in limiting aphid population growth. That is, the availability of these essential resources may be a major factor affecting syrphid oviposition and consequently aphid predation. This may be especially true in modern agroecosystems where agronomic practices have tended to reduce floral diversity (Boatman, 1989), removing the flowering arable weeds which are food sources for adult syrphids.

Several authors have studied the effect of sowing single species stands of pollen and nectar sources in field margins on the density of syrphids in the vicinity of the margin. Klinger (1987) examined the effect of the presence of margin strips of *Sinapsis arvensis* and *Phacelia tanacetifolia* on the numbers of aphid predators in the adjacent field. Polyphagous predators were recorded in higher numbers in the margin strips and in adjacent fields than in wheat plots without a margin strip. Syrphid adults were recorded in higher numbers in the margin strips than in the field, presumably as a result of the flies foraging on the *P. tancetifolia* and *S. arvensis*. No quantification of the impact of different predatory groups on aphid populations was provided although a trend towards lower aphid densities in the field adjacent to the *P.tanacetifolia* and *S. arvensis* plots was observed. Sengonca and Frings (1988) reported that although syrphid adults were recorded in higher numbers in sugar beet plots with *P. tanacetifolia* margin strips than in control plots without *P. tanacetifolia*; the density of syrphid eggs and larvae was highest in control plots where aphid density was highest.

In addition to manipulative experiments involving high densities of selected flowering plants, several authors have studied the relationship between the species composition of naturally occurring field margins and the density and diversity of syrphid species.

Molthan and Ruppert (1989) studied the species composition of syrphids in three naturally occurring field boundaries; the number of species and abundance of flies in narrow margins consisting of grasses was significantly lower than in wider (1.5-2m) margins consisting of a range of dicotyledonous plants. The greatest diversity and largest number of individuals were recorded from an 8m wide margin with an adjacent embankment and a high diversity of flowering plants. Kühner (1988) recorded the relative abundance of syrphids and parasitoids in herbicide-free and herbicide-treated crop edges in three locations in Hesse, Germany. At two of the locations the crop edges comprised a range of flowering plants; syrphids were more abundant at these locations than in the third area where the herbicide-free crop edge was characterised by different species of grasses and few flowering plants. Most of the beneficial species in the latter area belonged to the parasitic Hymenoptera.

Kühner also recorded the number of cereal aphids in plots of sprayed and unsprayed crop edge at the three locations; aphid density was lower in herbicide free plots than in herbicide treated plots in areas where naturally occurring boundaries consisted of a range of flowering weeds; however, in the area in which grasses predominated in crop edges there was no significant difference in aphid density between the two treatments. Felkl (1988) recorded the numbers of syrphid larvae in herbicide free and herbicide treated crop edges; larvae were more numerous in border strips treated with herbicide where aphid infestations were higher. However, carabids, staphylinids and spiders were more abundant in the herbicide free edges.

With the exception of the studies of van Emden (1965) and Pollard (1971) no studies of the impact of field margin composition or manipulation on the diversity and density of syrphids exist in the UK. However, since 1988 agricultural policy in UK has been concerned with the reduction of cereal surpluses, in particular via the introduction of the "Set-Aside" scheme. This has stimulated research into management options for field margins, including those which are beneficial to natural enemies of crop pests.

The present study was undertaken as a result of these changes with the aim of examining the foraging behaviour of adults of commonly-occurring syrphid species on farmland. In particular the aim was to identify which naturally occurring, non-crop plants are important food sources for the flies and to examine the effect of a management technique ("conservation headlands"- see later) which encourages the growth of at least some of these non crop plants, on the distribution of syrphid adults. In addition, field experiments were carried out to examine the factors influencing the distribution of syrphid eggs within wheat crops.

CHAPTER TWO

THE SELECTION OF FLOWERS BY SYRPHIDS

Introduction

The earliest reports of the association between syrphids and flowers were records of the presence of the flies on various flowers (Müller, 1883; Drabble & Drabble, 1917, 1927; Hamm, 1934). Later work provided quantitative information on the flower-visiting patterns of certain syrphid species (Jones, 1954, 1955; Grinfeld, 1955; Parmenter, 1956; Kugler, 1970; Kay, 1976; Gilbert, 1980; Ruppert and Klingauf, 1990) while El-Berry *et al.* (1974a,b), Stelleman & Meeuse (1976), Leereveld, *et al.* (1976) and Lack (1982) examined these patterns in the context of pollination.

Dauman (1932, 1935) and Kugler (1950) have shown that syrphids can distinguish the shapes of flowers and concluded that the approach of syrphids to flowers was purely an optical response. At short range, scent induced the flies to alight. Ilse (1949) and Kay (1976) showed a preference for white and yellow flowers in *E.tenax*. However, Haslett (1981) reported that *E. tenax* showed an apparent preference for blue and red flowers over white and yellow, while *E. pertinax* preferred white and yellow flowers. *Rhingia campestris* appeared to specialize on blue and purple flowers (Gilbert, 1981; Haslett, 1989) while *Cheilosia albitarsis* preferred low u.v yellow.

In addition to direct observation of foraging behaviour, analysis of the gut contents of syrphids has been used to study the flower visiting patterns of the flies. Schneider (1969) analysed the gut contents of *Scaeva pyrastri* and concluded that this species did not confine itself to a single species or specific group of flowers. In contrast, several *Platycheirus* species have been shown to have a clearly restricted range in pollen feeding (van der Goot & Grabandt, 1970). Haslett (1989) examined the extent to which six syrphid species were selective in their diets; some species showed a substantial degree of pollen selectivity, while others showed a more generalist approach to foraging.

Observations of the syrphids associated with garden habitats and ancient woodland have recorded inter-specific differences in the type of flower visited and the food taken (Gilbert, 1985). The differences appeared to be closely connected with morphology. Relative proboscis length and labellar size were the main morphological differences between species and Gilbert (1985) suggested a relation between these characters and differences in the proportions of pollen and nectar in the diets of the flies. There were increases in the proportion of the time spent foraging on nectar with increases in body size although some species were pollen specialists which almost exclusively took pollen. Haslett (1989) has claimed that pollen is taken in large quantities by many syrphids, irrespective of proboscis length or body mass.

In species foraging on nectar, Gilbert suggested that the flower species visited can be explained, in part, by the relationship between proboscis length and corolla depth. Syrphids with relatively long probosci may be discouraged from visiting flowers with short corollae through a combination of the handling time associated with visiting flowers of differing corollar depth and the greater amounts of energy available from flowers with long corollae (Prys-Jones,1982).

Pollen specialists satisfy their metabolic requirements with pollen. Nutrients are obtained from pollen when the grains exude their contents into the gut lumen of the fly. Exudation may be initiated by the germination of the pollen tube, after which a general rupture of the grain takes place (Haslett, 1983). Enzymes have been recorded from the guts of syrphids (Schiemenz, 1957; Zimina, 1957; Nayar, 1967; Kevan, 1970) so enzymic action may also be responsible for the liberation of nutrients into the gut lumen. In either case it is probable that the release of energy from pollen is too slow to fuel the activities of larger hoverflies (Gilbert, 1985). This would account for increasing proportion of nectar in the diet of larger syrphids and the absence of large species of hoverfly feeding exclusively on pollen. Furthermore, immature male syrphids, for example, *S.ribesii,* have been observed feeding on pollen while mature males, which have particularly high energy requirements because they hover in leks (Heinrich and Pantle, 1975), switch to nectar and honeydew (Gilbert, 1984). Species-specific differences between plants in the nutritive value of pollens (Stanley & Liskens, 1974) may be important in determing which flowers are visited.

An understanding of the selection of flowers by syrphids which have aphidophagous larvae is important in an agricultural context because of the potential for manipulating the distribution of syrphids within the agroecosytem by the provision of appropriate flower species. Molthan & Ruppert (1988) have shown that the provision of flowers in a sufficiently wide boundary strip affects both the species diversity and density of syrphids in the vicinity of the boundary strip.

The work presented in this section is a quantitative assessment of the use of non-crop plants by some commonly occurring syrphid species. In particular, the study concentrated on the use of arable weeds and other plants which occur in the margins of cereal fields. The aim was to obtain information on the relative importance of various flowers to the flies. This information will facilitate the development of guidelines for the management of field-boundaries, which aim to increase the number of adult syrphids and therefore potentially the numbers of larvae in the crop.

Materials and methods

Field Sites

Two field margins with differing floral composition were selected from a mixed arable\livestock farm in North-West Hampshire. The sites were paired for aspect and cropping pattern; their location is shown in Fig. 1. One sampling site (50mx1m) was established in a randomly allocated position in each margin. All observations of syrphid behaviour were restricted to these sites.

Site One: Field 14.

Field 14 consisted of an established hedgerow, approximately two hundred metres long. The hedgerow was bordered by perennial rye-grass, and was separated from a 21.9 ha field of winter-wheat, c.v. Rendevous, by a three metre-wide farm track

The hedgerow vegetation included hawthorn, *Crateagus monogyna*, bramble *Rubus fruticosus*, elder *Sambucus nigra*, dogwood *Cornus sanguinea* and spindle *Euonymus europaeus.* A range of

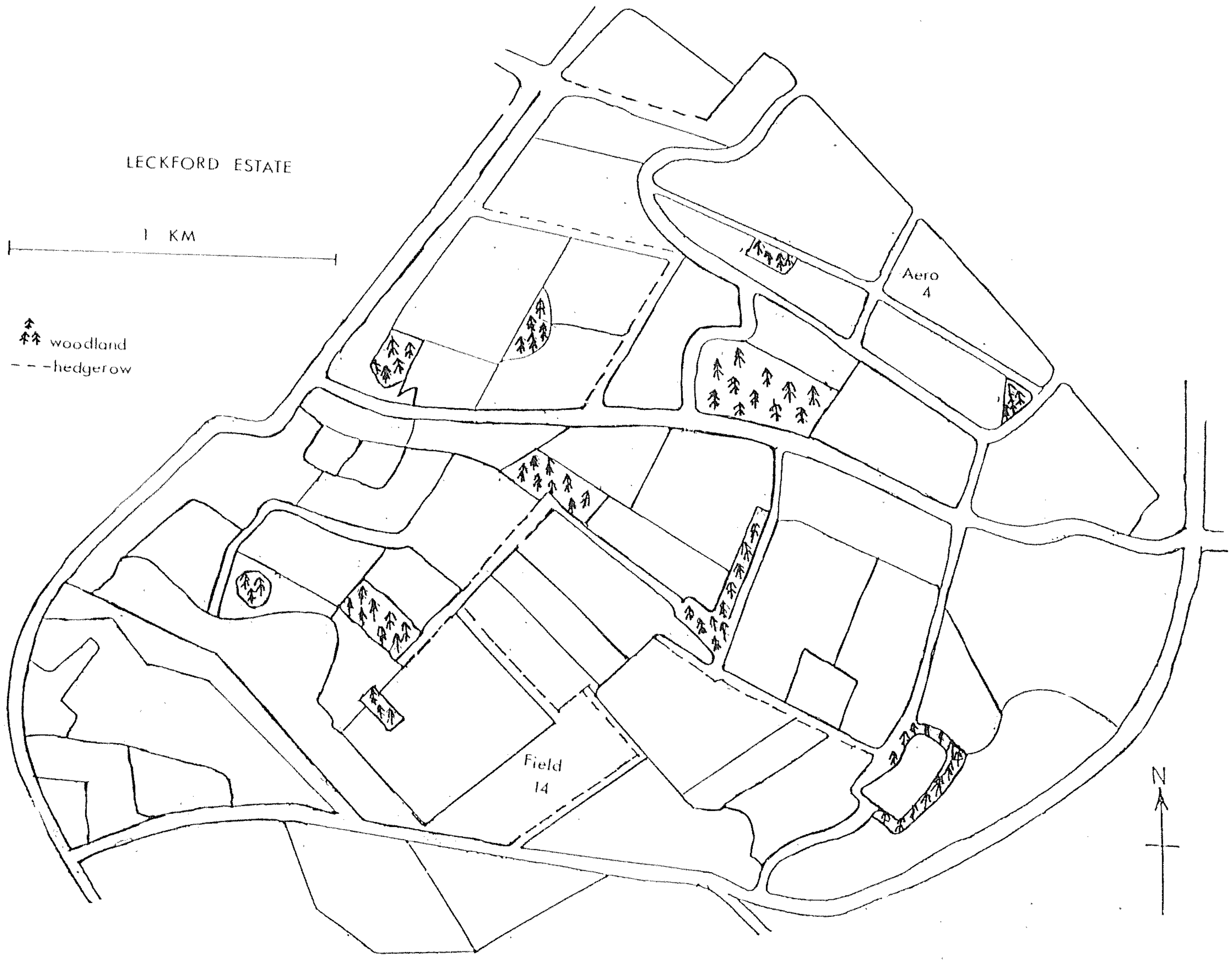


Fig. 1. Map of the Leckford Estate, Hampshire, showing the position of the two study sites.

spring flowers gave way to grasses in the summer and autumn. By early summer grasses such as *Lolium perenne*, *Dactylis glomerata*, *Arrhenatherum elatius* and *Agrostis* species, together with rough chevril, *Chaerophyllum temulentum*, formed the dominant herb layer. In late summer, the available flower species comprised *Heracleum sphondylium*, *Rubus fruticosus* and *Rosa canina*.

Site Two: Aero 4

Aero 4 comprised a one metre wide fallow strip adjacent to a 25 ha field of winter-wheat c.v. Avalon. The strip was separated from a field of perennial rye grass by a five metre wide farm track. The fallow strip was colonised by a range of arable weeds. In the spring the predominant weed species were *Lamium album*, *Silene vulgaris* and *Silene alba*. *Sinapsis arvensis, Lapsana communis, Sonchus* species and *Matricaria perforata* became abundant as the summer progressed.

Syrphid foraging behaviour

Data obtained in 1988 from standard census walks taken in the two field margins described above was used in the analysis of syrphid foraging behaviour. At each site a set route of fixed size (50x1m) was traversed at a constant speed. All the syrphids encountered were identified to species and the behaviour at the time of first siting, along with the weed species involved, were recorded onto a microcassette tape recorder. Each observation had a corresponding recording of the time of day, cloud cover, wind speed, temperature and relative humidity. Measurements of temperature and relative humidity were made using a Grant "Squirrel" datalogger. Wind speed was estimated using the Beaufort scale.

Census days were chosen according to weather conditions; cold, wet days were avoided. Overall, conditions in 1988 were good and few days were lost as a result of bad weather. It was usually possible to cover the two field-margin sites on adjacent days. Censuses took place between early June and the end of August, usually beginning at 05.30 G.M.T. and ending between 16.00 and 16.30 G.M.T.

Haslett (1989) has critised the use of observational methods to study flower selectivity, because of the variation in handling times between flower species. He has suggested that the identification of pollen grains from the guts of syrphids could be used as an alternative approach to direct observation. However, the pollen productivity of flowers differs between species (Percival, 1956) from 0.005mg to 55mg per day per "flower form" (inflorescence or single flower).Therefore, it would be inaccurate to use the abundance of flowers as a measure of pollen availability. Without an assessment of the rate of pollen production for the flower species involved it is not possible to asses the degree of selectivity. In the present study the absence of accurate assessments for the rates of pollen and nectar production for the various flower species resulted in total floral abundance being used as a measure of resource abundance. Although these values did not represent a measurement of the actual resource availability, the fact that the selection of flowers by syrphids is a discrete behavioural act may justify this approach. That is, consumer individuals do not choose resources by joule or by gram but rather item by item (Rotenberry, 1990).

Flower sampling

Total floral abundance in each sampling area was measured weekly from June to the end of August using a line of fifty 1m^2 quadrats. The number of open flowers, flower heads or flower-bearing stems was recorded for each flower species. These sampling units were chosen to represent the flower visitors view as closely as possible. That is, it was assumed that syrphids would distinguish individual flowers if these were spatially separated and on the same size scale as the fly, but would distinguish racemes if the flowers were small and densely packed.

Analysis of flower visitation patterns

Several analytical techniques exist for the comparison of the use and availability of resources, for example, Ivlev's electivity index, E (Ivlev, 1961), Ivlev's Forage ratio, E' (Ivlev, 1961) and its modifications (Jacobs, 1974, Chesson, 1978) and the indices α and β (Manly, Miller and Cook, 1972). These techniques have been widely used to determine "preference" (for example, Dennis, 1990; Menge, 1972). A resource has been termed "preferred" if its usage exceeds its availability in the habitat. However, Johnson (1980), has recommended that the term preference be restricted to a description of the likelihood of a component being chosen when it is offered on an equal basis with others. In the field, resources seldom occur on an equal basis; in these situations resource usage is described as selective when components are used disproportionately to their abundance in the habitat. Conclusions about whether an individual flower species is used above, in proportion to, or below its availability are dependent upon the assumptions made as to the relative availability of flower species to syrphids. The inclusion of flowers unimportant to the flies will influence the rating of the flower species which are used by the flies.

Johnson (1980) proposed a method for the comparison of use and availability measurements which is based on ranks and is therefore less sensitive to the inclusion of questionable components. However, Alldredge and Ratti (1986) have shown that the method described by Johnson is unable to detect even large differences in use and availability when their rank orderings are the same. In the present study a technique comparing the absolute numbers of flowerheads with the number of visits to individual flower species has been used. The caveat mentioned earlier resulted in the calculated values being used to indicate only the relative value of an individual flower species, in comparison with others, and not to make absolute statements about avoidance or preference.

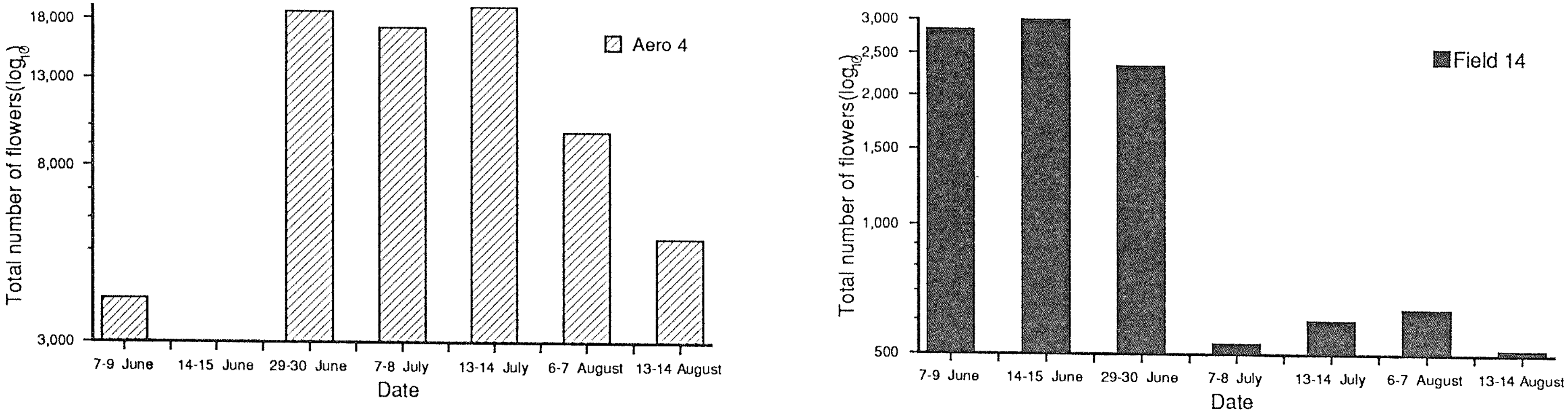
Results

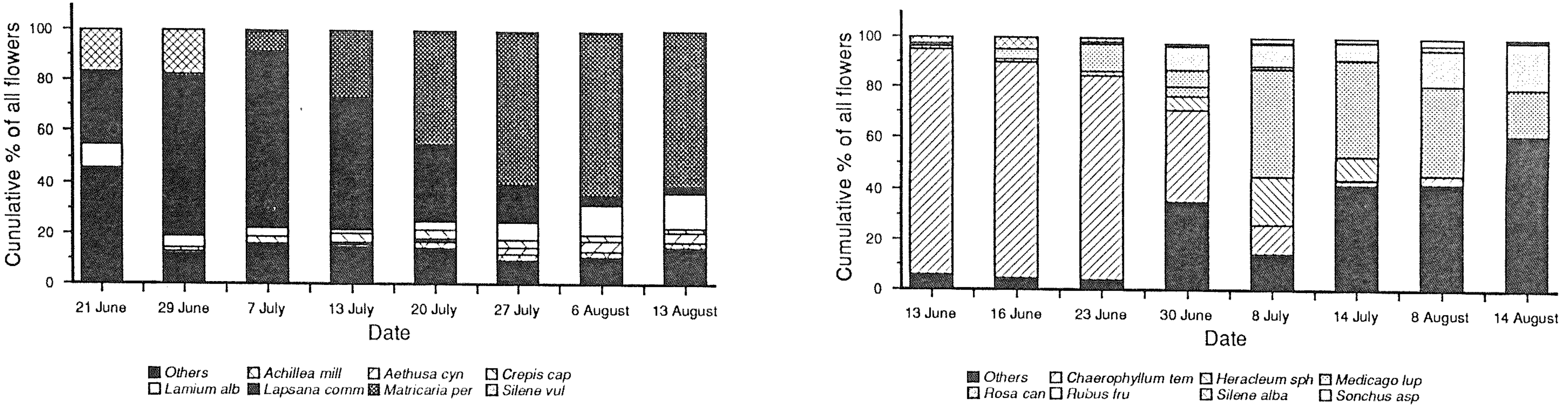
Abundance of flowers

Fig.1(a) summarises the total number of flower heads, of all species, recorded from the two sites. Analysis of the data using Wilcoxon signed ranks showed that there were consistently higher numbers of flower heads recorded at Aero 4 throughout the study ($Z= -2.80224$, $P< 0.005$). The family and species composition of the flowers is shown in Figs. 2(a) and 1(b). The Compositae accounted for more than 70% of all the flowers at Aero 4 during July and August; *Lapsana communis* and *Matricaria perforata* were the dominant species during this period. The umbellifer, *Chaerophyllum temulentum*

Table 1. Key to the flower species represented in Figs. 1-14.

Abbreviation in fig.	Flower species.
Achillea mill.	*Achillea millefolium*
Aegopodium pod.	*Aegopodium podgraria*
Aethusa cyn.	*Aethusa cynapium*
Agrimonia eup.	*Agrimonia eupatoria*
Anagellis arv.	*Anagellis arvensis*
Artemisia vul.	*Artemisia vulgaris*
Centaurea nig.	*Centaurea nigra*
Chaerophyllum tem.	*Chaerophyllum temulentum*
Cirsium arv.	*Cirsium arvense*
Cirsium vulg.	*Cirsium vulgaris*
Convolvulus arv.	*Convolvulus arvensis*
Crepis cap.	*Crepis capillaris*
Daucus car.	*Daucus carota*
Heracleum sph.	*Heracleum sphondylium*
Lamium pur.	*Lamium purpureum*
Lamium alb.	*Lamium album*
Lapsana comm.	*Lapsana communis*
Leontodon aut.	*Leontodon autumnalis*
Matricaria per.	*Matricaria perforata*
Medicago lup.	*Medicago lupulina*
Polygonum avi.	*Polygonum aviculare*
Ranunculus rep.	*Ranunculus repens*
Rosa can.	*Rosa canina*
Rubus fru.	*Rubus fruticosus*
Silene vul.	*Silene vulgaris*
Silene alb.	*Silene album*
Sinapsis arv.	*Sinapsis arvensis*
Sonchus arv.	*Sonchus arvensis*
Sonchus asp.	*Sonchus asper*
Taraxacum off.	*Taraxacum officinale*
Veronica per.	*Veronica persica*
Grasses and plantains	
Agrostis sto.	*Agrostis stolonifera*
Arrhenatherum ela.	*Arrhenatherum elatius*
Dactylis glo.	*Dactylis glomerata*
Lolium per.	*Lolium perenne*
Plantago lan.	*Plantago lanceolata*
Plantago maj.	*Plantago major*



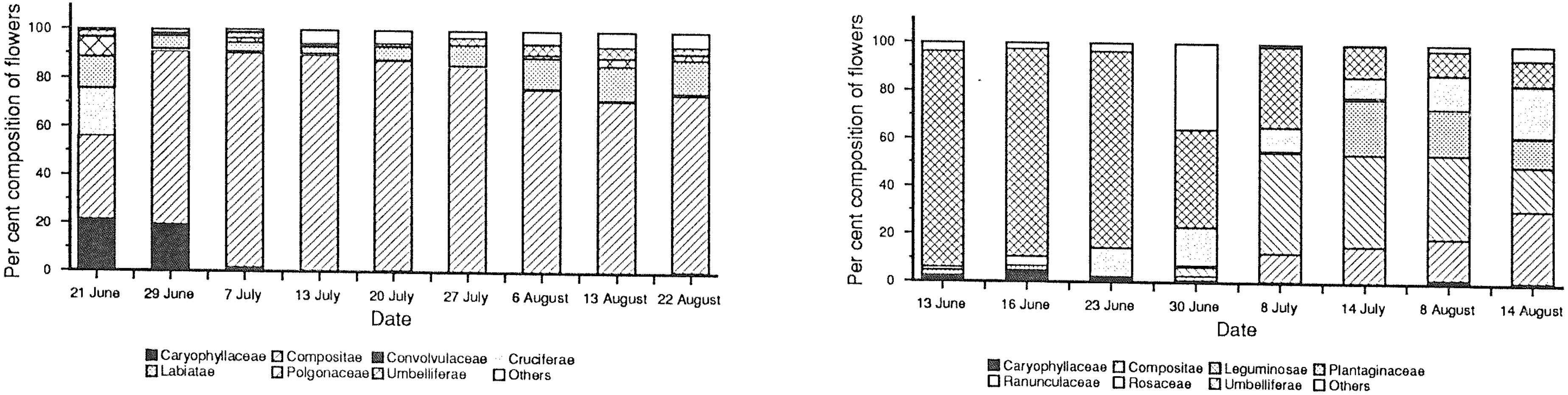


Aero 4

Field 14

Fig.1(a). The total number of flowers at the two field sites in 1988.

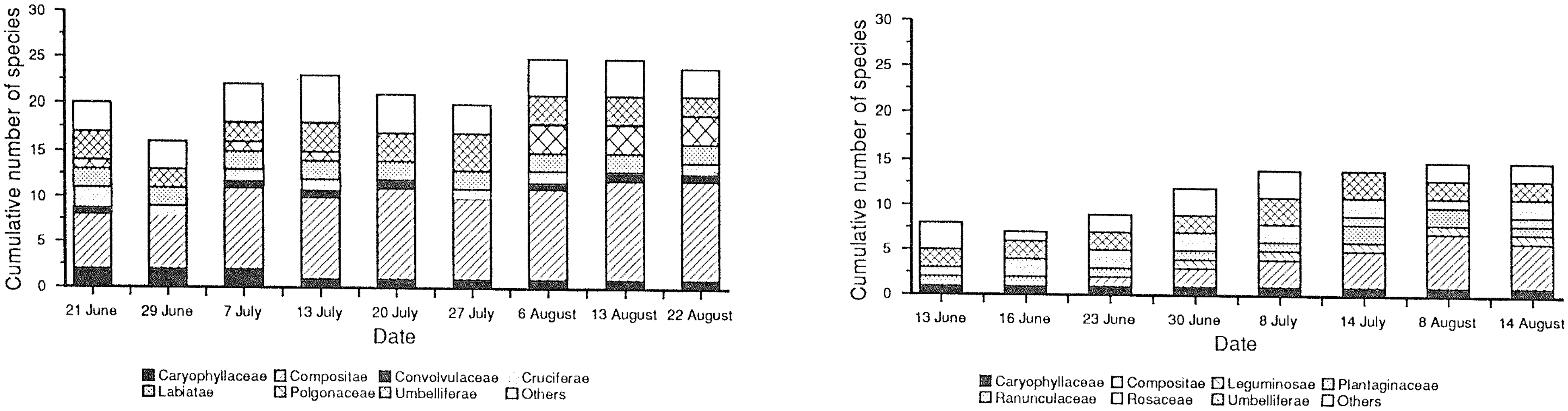
Fig.1(b). The percentage species composition of the flowers at the two sites.



Aero 4

Field 14

Fig.2(a). The family composition of flowers at the two sites 1988.



Aero 4

Field 14

Fig.2(b). The total number of flower species recorded in each family at at the two sites in 1988.

was the dominant species at Field 14 during June; in July and August the flowers comprised a mix of species from several families. Fig. 2(b) shows that there were fewer species at Field 14 throughout the study.

Flower selection

A total of 1186 observations of the foraging behaviour of 15 species of syrphid were recorded from the two sites, during the period 15 June to 22 August 1988. (Appendix 1 summarises the total number of observations of foraging behaviour for each of the 15 species). *E. balteatus* accounted for 37.18% of the observations. The majority of the remaining species were recorded in low numbers during the study; some species had peaks of abundance according to the phenology of the flies. Only four species were recorded in sufficient numbers to allow statistical analysis of the data: *E.balteatus, E. tenax, M.corollae,* and *P.peltatus.* Although *M. scalare* and *S.pipiens,* accounted for 10.96% and 10.03% of the total observations the rate of observation on individual census dates was low; therefore no analyses were performed on the data. The flies, with the exception of *M. scalare*, occurred in low numbers at Field 14 and unless otherwise stated the results refer to data from Aero 4.

M. scalare was atypical when compared with the majority of the species recorded in the study; it was observed foraging on grasses and plantains (*Plantago* spp.) in addition to dicotyledons. As no measurements of the abundance of grass flower heads were made during the study it was not possible to analyse the distribution of flower visits by this species. Fig.3 shows the distribution of flower visits as a percentage of the total number of observations per date. On five of the six sampling dates, over 50% of the observations of this species were individuals foraging on grasses and plantains. Data for *S. pipiens* is also presented in this form in Fig.4. Fig. 5 shows the distribution of flower visits as a percentage of the total number of observations per date for the six least commonly observed syrphid species: *P. albimanus, P.manicatus, R. campestris, S. scripta, E. nemorum* and *E. arbustorum.*

E. tenax, M. corollae, and *P. peltatus* accounted for 9.61%, 7.93% and 9.44% of the total observations, respectively. Figs. 6,7,8 show the observed and expected number of visits to individual flower species for these flies. The observed values refer to the number of visits to a particular flower species, at Aero 4, on that date. The expected values were calculated according to the relative abundance of the flower species in the habitat. A Kolmogorov-Smirnov test was used to compare the observed and expected distribution of flower visits. This test was chosen because it was possible to analyse small sample sizes without having to group data. Although the test is properly applied only to continuous frequency distributions it can be used as an approximate test with discrete frequency distributions; in this case the tabulated critical values of the test statistic, D, are conservative (Neave and Worthington, 1988).

On six of the seven sampling dates, between 21 June and 6 August, the observed distribution of flower visits for *E. tenax* differed significantly from the expected distribution. (D_{45}= 0.6193, $P<0.01$; D_{66}=0.4164, $P<0.01$; D_{29}=0.5466, $P<0.01$; D_{19}=0.7514, $P<0.01$; D_{44}=0.2251, $P<0.05$; D_{20}= 0.175, NS; D_{46}= 0.5273, $P<0.01$). Fig. 6 shows the observed and expected distribution of flower visits on the six dates.

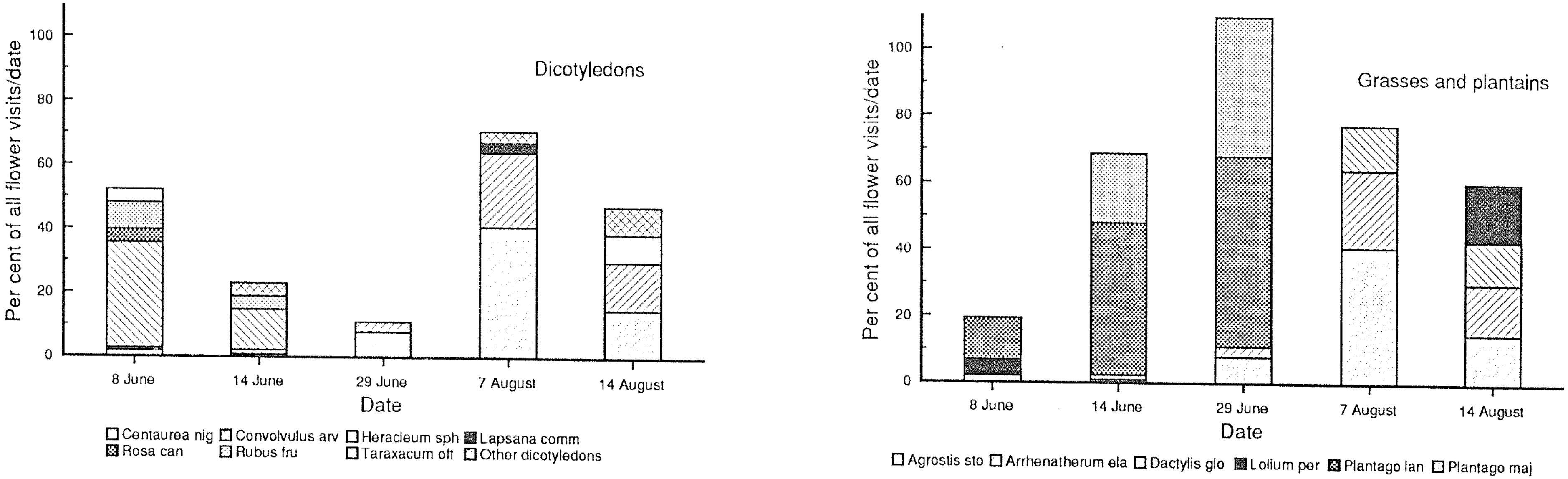


Fig.3. The number of visits to individual plant species, by M. scalare, expressed as apercentage of the total number of visits per date at Field 14. The data is divided into visits to dicotyledons and visits to grasses and plantains.

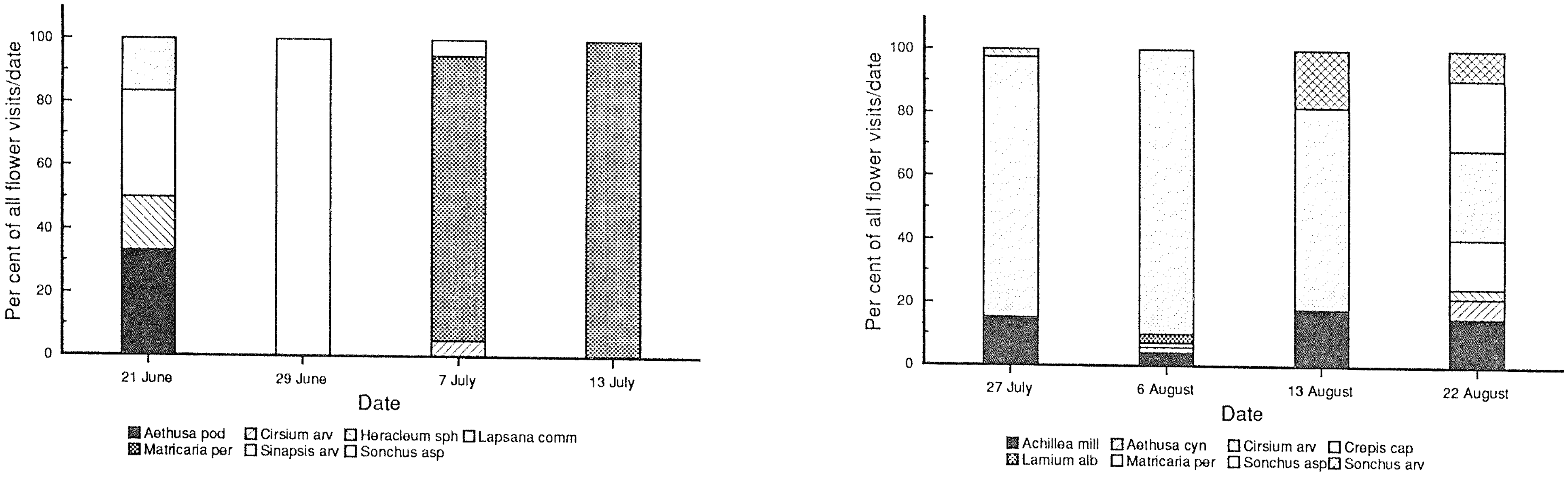


Fig.4. The total number of visits to individual flower species expressed as apercentage of the total number of visits by *S. pipiens* adults on each date at Aero 4.

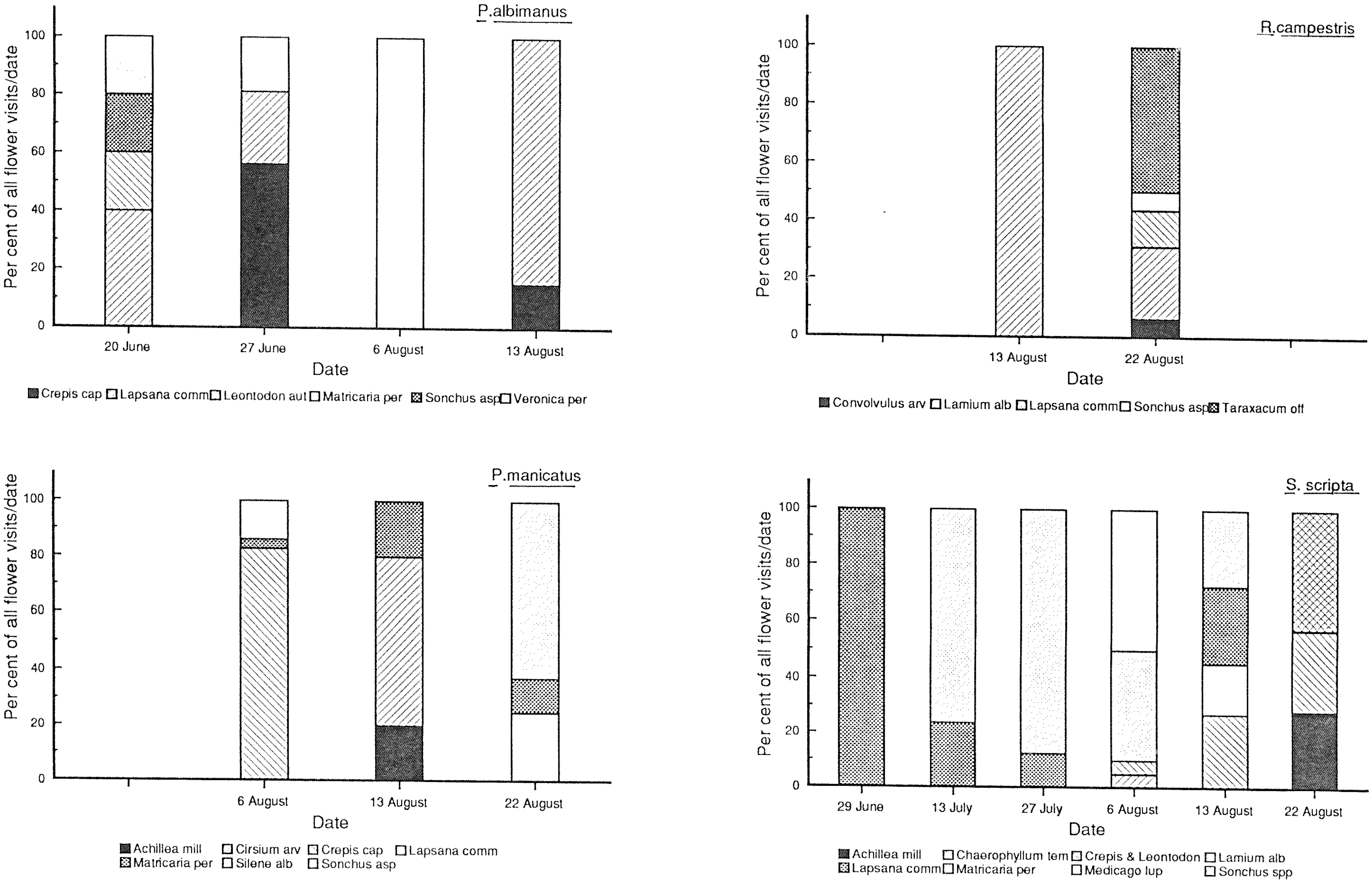


Fig.5. The number of visits to individual flower species, expressed as a percentage of the total number of visits per date for six of the least commonly observed syrphids at Aero 4.

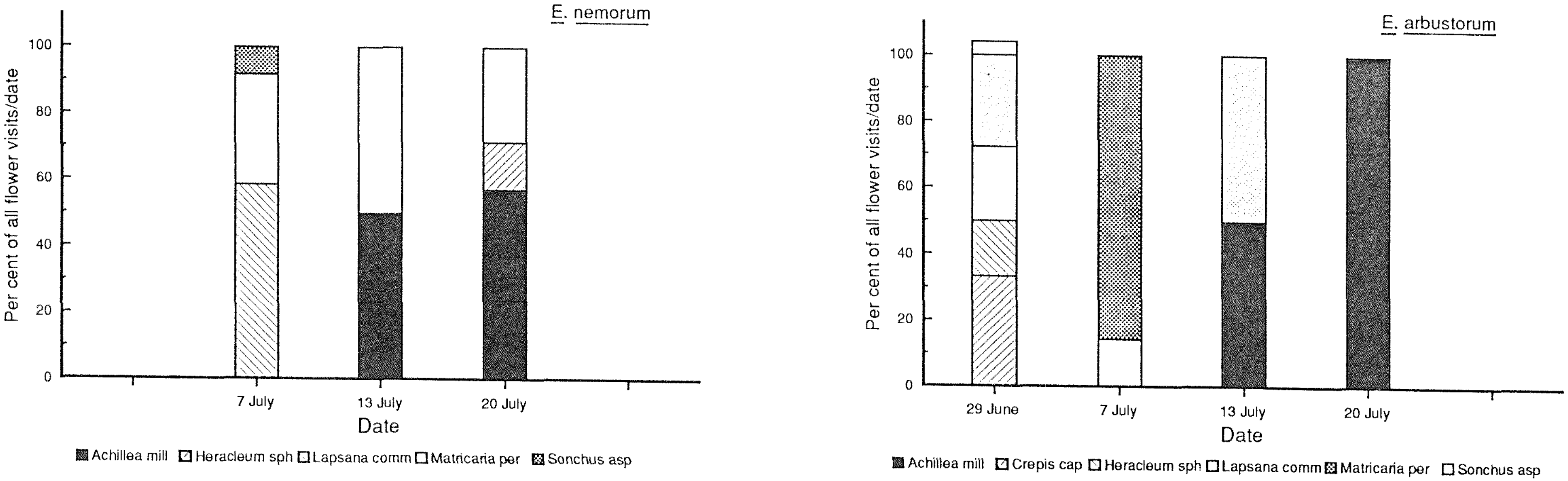
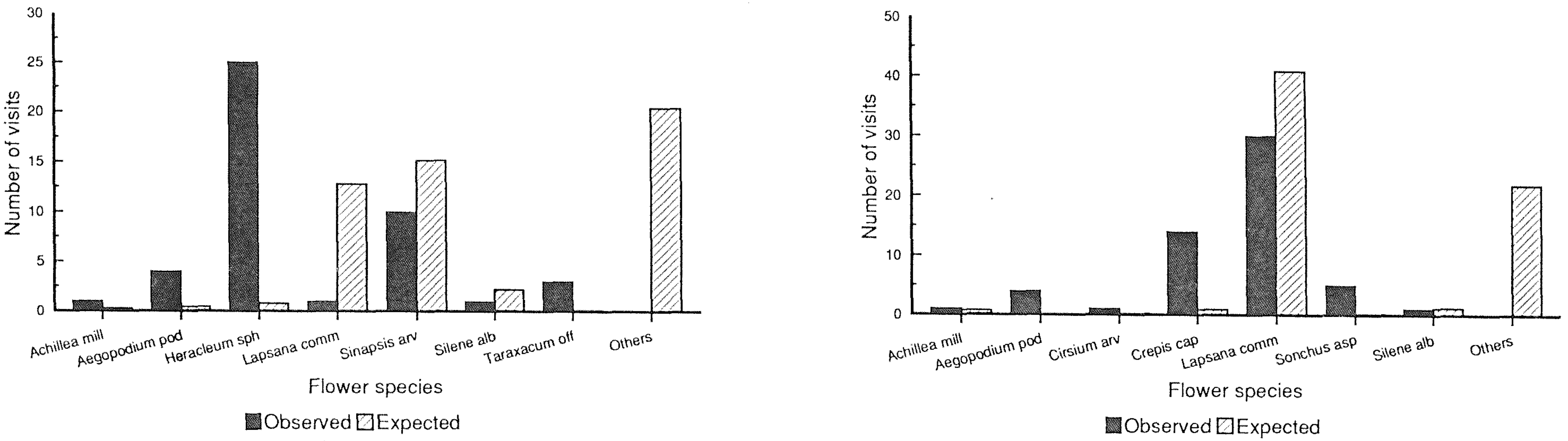
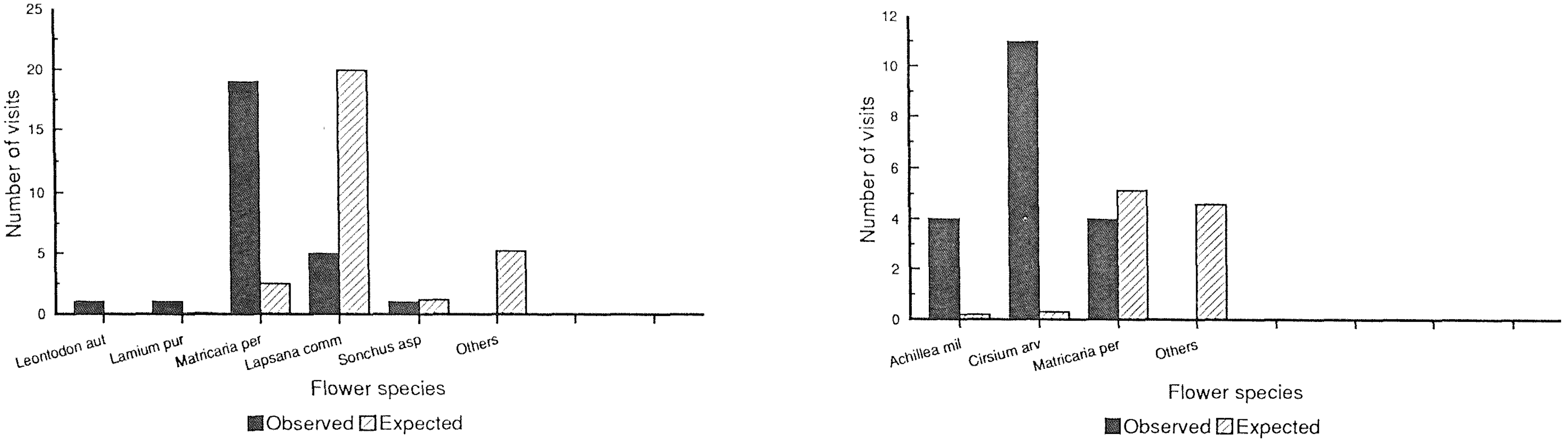


Fig.5(contd.) The number of visits to individual flower species, expressed as a percentage of the total number of visits per date for six of the least commonly observed syrphids at Aero 4.



21 June 1988

29 June 1988



7 July 1988

13 July 1988

Fig.6. A comparison of the observed and expected distribution of flower visits for *E. tenax* at Aero 4.

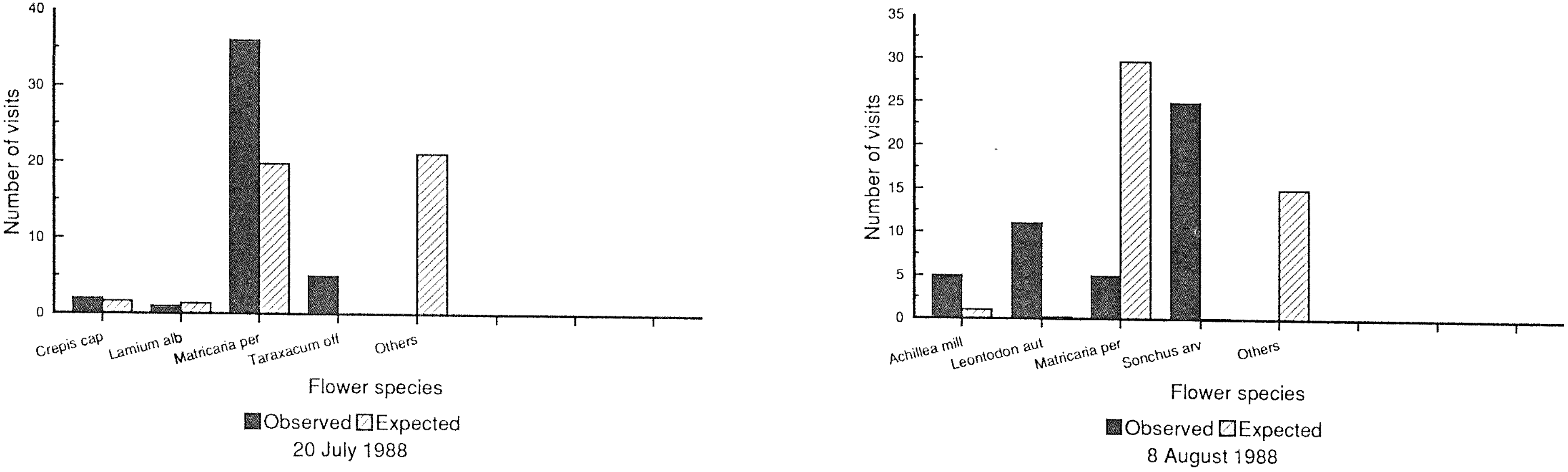
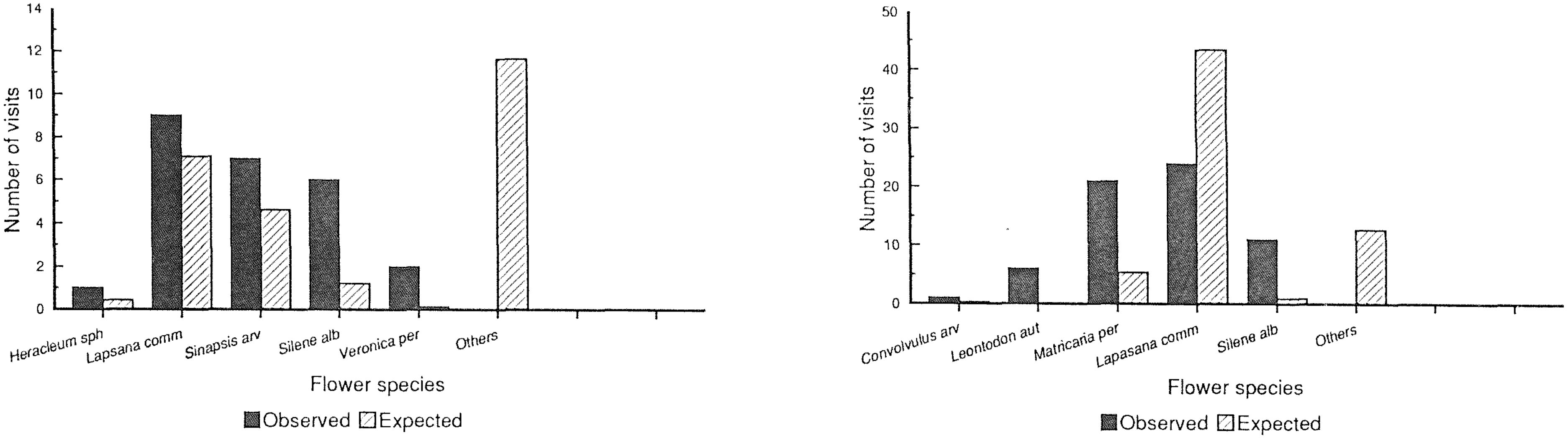


Fig.6(contd.). The observed and expected distribution of flower visits for *E. tenax* at Aero 4.



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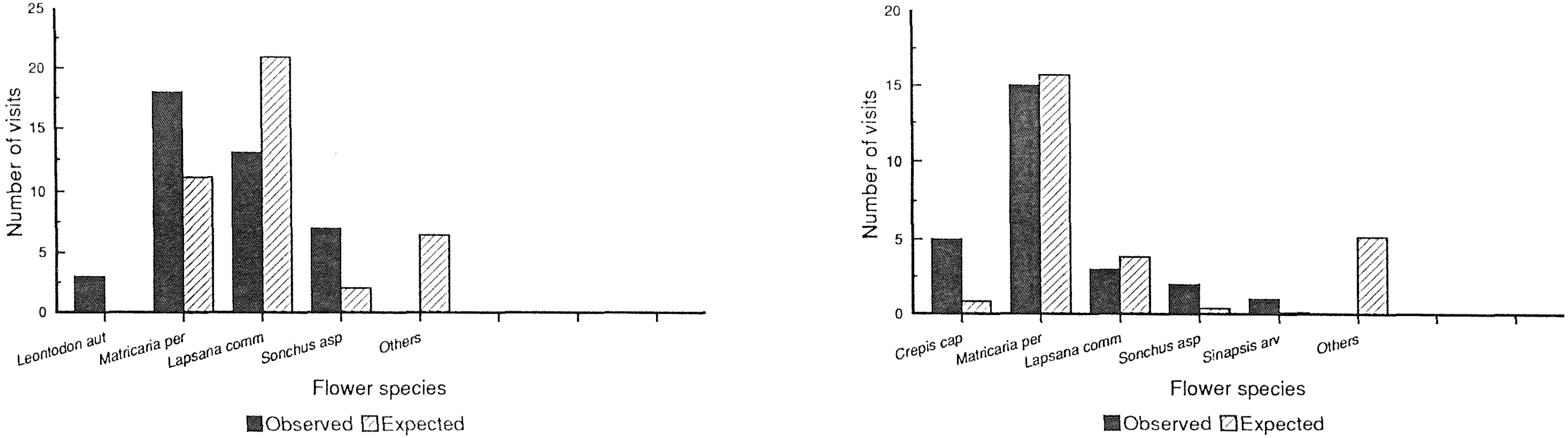

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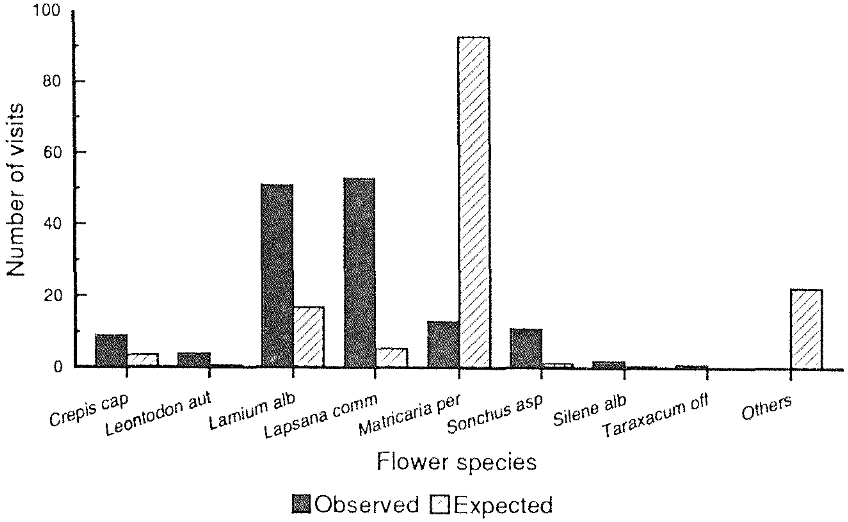
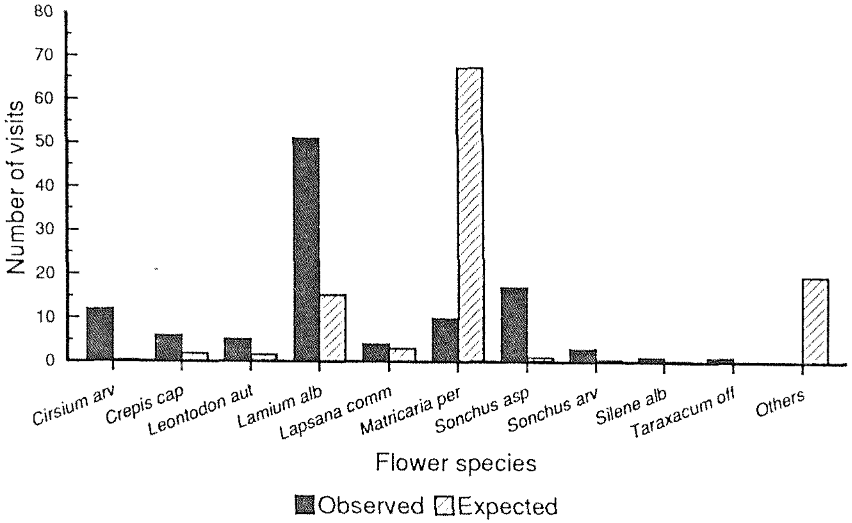
Fig. 7. A comparison of the observed and expected distribution of flower visits for M. corollae at Aero 4.



6 August 1988



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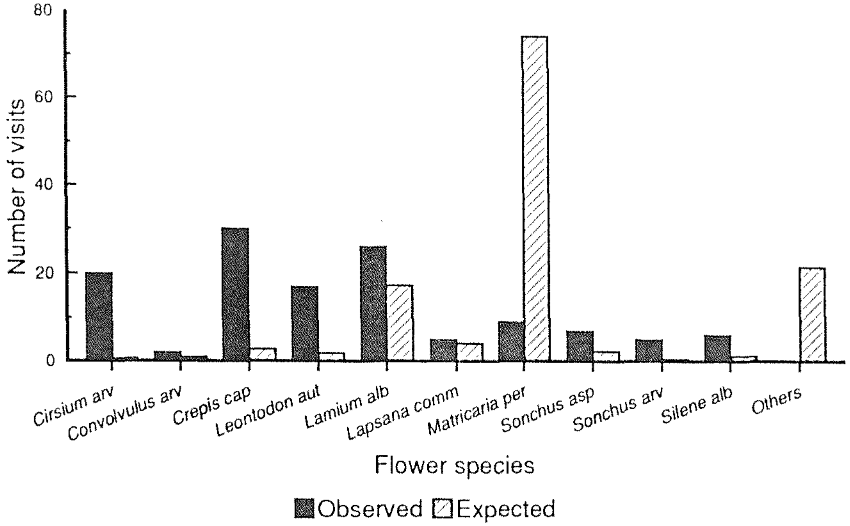
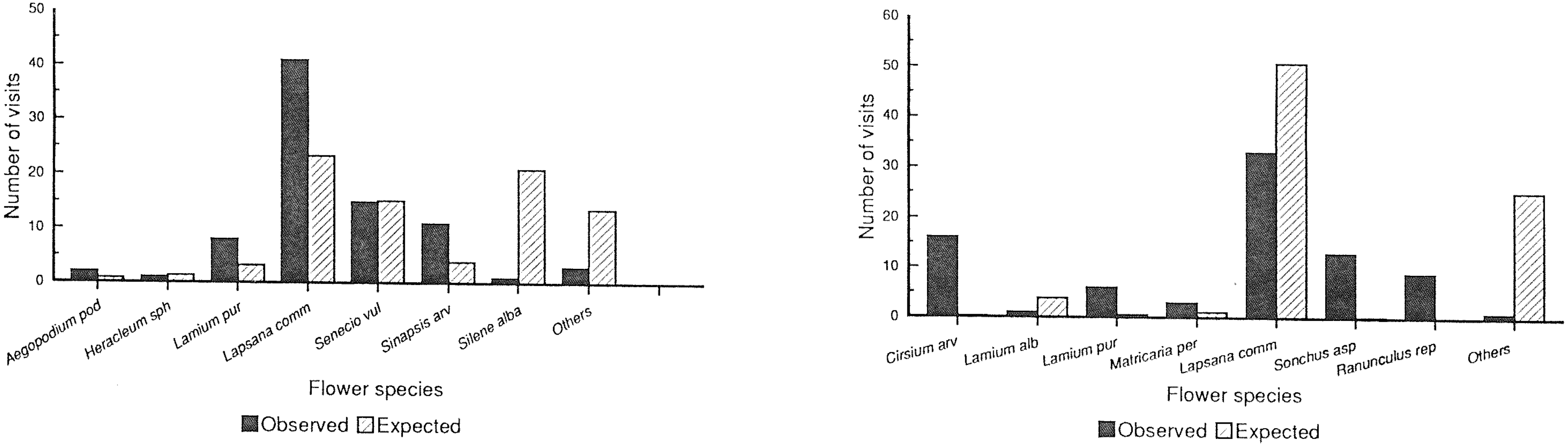


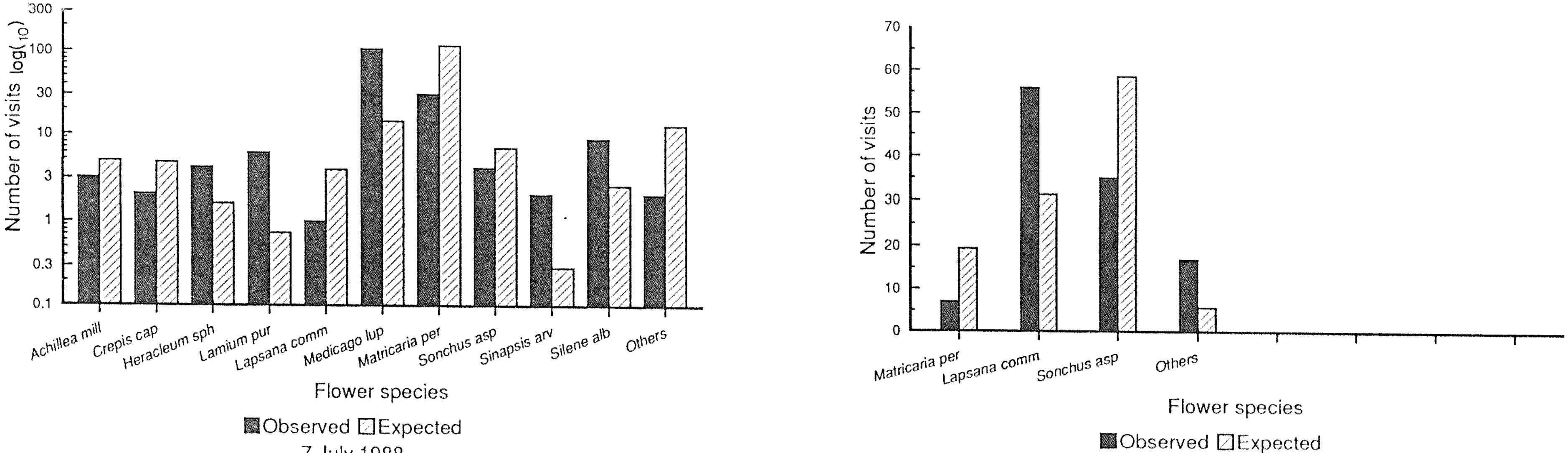
22 August 1988

Fig. 8. A comparison of the observed and expected distribution of flower visits for P. peltatus at Aero 4.



21 June 1988

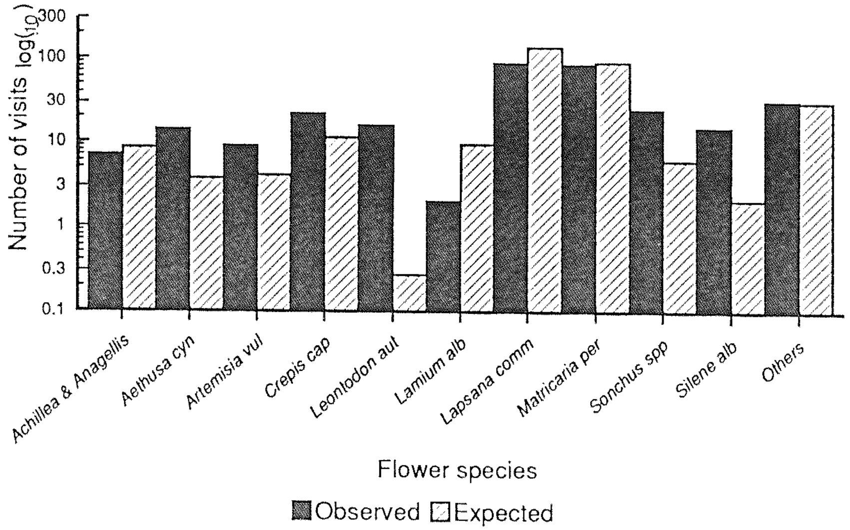
29 June 1988



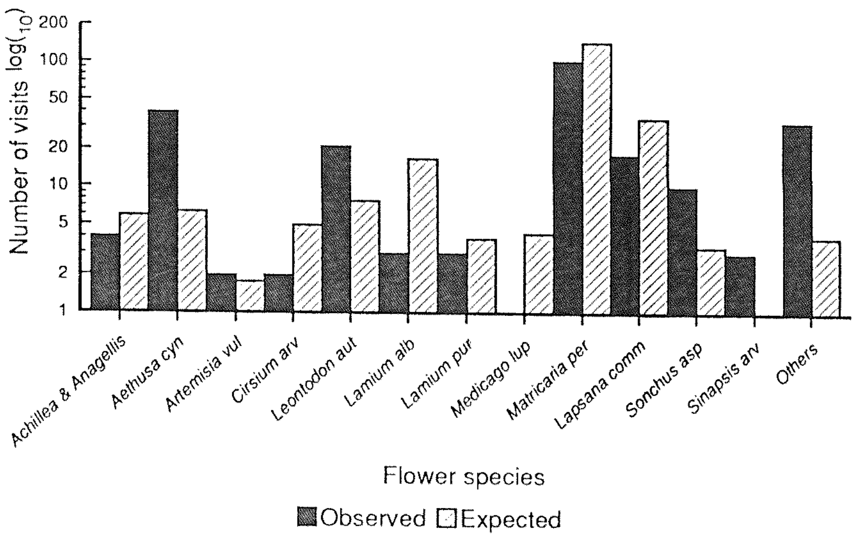
7 July 1988

13 July 1988

Fig. 9. A comparison of the observed and expected distribution of flower visits for E. balteatus at Aero 4.



20 July 1988



27 July 1988

13 August 1988

Fig. 9 (contd.). A comparison of the observed and expected distribution of flower visits for E. balteatus at Aero 4.

The data for *M. corollae* represented seven separate sampling dates between 21 June and 13 August; the two distributions were significantly different on four of the dates (D_{25}= 0.2489, $P_{0.05}$=0.26404; DI63= 0.1979, P< 0.05; D_{41}=0.1002, NS; D_{17}= 0.5437, P< 0.01; D_{26}=0.0814, NS; D_{40}= 0.5828, P<0.01; D_{18}=0.5322, P<0.01) with the values for the fifth date approaching significance at the 5% level. Fig.7 shows the observed and expected distribution of flower visits on the four dates.

P.peltatus was only recorded in sufficient numbers to allow statistical analysis of the data on three dates during August. Fig. 8 shows a comparison of the observed and expected distribution of flower visits on the three dates; the two distributions were significantly different on each date (D_{144}=0.5266, P<0.01; D_{110}=0.3751, P<0.01; D_{127}=0.514, P<0.05).

E.balteatus was observed foraging on a total of 27 flower species. This represented a broader range of flower species than the other syrphids recorded in the study; as a result a G-test was used to compare the observed and expected distributions of the flower visits. Fig. 9 shows a comparison of these values for individual flower species. On all the sampling dates between 21 June and 13 August 1988, at Aero 4, *E. balteatus* did not visit flower heads according to their abundance in the habitat (G_{adj}=70.291, P_9<0.01; G_{adj}=339.107, P_7<0.01; G_{adj}=381.529, P_9<0.01; G_{adj}=51.816, P_6<0.01; G_{adj}=120.489, P_{12}<0.01; G_{adj}=230.695, P_{13}<0.01; G_{adj}=4.847, P_5<0.05; G_{adj}=42.245, P_7<0.01; G_{adj}=3.144, NS).

Neither the Kolmogorov-Smirnov nor the G-test identified which flowers were visted more or less frequently than would be expected from their abundance in the habitat. Therefore, the data were further analysed using the Index C, (of for example, Murdoch (1969)) which compares the use and abundance of resources.

$$\text{Index C} = \frac{N_e/N_e'}{N/N'}$$

N_e, N_e'	the number of visits to species I and II.
N,N'	the abundance of species I and II.

The analysis of more than two species of flower was achieved by pooling additional species into the type II category. The index produces asymmetrical scales in which selective usage is indicated by values from one to infinity; when usage is not selective values between zero and one are obtained. Logarithms of the index were used to produce symmetrical scales.

The index was used to quantify the relative importance of individual weed species to *E. balteatus, M. corollae*, *E. tenax* and *P. peltatus*; the results are expressed graphically in Figs.10-13. The results for all species show that the selection index value, and therefore the ranking, of individual flower species differed according to the date. This might be expected as a result of changing resource patterns associated with the flowering phenologies of particular flower species.

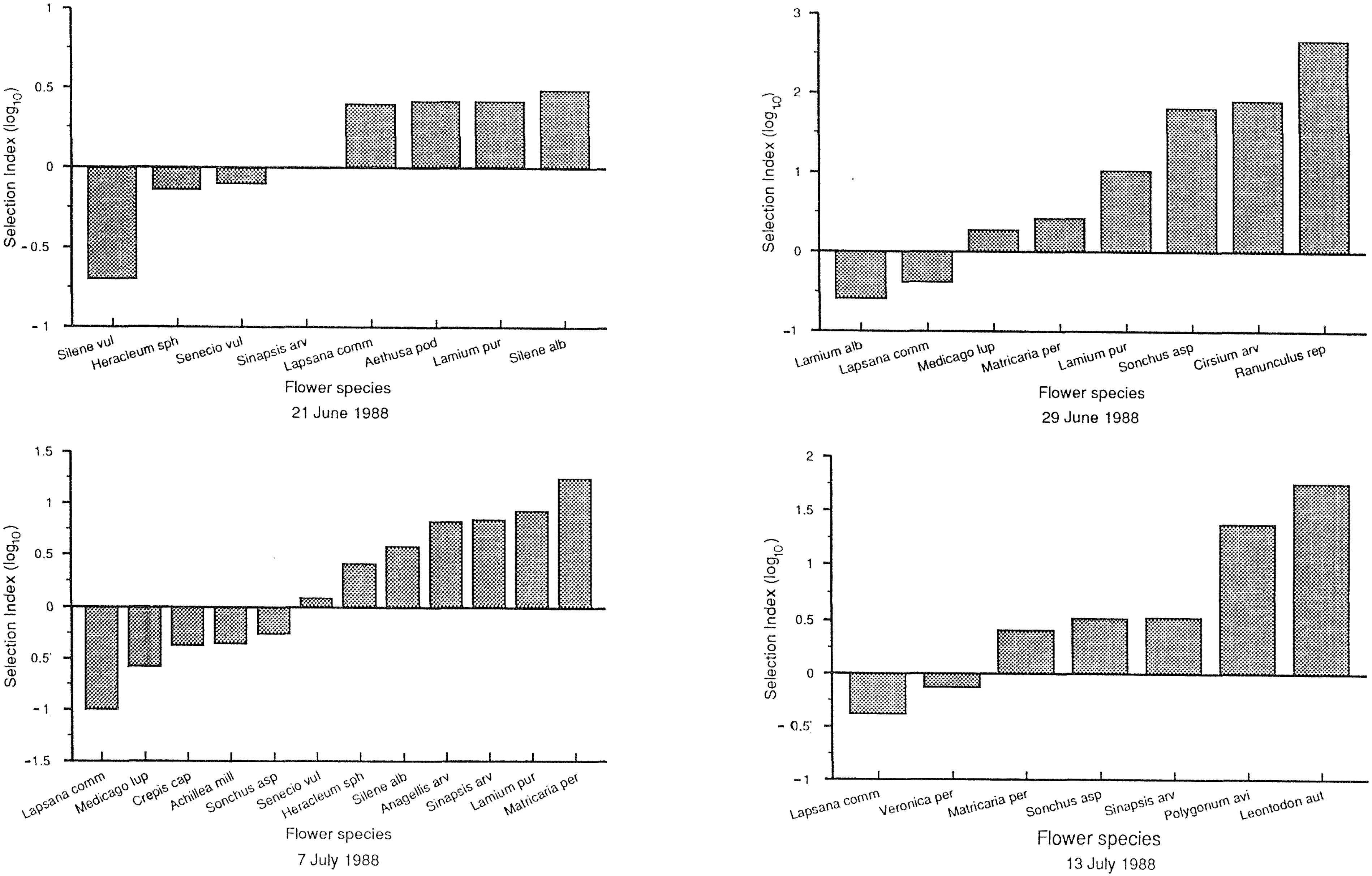
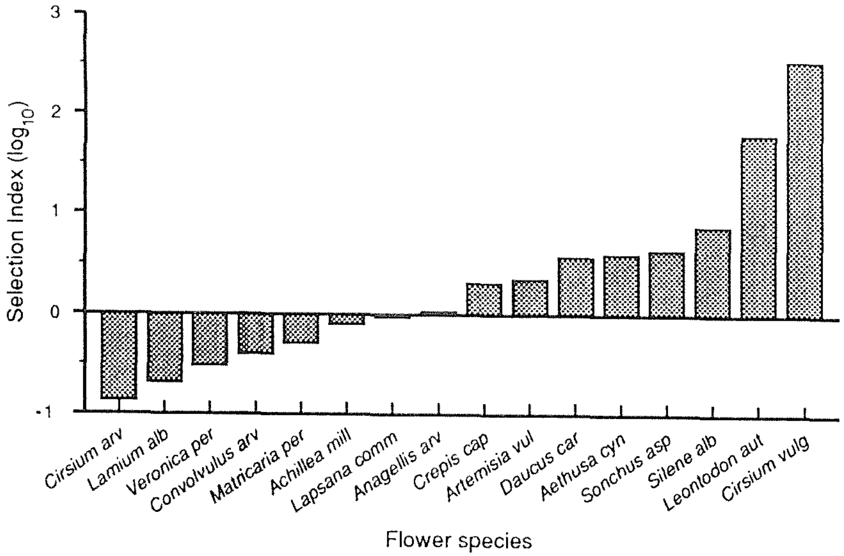
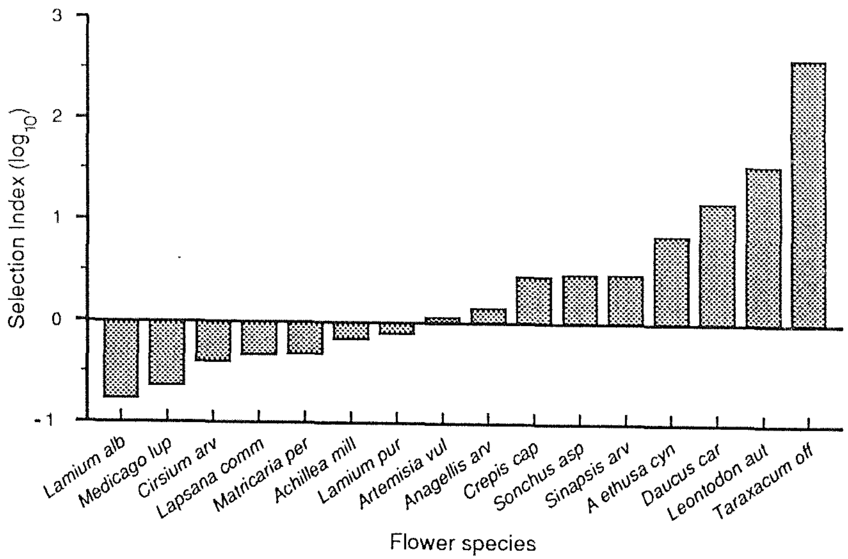


Fig.10. The calculated Selection Index values for E. balteatus.
Values greater than 0 indicated that the flowers were visited more often than would be expected from their relative abundance in the habitat.



20 July 1988



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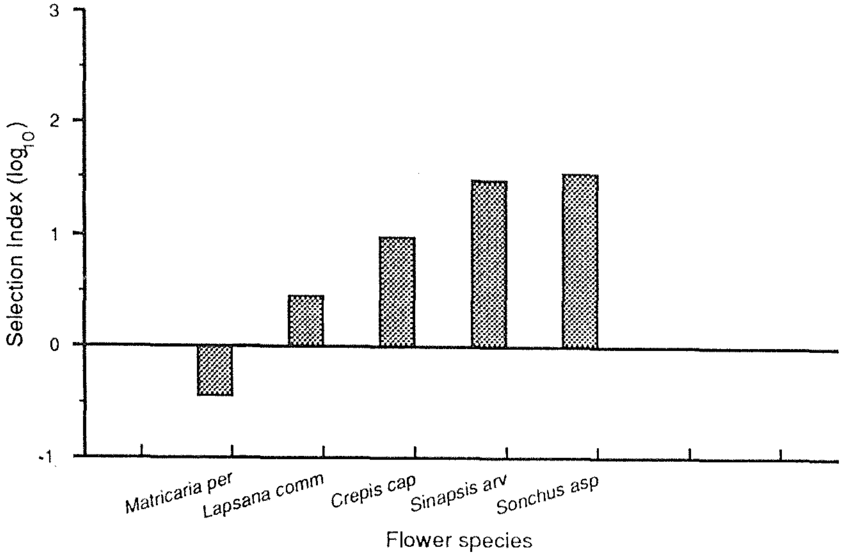

6 August

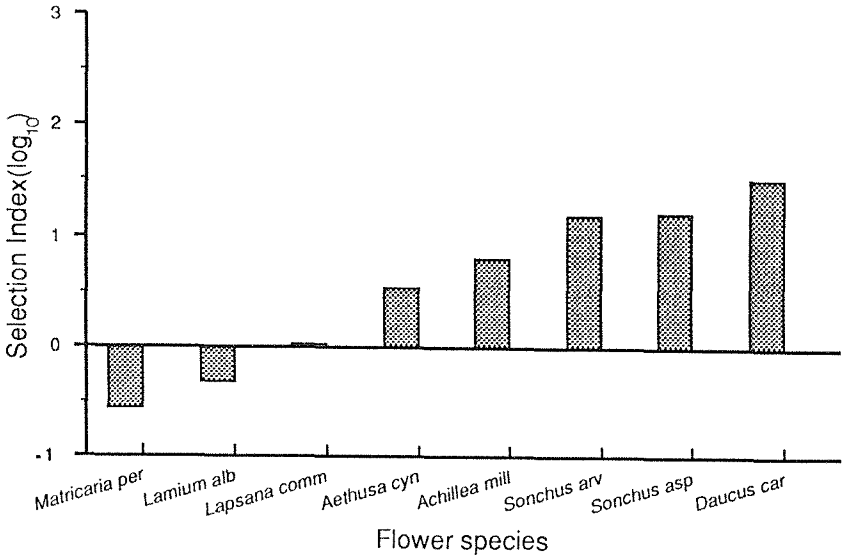

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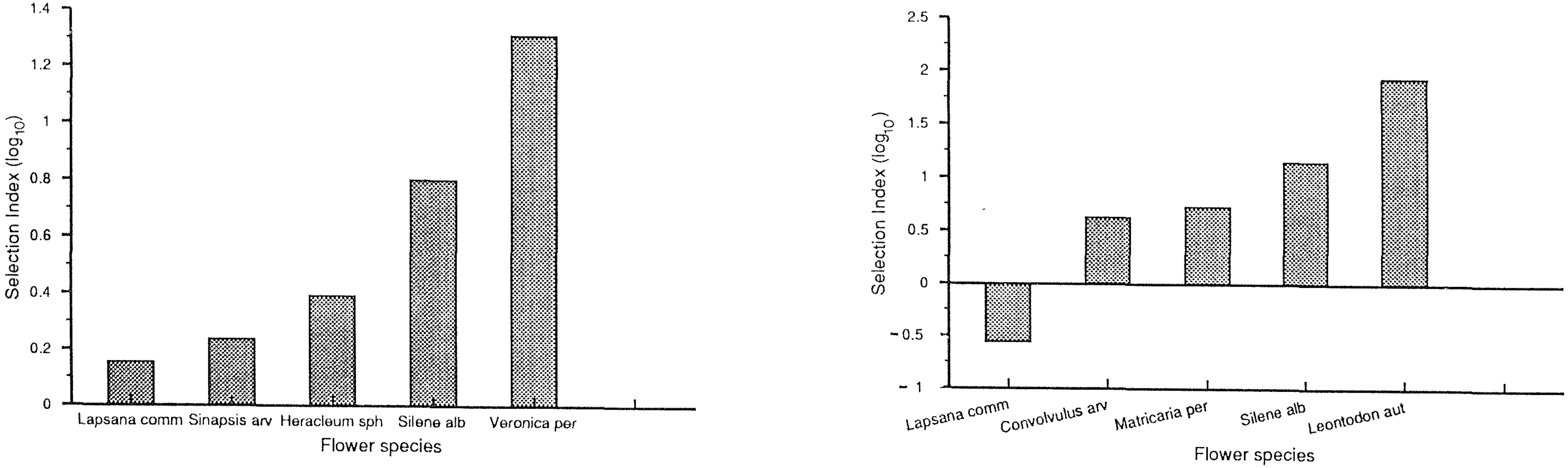
Fig. 10 (contd.). The calculated Selection Index values for E. balteatus



21 June 1988

7 July 1988

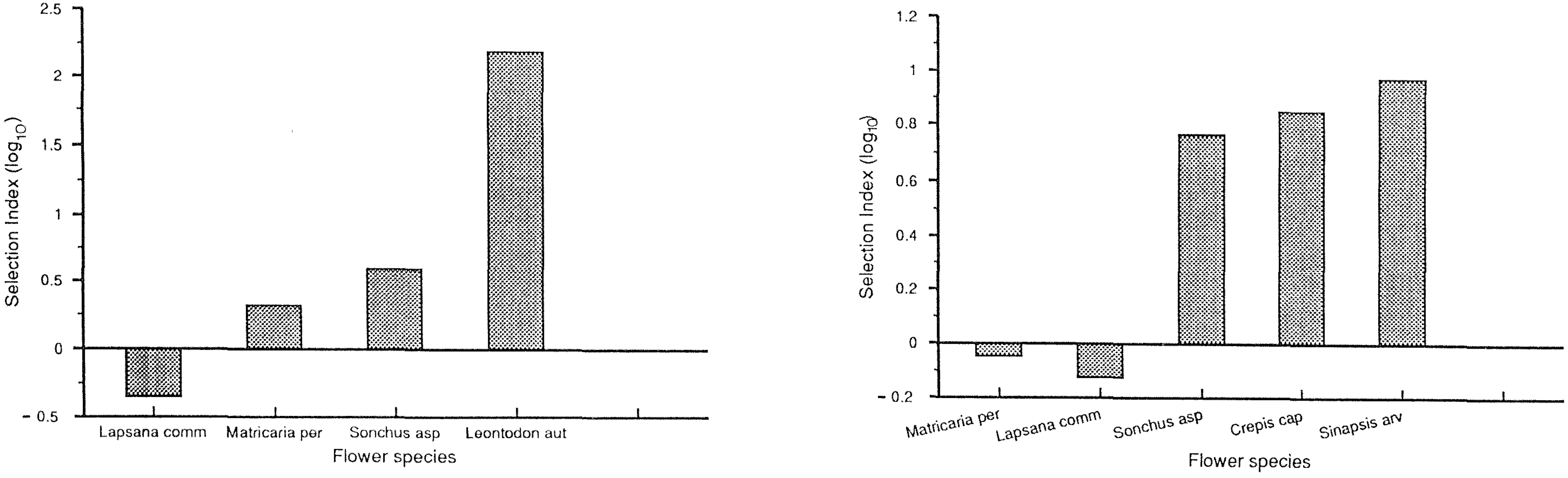


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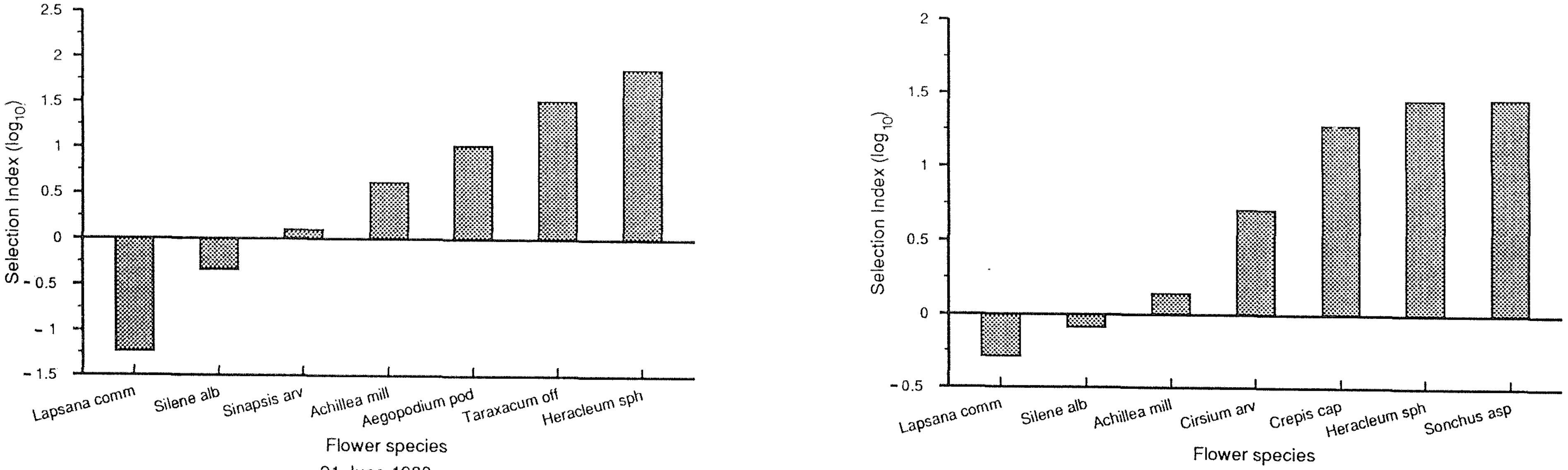
Fig. 11. The calculated Selection Index values for M. corollae.
Values greater than 0 indicate that the flowers were visited more often than would be expected from their relative abundance in the habitat.



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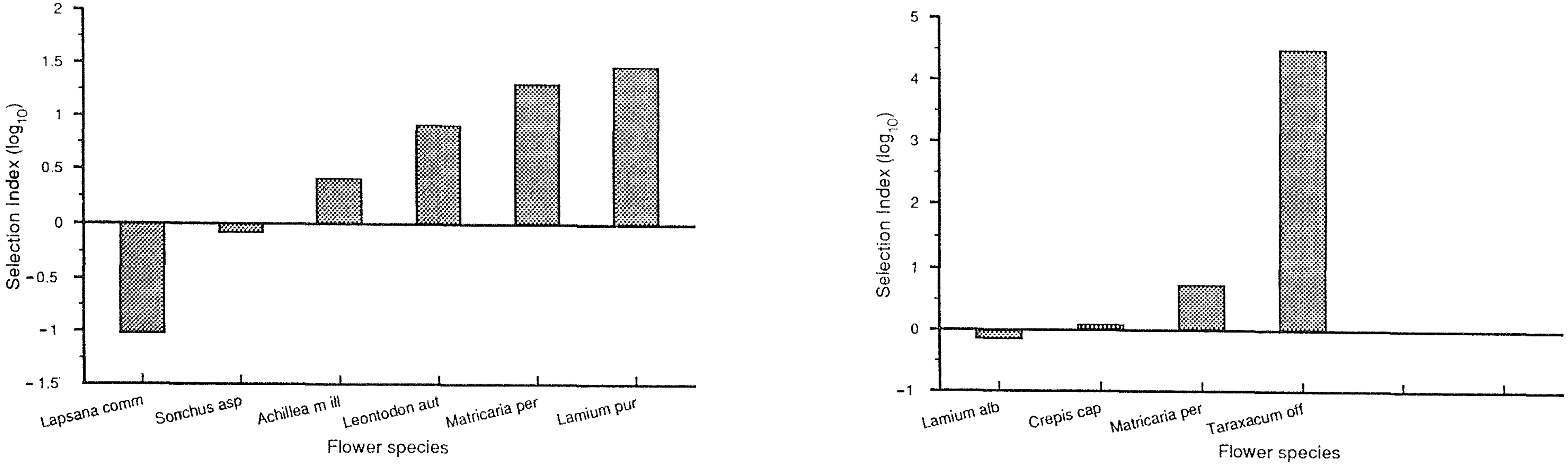
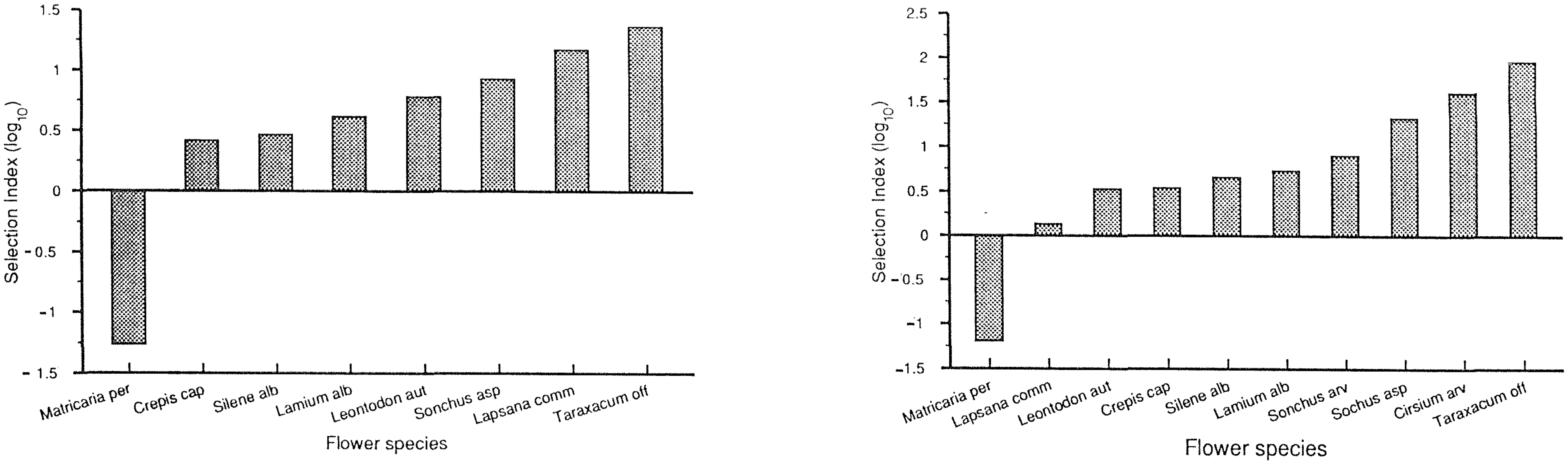
29 June 1988



7 July 1988

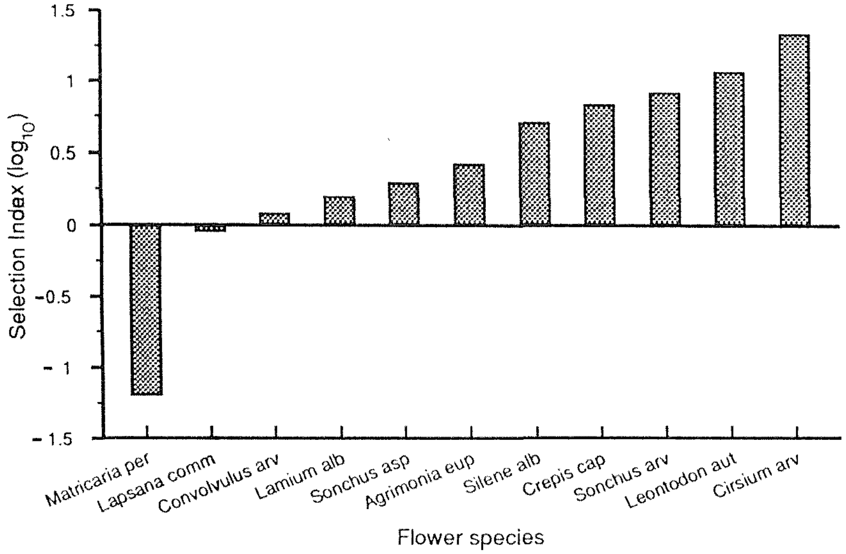
20 July 1988

Fig.12. The calculated Selection Index values for E. tenax.
Values greater than 0 indicate that flowers were visited more often than would be expected from their relative abundance in the habitat.



6 August 1988

13 August 1988



22 August 1988

Fig. 13. The calculated Selection Index values for P. peltatus.
Values greater than 0 indicate that flowers were vistited more often than would be expected from their relative abundance in the habitat.

The pattern of flower use by *E. balteatus* resulted in four flower species with calculated values($\log_{10}$) which were consistently greater than 0, that is, *Leontodon autmnalis, Aethusa cynapium, Daucus carota* and *Silene alba* were used selectively. Conversely, the calculated values($\log_{10}$) for *Lamium album* were invariably less than 0. Positive values were recorded, on three or more consecutive sampling dates, for several of the remaining species , for example, *Sonchus asper* and *Matricaria perforata.* However, from 20 June until 13 August a run of negative values was recorded for *M.perforata.*

P. peltatus was recorded visiting a total of 12 flower species during the study. The flowers were predominantly members of the family Compositae, however, it also visited *Lamium album* and was the only syrphid which used this flower selectively. *E. tenax* was observed foraging on a total of 16 flower species. *Lapsana communis* was consistently visited less often than would be expected from its abundance in the habitat. *A. millefolium* was invariably used selectively, as were *H. sphondylium* during June *M. perforata* during July. *M. corollae* was recorded visiting 11 flower species. Members of the genus *Sonchus* were used selectively during the study; the use of other members of the Compositae varied according to the date.

Discussion

Several authors have analysed resource use patterns in syrphids. Barendregt (1975), Gilbert (1980, 1981) and Ruppert and Molthan (1990) have used observational methods to quantify the flower visitation patterns of syrphids; all three authors concluded that syrphids use the available floral resources selectively. Haslett (1982,1989) used pollen analysis of the gut contents of syrphids to determine feeding preferences; some syrphid species were highly selective in their pollen diets while others foraged on a broader range of species. The study of the foraging behaviour of the syrphids associated with arable field margins presented in this chapter is consistent with these previous studies; syrphids did not visit flowers according to their abundance in the habitat.

Gilbert (1981, 1985) and Haslett (1981, 1989) have suggested different mechanisms to account for the observed patterns of resource utilisation by syrphids. Haslett concluded that the division of flower resources by the more selective syrphid species was at least partially dependant on the colours of the flowers. Gilbert related differences in the type of flower visited and the food taken to morphological differences among flies. Neither of the proposed mechanisms excludes the possibility that, in the case of individuals taking pollen, the pattern of flower visits may be related to the differing nutritional value of pollens (Baker and Baker 1979; Stanley and Liskens, 1974). This might account for the fact that in both studies there were pollen types which were completely ignored by the flies.

This study has made no attempt to determine the mechanisms underlying the observed patterns of foraging behaviour. Instead, the aim was to identify which of the commonly occurring arable weeds and hedgerow plants were selected by syrphids and to identify the degree of foraging specialisation of economically important syrphid species.

Table 2 (modified from Gilbert, 1981) summarises information from several authors and refers to the number of flower species visited by syrphids. The broad range of values for individual species

Table 2. The number of plant species visited according to various authors (modified from Gilbert, 1981).

Syrphid species	Authors				
	a	b	c	d	e
E. balteatus	10	11	9	122	27
Er. arbustorum	10	13	10	46	6
Er. tenax	6	9	11	67	15
Mel. mellinum	11	5	3	30	-
Mel. scalare	7	7	10	67	14
Met. corollae	11	15	0	67	14
Pl. albimanus	7	9	9	78	6
Pl. manicatus	11	10	6	13	7
Pl. peltatus	6	7	2	28	11
Sph. scripta	6	4	1	-	10
Syritta pipiens	6	7	5	55	12
Syrphus ribesii	13	15	6	90	-

Authors

a = Claussen (1980);
b = Nielson (1966, 1971, 1972);
c = Speight *et al.* (1975);
d = Gilbert (1981);
e = present study.

Generalistaions about the foraging behaviour of the syrphids (from Gilbert, 1981).

Generalists

Pollen feeders:	*E. balteatus*, *Syrphus ribesii*, *Scaeva pyrastri.*
Necatr feeders:	*Eristalis tenax*, *Eristalis pertinax.*
Mixed feeders:	*Metasyrphus corollae, Syritta pipiens, Platycheirus albimanus, Platycheirus peltatus, Platycheirus manicatus, Eristalis arbustorum.*

Moderate specialists

Pollen feeders	*Melanostoma scalare*
Nectar feeders	*Myiatropa florea*
Mixed feeders	*Sphaerophoria scripta*

Specialists

Pollen feeders	*Melanostoma mellinum, Pipizella aust*
Nectar feeders	*Rhingia campestris*
Mixed feeders	*Cheilosia pagna*
Leaf feeders	*Xylota* spp.

presumably reflects differing sample sizes. Ranta *et al.* (1981) suggested that the number of flower species visited can be used as an index of niche breadth. However, Gilbert (1981) pointed out that as this niche metric is a function of the number of observations it is probably a poor indicator of the "real" niche breadth. Nevertheless, in the present study the number of flower species visited by the syrphids has been used to categorise *E.balteatus, E.tenax, P.peltatus, S. pipiens* and *M.corollae* as generalists. This agrees with Gilbert's work in which all these species were classified as generalists on the basis of the number of visited plants, together with estimates of niche breadth.

Fox and Marrow (1981) suggested that geographical scale is important in identifying the degree of specialisation; some species are generalists, but their constituent populations may be specialists on a local scale. However, the observations in Table 2 cover a range of geographical locations and habitat types and the general trends still remain consistent between the studies.

Rotenberry (1990) studied the degree of temporal resource heterogeneity in a system consisting of a community of insects and the plants they visit for pollen and nectar. He recorded that although insects foraging on the plants throughout the floral season could expect constancy in the relative timing of blooming, they were exposed to considerable temporal heterogeneity in flower resource abundance, both between and within years. He concluded that this heterogeneity would select either for an extreme specialist or a broad generalist. It seems probable that populations of insects which are associated with arable systems will experience both temporal and spatial heterogeneity in flower resource abundance on a range of scales. This might be expected to affect the behaviour and the composition of the insect community. This is reflected in the observation that the majority of species (with the possible exceptions of *M. scalare* and *R. campestris*) recorded in this study, are generalists.

Although the two economically important species, *M. corollae* and *E. balteatus*, were observed feeding on a range of flower species, within this range species were used selectively. This has implications for the production of guidelines for the management of field margins; guidelines which encourage the growth of these weed species will favourably modify the agroecosytem for syrphids. The flower species which were used selectively included *Cirsium* species, members of the genus *Sonchus*, *Matricaria perforata, Silene alba, Leontodon autumnalis* and *Aethusa cynapium*. The establishment of florally diverse field margins which contain these species is preferable to the establishment of single species stands. The encouragement of early flowering species may be particularly important, having the potential to influence the timing of oviposition. In practice, the management of field margins will involve some degree of compromise; the strategies must be economically and agronomically acceptable to farmers. For example, several of the plant species identified as important by this study are pernicious weeds and their encouragement would be agronomically unacceptable.

The development of guidelines which are aimed at enhancing the numbers of syrphids on farmland will benefit from additional information, on the selection processes which occur on a different scale from those discussed in this chapter. Levin (1978) has suggested that foragers are faced with decisions at several hierarchical levels, defined by levels of perception of the environment: where to search (habitat, patch), which species to feed from (flower) and which plants to feed from and in what sequence. Habitat selection by syrphids is probably influenced by hygrothermal stress (Gilbert, 1981).

The influence of micro environmental factors on syrphid activity and distribution patterns is discussed in Chapter six.

Thomson (1981) has studied the response of flower visitors to patches of varying flower density. The block sizes at which insects assessed flower density differences were estimated to be approximately 1000m^2 for solitary bees and flies visiting *Potentilla* species. In addition, there was a time lag of 1.5 days in the assessment of flower density. In an applied context it will be important to understand the perception and utilisation of patches of non-crop habitat by syrphids; in addition to the extent of between patch movement. Both *M.corollae* and *E. balteatus* are known to be highly mobile; *E.balteatus* is known to undertake long migrations (Johnson, 1961) and Lyon (1965) has claimed that *E. balteatus* can fly up to 10 km per day. However, little is know about the non migratory movements of these species; this problem is addressed in Chapter seven.

In recent years field margins, (terminology from Greaves and Marshall, 1987) have presented increasingly difficult weed control problems for farmers (Smith and McDonald, 1990). The accidental application of fertiliser, and herbicide spraying have resulted in species-poor communities which are dominated by a few species of pernicious weed. A potential solution to this problem might be the establishment of "diverse, grassy, perennial swards" (Smith and Macdonald, 1990; Nowakowski and Marshall, 1990). The timing and frequency of mowing of these swards could be used to control the perennial weed species, while the annual weeds would be unable to compete in the perennial sward. Although the conservation value of these swards, in terms of plant species, may be limited their permanent establishment has the potential to be of benefit to insects which forage on pollen and nectar.

An alternative approach to the management of field margins, which has already been shown to have benefits for wildlife, involves the selective use of herbicides in the headlands of cereal fields (Sotherton *et al.* 1989). The modified herbicide regime in these "conservation headlands" encourages the growth of annual, arable weeds. Both of these techniques have potential for influencing the distribution of syrphids on farmland. The conservation headland technique is already widely employed; there were a total of 474 miles and an area of 1171 acres of conservation headland in the UK in 1989 (Thomson, 1990). The affect of the presence of plots of conservation headland on the distribution of adult syrphids, and on oviposition are discussed in Chapter three.

In the long term, a greater understanding of the use of arable weeds by beneficial insects may influence the pest status and calculations of economic thresholds for individual weed species.

CHAPTER THREE

THE EFFECT OF NON-CROP PLANTS WITHIN THE CROP ON THE NUMBERS OF SYRPHID ADULTS AND THE DISTRIBUTION AND SPECIES COMPOSITION OF SYRPHID EGGS.

Introduction

Several authors have studied the relationship between the species composition of naturally occurring field margins and the density and diversity of syrphid species. Molthan and Ruppert (1989) studied the species composition of syrphids in three naturally occurring field margins; the number of species and abundance of flies in narrow margins consisting of grasses was significantly less than in wider (1.5-2m) margins consisting of a range of dicotyledonous plants. The greatest diversity and largest number of individuals were recorded from an 8m wide margin with an adjacent embankment and a high diversity of flowering plants.

Kühner (1988) recorded the relative abundance of syrphids and parasitoids in herbicide-free and herbicide-treated crop edges in three locations in Hesse, Germany. At two of the locations the crop edges comprised a range of flowering plants; syrphids were more abundant at these locations than in the third area where the unsprayed crop edge was characterised by different species of grasses and few flowering plants. Most of the beneficial species in the latter area belonged to the parasitic Hymenoptera.

Comparisons of the numbers of syrphid adults in herbicide-treated and herbicide-free plots of field margin showed higher numbers of adults in the herbicide treated areas (Ruppert and Molthan, 1991). The authors suggested that the higher numbers were a result of the higher aphid densities in the herbicide treated margins. Mature syrphid females were presumably retained in the area as a result of an aggregative numerical response. Felkl (1988) recorded that syrphid larvae were more numerous in the margins of cereal crops treated with herbicide where aphid infestations were higher than in nearby herbicide-free margins. Similarly, Horn (1981) recorded the number of syrphid eggs and larvae in weedy and weed-free plots of collards. Initially there were higher numbers of syrphid larvae in the weedy plots. Later in the season higher numbers were recorded from the weed-free plots; presumably as a result of the higher aphid densities in these plots.

Smith (1976) studied the distribution of syrphid eggs between weedy and weed-free plots of Brussels sprouts. *E. balteatus* females oviposited on sprout plants in the weedy plots early in the season when aphid density was low. Later in the season when aphids were more abundant aphid density was the most important factor determining the distribution of the eggs. Oviposition by *Melanostoma* species was greatest in the weedy plots; greater numbers of eggs were laid on the weeds than on the Brussels sprout plants themselves. *Platycheirus* species tended to lay more eggs on sprouts in bare soil than in the weedy plots. However, on some occasions oviposition on weeds resulted in the total number of eggs per unit area being similar in weedy and weed-free plots.

In species such as *E. balteatus* and *M. corollae* plant-related factors are relatively unimportant in providing the stimulus to oviposit; females respond primarily to aphid colonies (Chandler 1968a,b). However, in the majority of *Platycheirus* species and *Melanostoma* species aphid related factors are relatively less important in stimulating oviposition; more eggs are laid away from aphid colonies than close to them. Under similar conditions the site of oviposition by *M. luniger* and *P. manicatus* females in relation to *Brevicoryne brassicae* colonies on Brussels sprouts plants varied markedly. *M. luniger* laid more than 50% of its eggs in close proximity to aphids; fewer than 1% of the eggs occurred on uninfested plants. In contrast, *P. manicatus* females laid fewer than 5% of their eggs in close proximity to aphids and over 50% on uninfested plants (Chandler 1968c).

Chandler (1968 a,b) studied the host-plant and aphid related factors which stimulate oviposition in several syrphid species. Plant species and plant appearance were both important factors in effecting oviposition by *P. peltatus*. Females laid freely on uninfested Brussels sprouts plants but no eggs were recorded from uninfested field bean (*Vicia faba*) plants. When supplied with different forms of the same variety of Brussels sprout *P. peltatus* laid significantly higher numbers of eggs on "waxy" plants than on the "glossy " form. Other members of the genus also showed this response. However, when the two forms were infested with aphids, *Platycheirus* females showed a less distinct response.

Melanostoma species were relatively unaffected by the presence or absence of aphids and oviposited in consistently higher numbers on the waxy form. The nature of the substrate at the oviposition site affected the size of the egg batches laid there by *M. scalare, M. mellinum, P. peltatus* and *P.clypeatus*. Females of all these species laid larger batches of eggs on waxy sprout plants than on bean and turnip plants or blocks of polystyrene; Chandler (1968a) concluded that the stimuli governing batch size were mediated by sensilla on the ovipositor.

The observation that phytozetic species, such as the two *Melanostoma* species and most *Platycheirus* species, oviposit primarily in response to plant related factors, often at low aphid densities or in the absence of aphids, has implications for enhancing the biological control potential of syrphids. That is, by providing appropriate non-crop plants (oviposition sites) it may be possible to affect the number of eggs in the crop either as a result of an increase in the number of eggs laid by individual females (batch size) or an increase in the range of syrphid species which oviposit in the crop. Although a range of syrphid adults occur on arable land the majority of larvae recorded from winter wheat belong to the genera *Episyrphus* and *Metasyrphus* (Dean, 1982). *Platycheirus* larvae have also been recorded from cereals in areas containing low growing weeds (Dean, 1982); the presence of non-crop plants at the base of winter wheat crops may stimulate oviposition within the crop by these flies.

Phytozetic syrphid species tend to lay eggs in batches; the first larva to hatch cannibalises the others and then searches for aphids; syrphid larvae are capable of moving actively from plant to plant (Sol, 1966). Dean (1982) recorded *Platycheirus* larvae, particularly *P. manicatus*, attacking aphids on lower canopy weeds in cereals. If no aphids are present on adjacent non crop-plants the larvae may move onto the crop where they will supplement the action of larvae, which emerged from eggs which had been laid in close proximity to aphid colonies by aphidozetic females. The larvae of *M.mellinum* and *Platycheirus clypeatus* can consume a total of 135 and 150 aphids respectively during the larval stage (Bankowska *et al.*,1978). In the absence of aphids the larvae of phytozetic species have been recorded predating invertebrates in leaf litter and it has been suggested that some species can complete their development by ingesting leaf litter (Gilbert, 1986). *Melanostoma* species have been recorded feeding on decomposing chickweed (Hamrun, 1966); larvae of *M. scalare* have been reared to adults in bags of *Acer pseudoplatanus* leaf litter (Rotheray, 1989).

Several studies have examined the effect of the presence of weeds within crops on populations of pest species. For example, Dempster (1969) showed that the survival of *Pieris rapae* larvae was significantly higher in hoed, weed-free plots of Brussels sprouts than in unweeded plots; the latter contained higher numbers of the carabid *Harpalus rufipes*. Smith (1976) concluded that decreased natural enemy action was at least partly responsible for the initially greater abundance of *B. brassicae* in a weed-free crop of Brussels sprouts than in a weedy crop. The presence of broad-leaved weeds in cereals has been shown to influence the distribution and abundance of the carabid *Agonum dorsale*; positive correlations existed between beetle density and weed cover (Powell, Dean and Dewar 1985; Coombes and Sotherton 1986). Powell, Dean and Dewar (1985) also noted significant reductions in the numbers of *Tachyporus* species and some other polyphagous predators in herbicide treated crops. The relationship between predator density and weed density is not restricted to broad-leaved weed species. Speight and Lawton (1976) showed that the numbers of carabids and staphylinids in a cereal field were related to the density of *Poa annua* (the only abundant weed in the experimental plots). In turn the predation rate by the animals on *Drosophila* pupae was directly related to predator density. Vickerman (1974) showed that cereal aphids were significantly more abundant in areas where *Poa trivialis* had been removed by the application of herbicide than in unsprayed plots. He suggested that this could be due to a reduction in predation pressure in the sprayed plots. The spraying had resulted in the reduction in numbers of 16 of 49 insect taxa; the greatest reductions occurred in populations of predatory staphylinids.

With the exception of Smith (1969, 1976), Horn (1981) and Felkl (1988) who studied syrphid oviposition in Brussels sprouts, collard and cereal crops respectively there have been no studies which have been specifically designed to examine the effect of the presence of non-crop plants within crops on syrphid oviposition. Smith (1969; 1976; see above) was the only researcher to examine the oviposition response of individual syrphid genera to the presence of weeds.

The aim of the present study was to quantify the number of syrphid adults in weedy and weed-free plots of winter wheat and to examine the effect of the presence of weeds on the composition and distribution of syrphid eggs within and among the plots.

Materials and Methods

Field Sites.

The field study was carried out on a 8km^2 mixed arable/ livestock farm (South Allenford), at Damerham on the Hampshire-Dorset border. During 1989 the south facing headland of Side Scammel (see Fig.1(a), 1(b)) and the adjacent north facing headland of Mesh Bottom were used as study sites. The two fields were separated by a "green lane" which comprised a farm track. The margin of Mesh Bottom and the green lane consisted of a hawthorn hedge with umbellifers in its base. The margin of Side Scammel adjacent to the green lane consisted of a shelterbelt containing woody and herbaceous species. The composition of the shelterbelt was relatively homogeneous along its length and overall beech, *Fagus sylvatica*, sycamore, *Acer pseudoplatanus*, yew *Taxus* species and bramble *Rubus fruticosus* were the dominant species. During 1990 the south facing headland of Side Scammel was used as the study site (Fig. 1c).

Experimental design 1989

The headland in Side Scammel was divided into three replicates (plots) of two treatments which were arranged alternately along the length of the headland. Each replicate was 100 x 12m. The two treatments comprised (1) a fully sprayed regime, in which pesticide application occurred in accordance with normal farm practice, and (2) a conservation headland treatment, in which a modified pesticide regime was employed. The modified pesticide regime was based on guidelines, published by the Game Conservancy Trust (Sotherton *et al.,* 1989) which permit the growth of certain broadleaved weed species. The guidelines are summarised in Fig. 2.

The same experimental design was adopted in Mesh Bottom, however, because the headland was shorter at this site each replicate measured 75 x 12m.

From early May until late July weekly counts of the densities of weeds, aphids and syrphid eggs were recorded from 15 quadrats per replicate. Five quadrats were randomly scattered along three transects through each replicate. The transects were 1, 6 and 12 metres from the field edge; these positions were subsequently referred to as hedgerow edge, mid headland and tramline. In each quadrat the number of wheat stems was recorded. The ear and upper leaves of each stem were examined for aphids and syrphid eggs. Aphids were recorded to species and instar. The rooted weed density was also recorded. The weeds were examined for aphids and syrphid eggs. On most occasions the sampling extended over two adjacent dates.

Experimental design 1990.

The 1990 study was a modified version of that undertaken during 1989. The study was undertaken in the south-facing headland of Side Scammel and the adjacent green lane, from early May to late June 1990. As in 1989 the experimental design comprised replicates of the two treatments

Fig. 1a The Study Farm

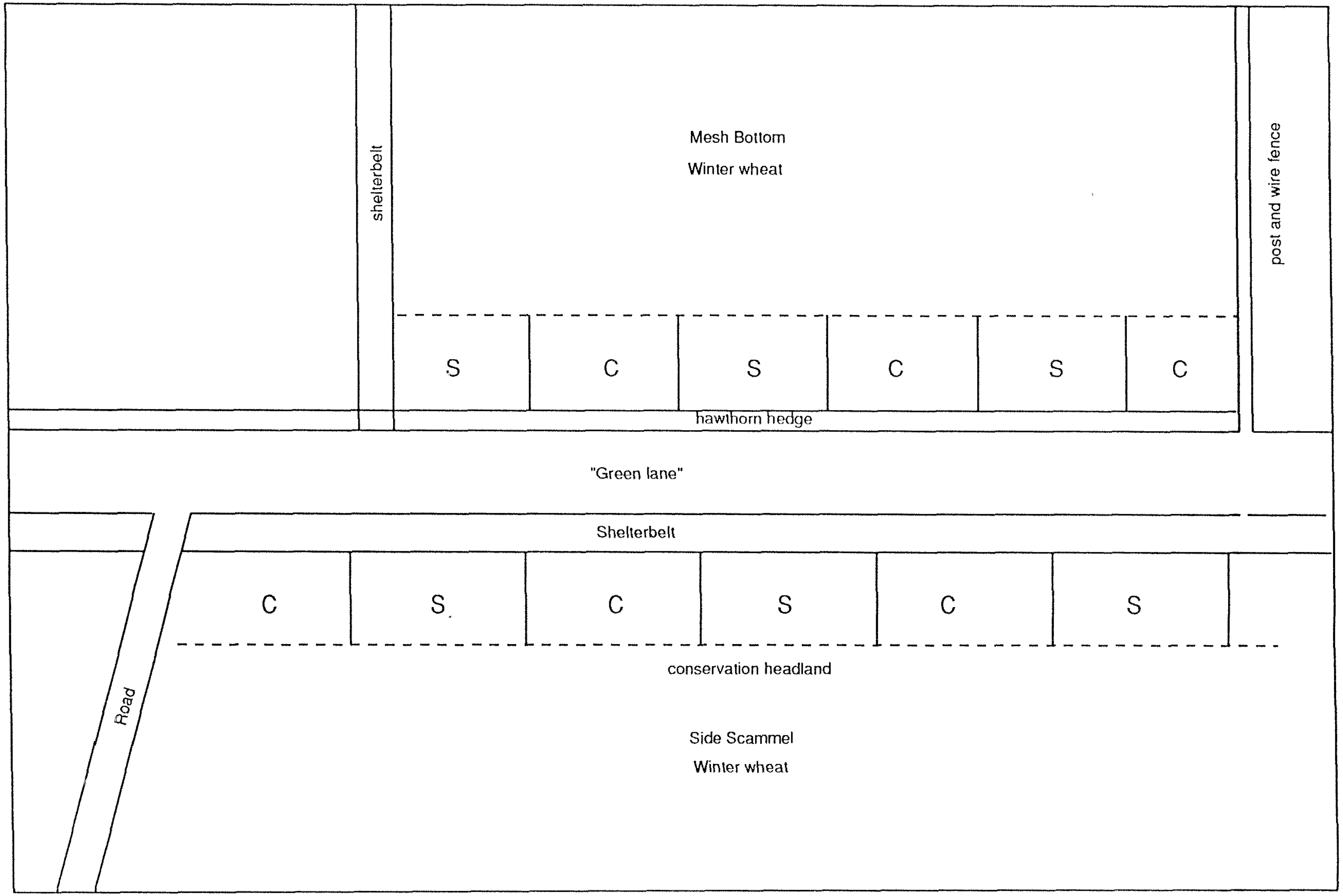


Fig. 1(b). The study site for the "conservation headland experiment" 1989. (not to scale).
Each plot at Side Scammel = 100 x 12m. Each plot at Mesh Bottom = 75 x 100m C = conservation headland plot; S = fully sprayed plot.

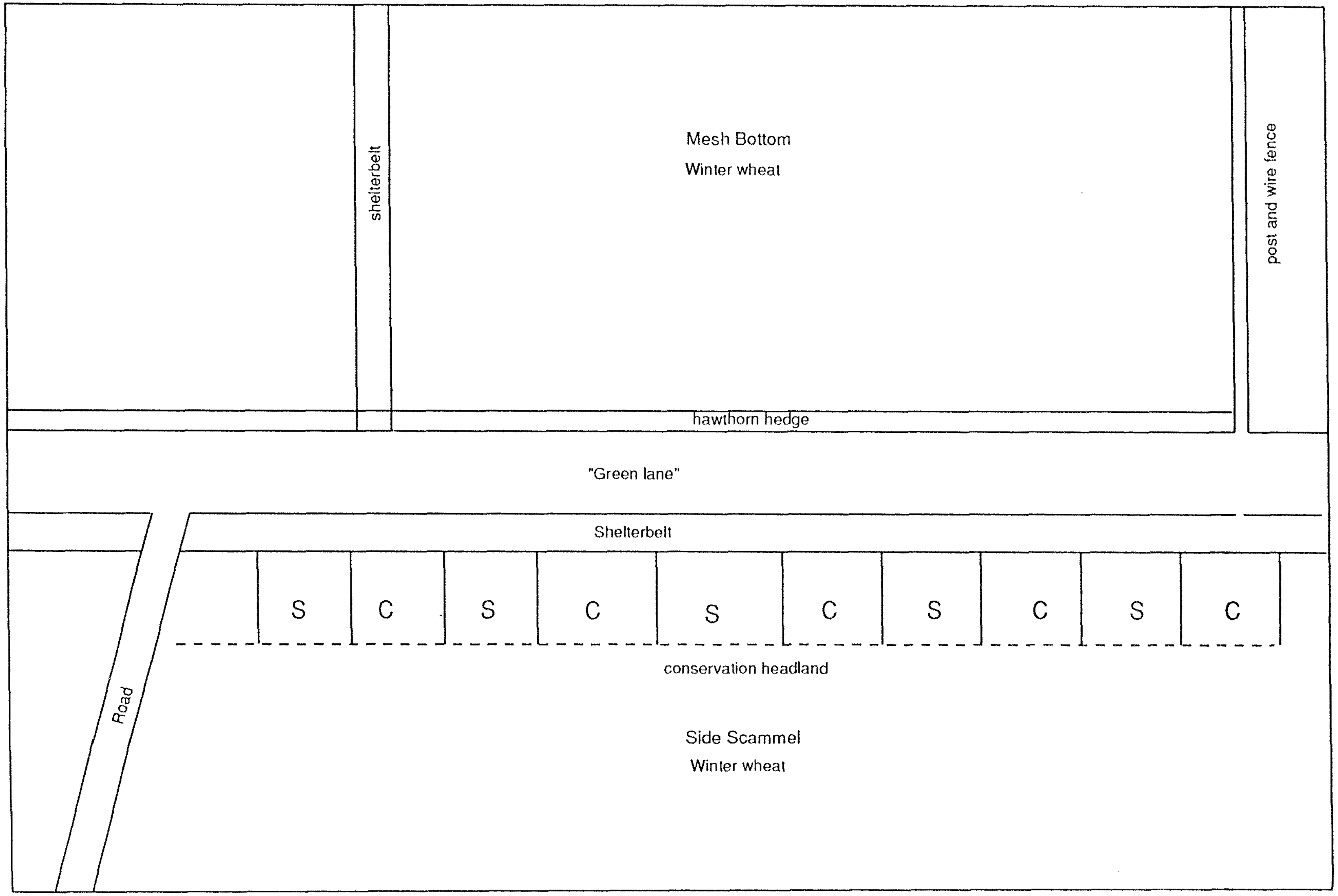
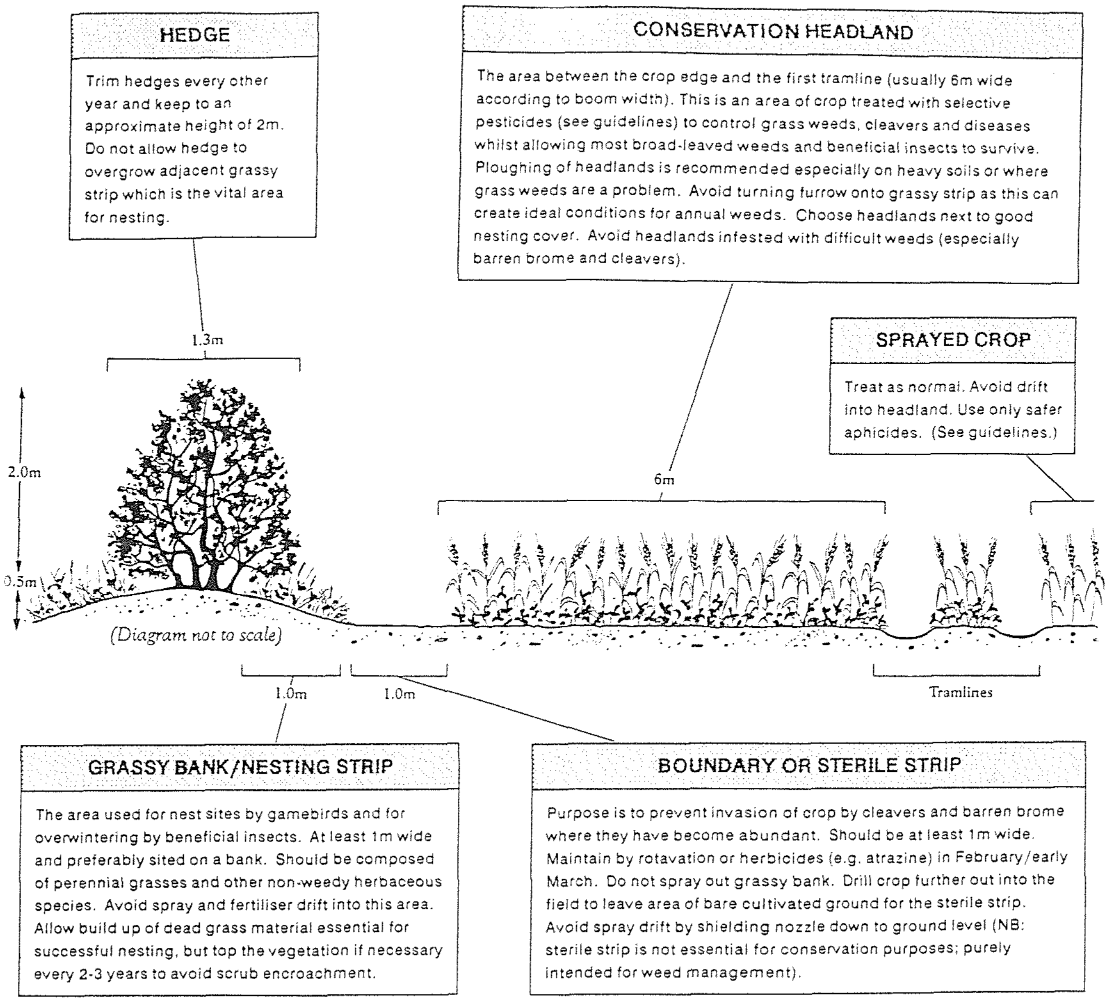


Fig.1c The study site for the "conservation headland experiment" 1990. (not to scale)
Each replicate (plot) = 75 x 12 m. C = conservation headland; S = fully sprayed treatment.



HEDGE

Trim hedges every other year and keep to an approximate height of 2m. Do not allow hedge to overgrow adjacent grassy strip which is the vital area for nesting.

CONSERVATION HEADLAND

The area between the crop edge and the first tramline (usually 6m wide according to boom width). This is an area of crop treated with selective pesticides (see guidelines) to control grass weeds, cleavers and diseases whilst allowing most broad-leaved weeds and beneficial insects to survive. Ploughing of headlands is recommended especially on heavy soils or where grass weeds are a problem. Avoid turning furrow onto grassy strip as this can create ideal conditions for annual weeds. Choose headlands next to good nesting cover. Avoid headlands infested with difficult weeds (especially barren brome and cleavers).

SPRAYED CROP

Treat as normal. Avoid drift into headland. Use only safer aphicides. (See guidelines.)

GRASSY BANK/NESTING STRIP

The area used for nest sites by gamebirds and for overwintering by beneficial insects. At least 1m wide and preferably sited on a bank. Should be composed of perennial grasses and other non-weedy herbaceous species. Avoid spray and fertiliser drift into this area. Allow build up of dead grass material essential for successful nesting, but top the vegetation if necessary every 2-3 years to avoid scrub encroachment.

BOUNDARY OR STERILE STRIP

Purpose is to prevent invasion of crop by cleavers and barren brome where they have become abundant. Should be at least 1m wide. Maintain by rotavation or herbicides (e.g. atrazine) in February/early March. Do not spray out grassy bank. Drill crop further out into the field to leave area of bare cultivated ground for the sterile strip. Avoid spray drift by shielding nozzle down to ground level (NB: sterile strip is not essential for conservation purposes; purely intended for weed management).

Fig. 2a. Summary of recommendations for pesticide use in "conservation headlands".

	Autumn-sown cereals	Spring-sown cereals
Insecticides	Only until 15th March	No
Fungicides	Yes (not pyrazophos after 15th March)	Yes (not pyrazophos)
Herbicides (grass weeds only)	AvadexBW, AvadexBW granular Avenge2, CheetahR*, Hoegrass, Commando, Muster, Roundup	AvadexBW, AvadexBW granular Avenge2, CheetahR*, Hoegrass Commando, Muster, Roundup
Herbicides (broadleaved weeds)	No	No
Growth Regulators	Yes	Yes

* wheat only

(conservation and fully sprayed headland) arranged alternately along the length of the headland (see Fig. 1c). There were five replicates of each of the two treatments; each replicate was 12 metres wide x 75 metres long.

During the period 13 May to 14 June 1990, weekly counts of the densities of weeds, aphids and syrphid eggs were recorded from 21 quadrats per replicate. Seven quadrats were randomly scattered along three transects through each replicate. The transects were 1, 6 and 12 metres from the field edge; as in 1989 these positions were referred to as the hedgerow edge, mid headland and tramline. In each quadrat, 20 randomly selected stems were examined for aphids and hoverfly eggs. The aphids were recorded according to species and instar. The position on the plant of any syrphid eggs was recorded. The eggs were removed, preserved in 70% alcohol and retained for subsequent identification. The rooted weed density and the number of flower heads of each of the weed species present in the quadrat were also recorded. The weeds were examined for aphids and syrphid eggs. On most occasions the sampling extended over two adjacent dates.

Measurements of the dimensions of commonly occurring flowers were taken during the study. The surface area of the flowers was calculated from these measurements by approximation to an appropriate geometrical shape. The product of the number of open flowers of each species and the mean surface area for that species was used to calculate a value for the total floral area per quadrat. It was not possible to obtain quantitative estimates of the pollen and nectar productivity of individual plant species.

The distribution of adult syrphids

1989

A standard census walk was used to provide a quantitative estimate of the number of syrphid adults in each of the replicates of the two treatments. Census days were chosen according to weather conditions; cool, overcast days were avoided. During the standard census a set route through the treatment replicates was walked at a constant speed. All the adult syrphids encountered during a fixed time interval were identified to species and the behaviour at the time of first siting was recorded onto a microcassette tape recorder. Each observation had a corresponding recording of the time of day, cloud cover, wind speed, temperature and relative humidity. Temperature and relative humidity measurements were made using a Grant "Squirrel" data/logger. Wind speed was estimated using the Beaufort scale.

Syrphid behaviour was categorised, using criteria modified from Gilbert (1981), as follows:

Foraging
Hovering
Grooming
Flying
Copulating

Inactive
Ovipositing
Imbibing water
Courtship/territorial

Syrphid Identification

The standard walk technique did not allow for the capture and removal of syrphids from the field site. Therefore, after an initial period of familiarisation, the majority of identifications were made in the field by sight alone (nomenclature mainly follows Stubbs and Falk, 1983). In the field it was possible to distinguish the members of several genera:

Genus *Platycheirus*

The taxonomy of this group has recently been revised. Speight & Goeldlin, (1990) have described twelve European *clypeatus* group species, increasing the number of *Platycheirus* species which may be listed for Europe to thirty-eight. Only five species were common at the two sites during the period of this study; of these it was possible to distinguish between the sexes of *P. manicatus, P. peltatus* and *P. albimanus.* Records referring to *P. clypeatus* were discarded; the absence of voucher specimens for the site made it impossible to determine which of the members of *clypeatus* group were present.

Genus *Melanostoma*

Three species belong to this group, the members of which resemble *Platycheirus* species. In the field it was possible to distinguish between individuals of *M. mellinum* and *M. scalare*; individuals of the third species, *M. dubium* were seldom recorded from the field.

Genus *Sphaerophoria*

Members of the genus *Sphaerophoria* are readily distinguishable from other syrphid genera, however, within the group itself the identification of individual species is more complicated. Stubbs and Falk (1983) list nine distinct species in addition to a form of undetermined taxonomic status. Identification of individuals to species is based on the genitalia of the fly, making accurate identifications in the field impossible. However, the male of one species, *S. scripta*, can be recognised by its very long abdomen which extends beyond the wing tip. During this study all the *Sphaerophoria* males observed were identified as belonging to this species; it was assumed that the majority of females also belonged to this species.

Genus *Scaeva*

Of the four known species in this genus only two occur regularly in Britain (Stubbs and Falk, 1983). These two species can be distinguished according to the markings on the 3rd and 4th tergites. *Scaeva* *pyrastri* was the only member of the genus observed during the study.

Genus *Metasyrphus*

In the sub-genus *Metasyrphus* there are two fairly distinct groups of species, containing six species in total. *Metasyrphus corollae* and *M. luniger* were the most commonly recorded species.

Genus *Syrphus*

Three species have been recorded from Great Britain. The females of *S. vitripennis* and *S. ribesii* are separable in the field provided a clear view of the hind femora is obtained although Plant (1990) reported that this technique is unreliable if the flies are teneral adults. The third species, *S.torvus* superficially resembles the other species. The males of all three species are inseparable without capture.

Genus *Episyrphus*

The single member of the group, *E. balteatus* has distinctive markings and is easily recognised in the field.

Genus *Eristalis*

Members of *Eoseristalis* sub-genus were the most commonly occurring flies with non-aphidophagous larvae. Three of the nine known species were recorded and could be distinguished according to several characters.

The duration of the standard census walk, that is, the time taken to transverse the length of the headland was approximately 90 minutes. It was usually possible to complete five such censuses on a single date. The starting point for the standard census walk was allocated randomly, as was the direction of the walk along the headland. These decisions minimised the risk of introducing bias into the data as a result of sampling the same plot at the same time each week.

On the day of each census the number of open flower heads present in 15 randomly allocated quadrats was recorded. The mean floral area was calculated from these values using the method described above.

1990

During 1990 a single standard census of the headland plots and adjacent "green lane" (see Fig. 1c) was taken at weekly intervals from early May to early July. The census usually began at 7.00 GMT. As in 1989 the starting point and the direction of the standard census walk was allocated randomly.

Experimental design and the assumptions of analysis of variance.

The experimental design employed in this study comprised three (1989) and five (1990) replicates of two treatments arranged alternately along the length of a headland. The design violates the basic assumption of the analysis of variance which is that treatments are randomly allocated. This section describes the factors which resulted in the use of such a design.

The aim of the experiment was to examine the effect of the presence of flowering weeds in the headland on the distribution of syrphid adults and on the distribution and composition of syrphid eggs. The standard census walk was used to obtain quantitative estimates of the numbers of syrphids in the replicates of each of the two treatments. In addition the quadrat samples taken in the headland (crop and non-crop plants) provided information on the numbers of aphids and syrphid eggs in the two treatments.

Preliminary observations of the behaviour of adult syrphids during 1988 suggested that to examine the effect of flowering weeds on the distribution of syrphid adults it would be necessary to use large replicates (>50m long) to minimise any edge effects. This requirement placed several constraints on the experimental design. Firstly it was necessary to find a study site with a sufficiently long and homogeneous field margin. It was not possible to use several field margins from different locations because of the need to minimise variation due to aspect, margin type and the cropping patterns of adjacent fields. In addition, the use of several study sites would have been too labour intensive.

Secondly, to obtain an accurate estimate of the number of flies per plot it was necessary to spend a minimum of ten minutes censussing each plot. As a result the length of time required to traverse the whole headland was in excess of 90 minutes. The random allocation of the treatments may have resulted in two or more replicates of a single treatment occurring adjacently along the headland. In turn this would concentrate the censussing of the treatment replicates into a short period of time, relative to the total census time. Lewis and Taylor (1964) concluded that the timing of flight activity in insects is affected by light intensity, whereas the amplitude (numbers seen) is influenced by temperature (Gilbert, 1985). Temperature will vary considerably according to the location in the headland and with time of day. Therefore, the concentration of the majority of observations for either treatment into a one area of the headland or one time period may have resulted in environmental factors masking any treatment effects. In addition, two adjacent replicates of the same treatment would have been equivalent to a single large plot of the treatment. The perception of patches of floral resources has not been extensively studied for syrphids. Therefore, it was considered necessary to employ a design in which the all plots were distinct and of the same size. After considering all these factors it was decided that the most appropriate design would be the alternate arrangement of treatment replicates along the length of the headland.

t-tests or one-way analyses of variance were used to compare the √ arc sine proportions of the total number of adults in each treatment. The effect of microclimatic factors on the activity of the adults and the mobility of the flies was assumed to minimise any bias introduced as a result of the failure to randomly allocate the treatments.

In the case of aphid density a nested analysis of variance was performed on transformed data to examine the variation among treatments and the plots, together with transects of an individual treatment. Using this approach it was possible to test if the variation among the treatments was greater than that to be expected on the basis of observed variation among and within the replicates of one treatment.

In the case of the remaining headland variables (weed density, the numbers of syrphid eggs and the numbers of eggs per aphid) transformation failed to produce data which conformed to the assumptions of analysis of variance (that is, the data was not normally distributed). Therefore, non-parametric analyses were performed on the data. A Mann-Whitney U test was used to compare the between-treatment variation and Friedman's two-way analysis by ranks was used to examine within-treatment variation due to replicate and transect. In many cases the analyses highlighted significant within-treatment variation. In these cases it is not strictly accurate to refer to the plots as treatment replicates or as conservation headland plots and fully sprayed plots; however, this terminology has been retained for ease of understanding.

Identification of syrphid eggs.

1990

During the study, mature female syrphids were captured from the field and identified using Stubbs and Falk (1983). The flies were subsequently placed in tubes containing vegetation infested with aphids; under these conditions females of several species were induced to oviposit. The eggs obtained by this method were used as reference specimens.

Eggs collected during the study were examined using a transmitted-light microscope. The eggs were illuminated from above, to allow the surface patterning to be viewed. Eggs were identified using the reference specimens in conjunction with the key produced by Chandler (1968). The light microscope produced a clear image only at low magnifications. Therefore, scanning electron microscopy (S.E.M.) was used to check the accuracy of a randomly selected sample of eggs which had been previously identified using the light microscope. S.E.M. was also used to identify any eggs which could not be identified with certainty using light microscopy.

Scanning electron microscopy

Eggs were preserved in 70% alcohol, transferred to 100% alcohol and critical point dried in a polaron E3000 critical point drier. The eggs were coated with gold palladium alloy in a sputter coater and the structure of the exochorion was examined using a Joel P15 scanning electron microscope. In addition to the reference specimens plates showing the morphology of the eggs of less common syrphids, were available from the literature (Kula, 1989; Kuznetsov, 1988). Using a combination of light microscopy and S. E. M. it was possible to identify all the collected eggs to genus.

Results

The distribution of adult syrphids between the treatments.

1989

The distribution of adult syrphids between the headland plots was recorded during the standard census walk. The proportion of the total number of individuals observed during the census, in each plot, was calculated from the census records. There was a minimum of four censuses per date; the values from each census were used to calculate the mean proportion of adults in each plot. A t-test was used compare the √ arc sine transformed mean proportion of adults in the two treatments. *E. balteatus* was the only syrphid which occurred in sufficient numbers on all the dates to allow statistical analysis of the data. In addition, individuals of the two *Melanostoma* species were sufficiently numerous during July to allow analysis of the data. With the exception of 13 June all the censuses took place in the headland of Side Scammel.

On the census days in July there was no significant difference in the mean proportion of *Melanostoma* adults in the two treatments ($t = -1.29$, N.S.; $t = -1.69$, N.S.; $t = 1.62$, N.S.). There was no significant difference in the mean proportion of *E. balteatus* adults between the two treatments throughout the study. However, the calculated t-values did approach significance at the 5% level on 13 June and 12 July ($t = -1.97$, N.S; $t = -2.73$, $P = 0.053$; $t = -2.18$, N.S.; $t = -2.62$, $P = 0.059$).

On each census day 15 randomly allocated $0.5m^2$ quadrats per plot were used to obtain an estimate of the number of flower heads per plot. These values were used to calculate the mean floral area ($mm^2/0.5m^2$) per plot using the technique described in the materials and methods section. Fig. 3(a) shows the relationship between the mean floral area per plot($\log_{10}$) and the proportion of the total number of *E. balteatus* adults for all the census dates. Analysis of the relationship using Spearman's rank correlation produced a significant, positive r_s value ($r_s = 0.578$, $P < .001$, $n = 36$).

Fig. 4 shows the behaviour of *E. balteatus* adults in the six headland plots on four census dates. The data from the five individual censuses per date was pooled and the proportion of the total number of observations in each behaviour category in the six headland plots was calculated. The values for each of the treatment replicates were used to calculate the mean proportion of each behaviour in the two treatments. Between-treatment differences in the mean proportion of observations in each behaviour category were analysed using a Mann-Whitney U test; individual census dates were treated as replicates. There was no significant difference in the mean proportion of flies which were flying, foraging or inactive in the two treatments ($U = -1.202$; N.S.; $U = 1.671$; N.S.; $U = -0.836$, N.S.). The remaining categories of behaviour (courtship, oviposition, basking) were pooled to form the category "other". There was no significant difference in the mean proportion of "other" behaviour between the conservation and sprayed headland plots ($U = 0.1078$; N.S.).

Fig. 5 shows the behaviour of *Melanostoma* adults in the six headland plots on three census dates. The mean proportion of observations in each of the four behaviour categories was calculated as described above and the data analysed using Mann-Whitney U tests. There was no significant difference in the mean

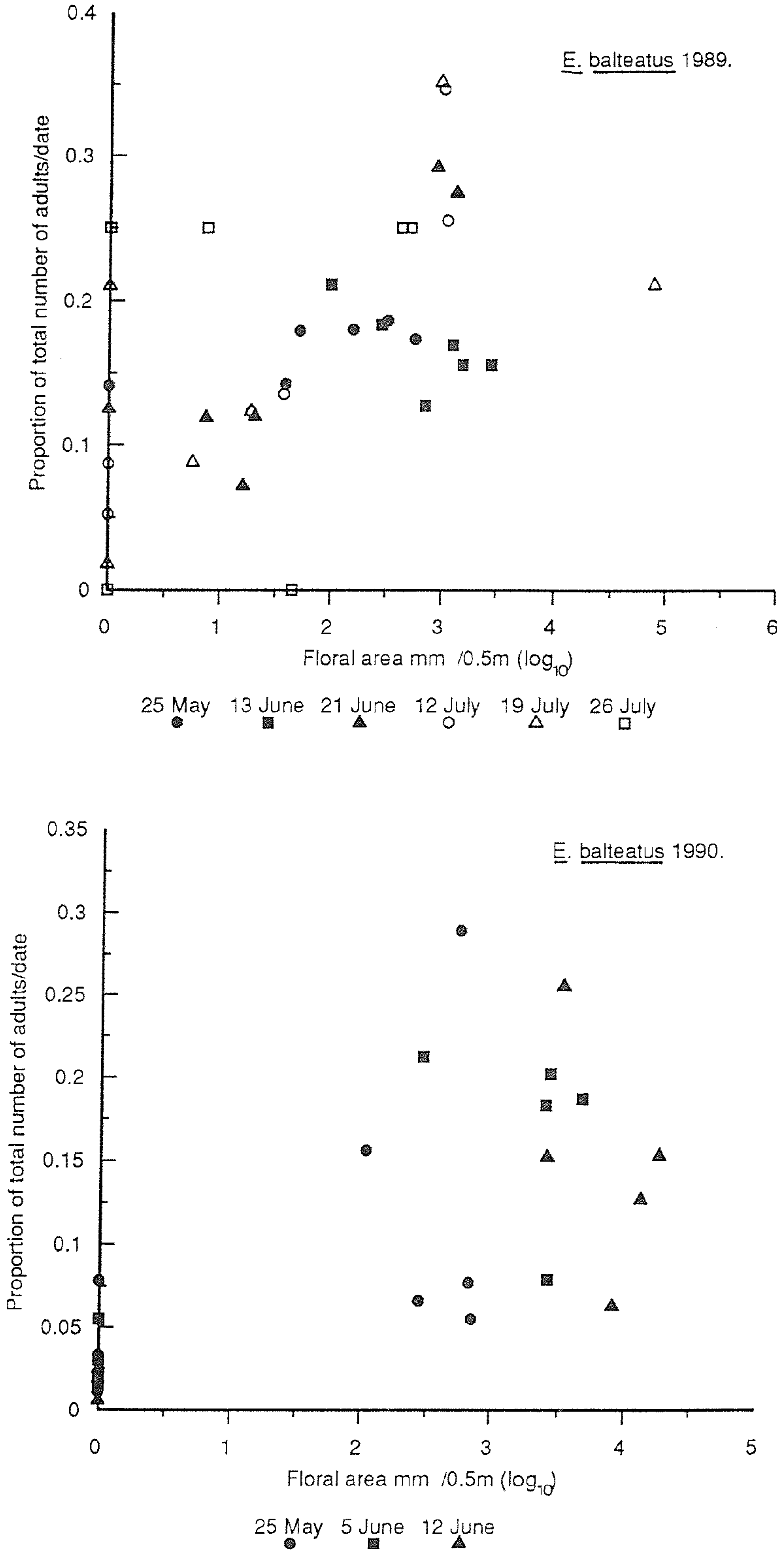


Fig. 3(a) and (b). The relationship between mean floral area per plot($\log_{10}$) and the proportion of the total number of flies recorded per plot.
Data from several census days was pooled for analysis; symbols distinguish the individual census dates.

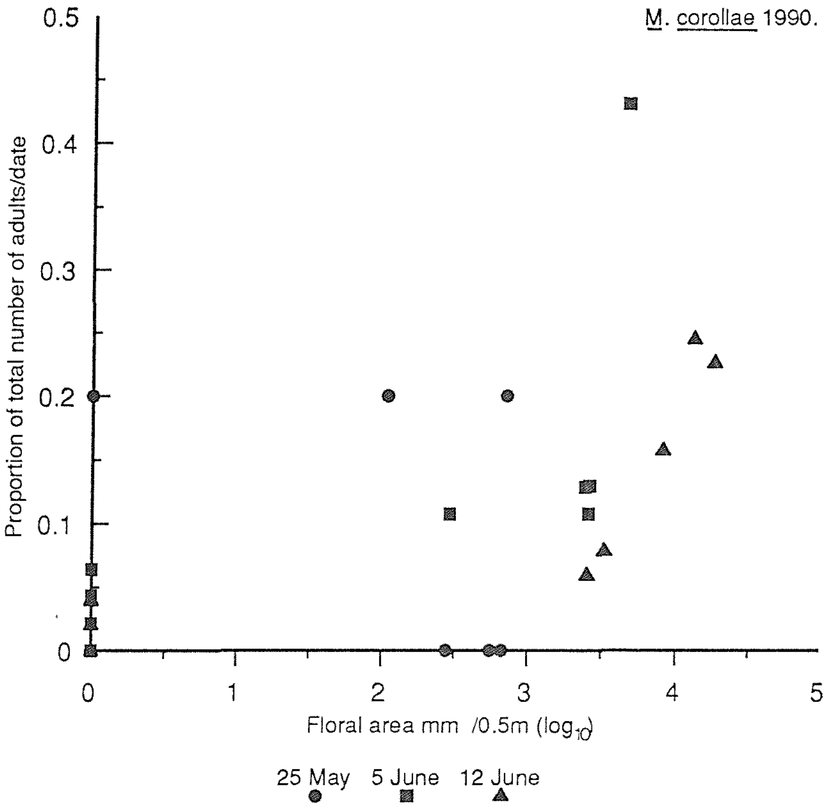
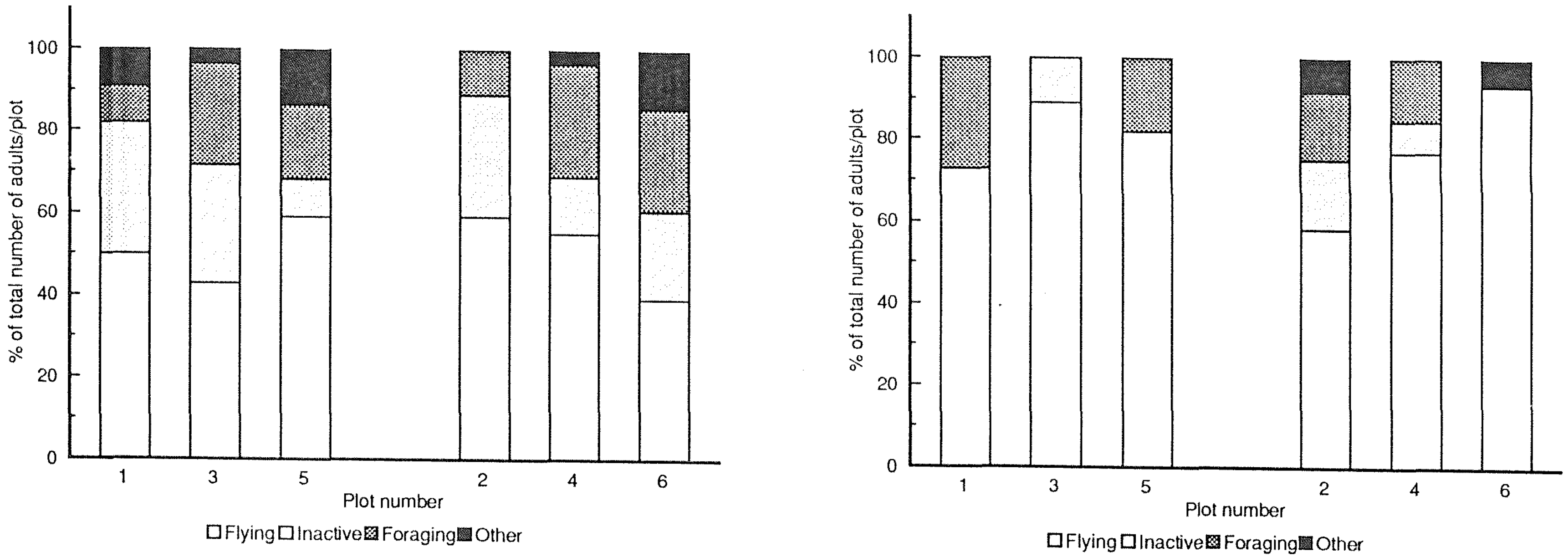
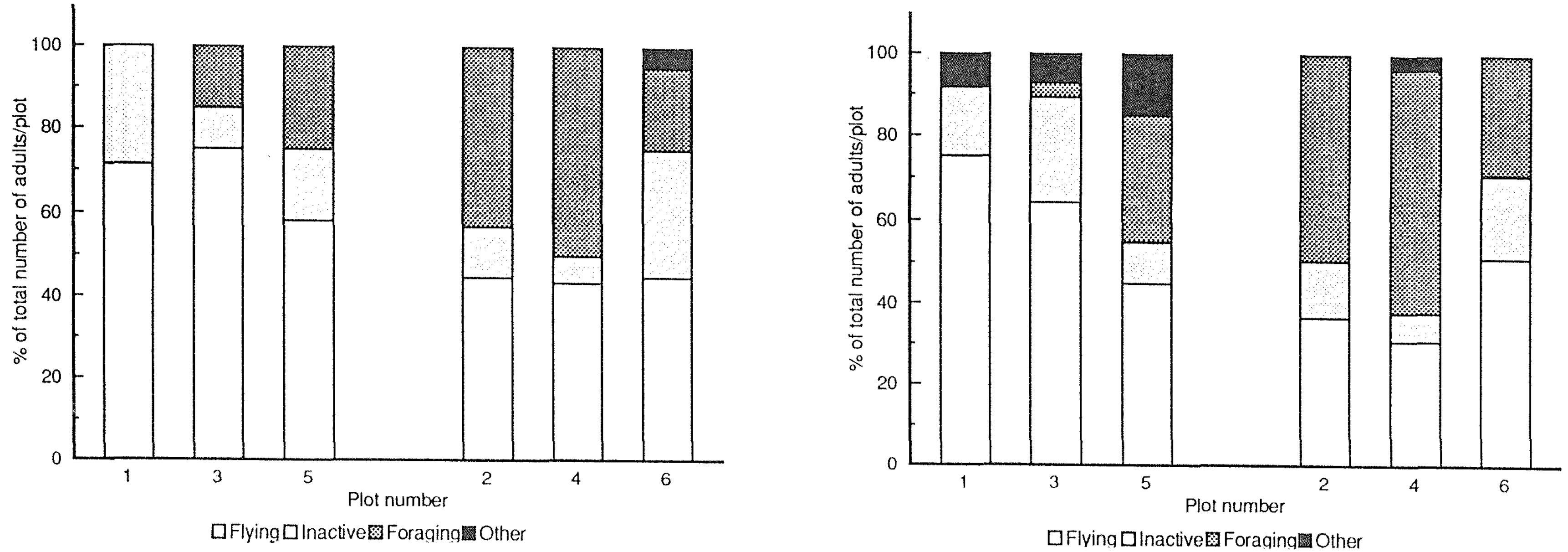


Fig. 3(c). The relationship between mean floral area per plot($\log_{10}$)
and the proportion of the total number of flies recorded per plot.
Data from several census days was pooled for analysis; symbols distinguish the individual census dates.



25 May

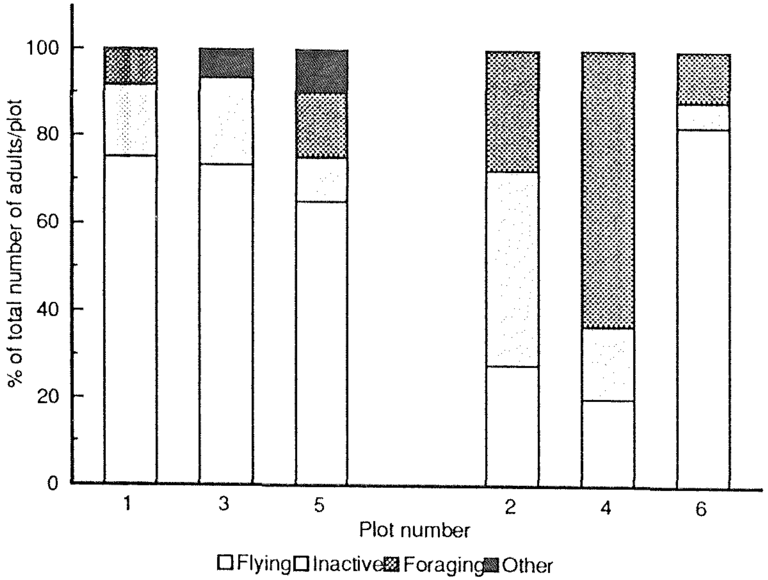
13 June



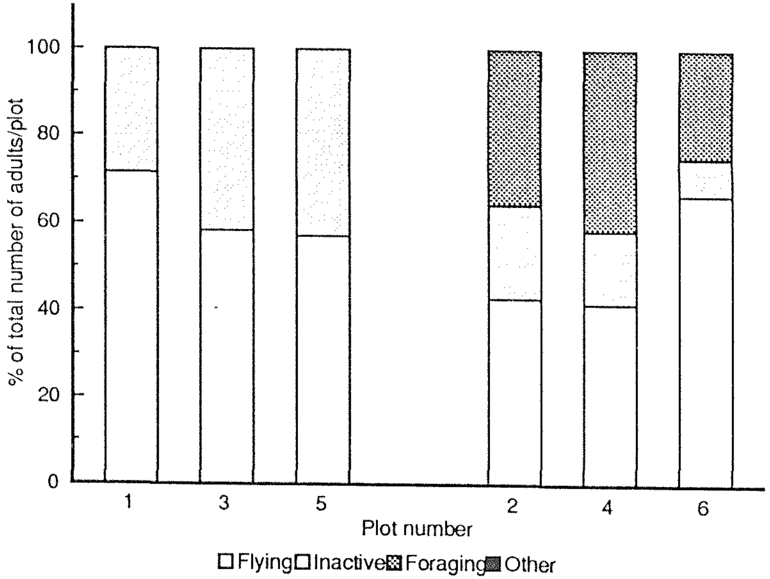
21 June

7 July

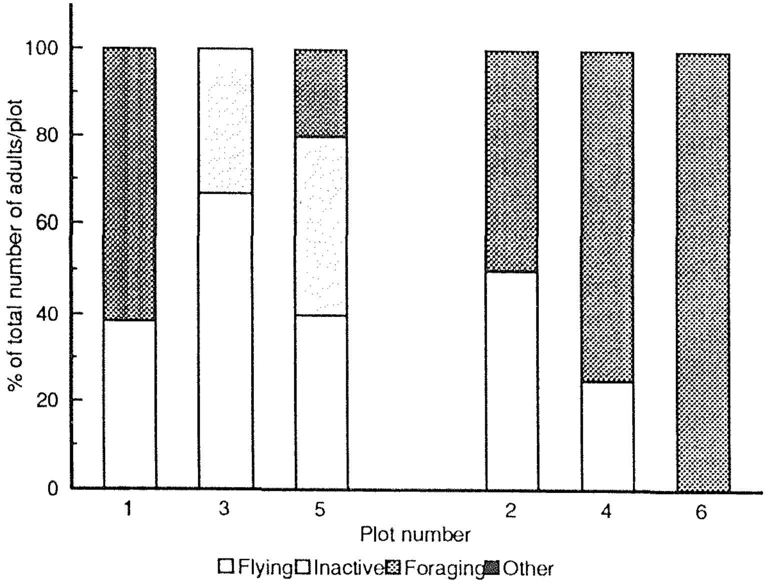
Fig. 4. The behaviour of *E. balteatus* adults in the six headland plots in 1989.
The bar segments represent the mean % of observations in each of the four behaviour categories. The values were calculted from observations made during five censuses of the headland on each date. 1,3,5 = fully sprayed treatment; 2,4,6 = conservation headland treatment.



7 July



14 July



21 July

Fig.5.The behaviour of Melanostoma spp. adults in the six headland plots in 1989
The bar segments represent the mean % of observations in each of the four behaviour categories. The values were calculated from observations made during five censuses of the headland on each date. 1,3,5 = fully sprayed; 2,4,6 = conservation headland treatment.

proportion of any of four categories between the two treatments (flying; U = -1.31, N.S.; foraging; U = 1.75, N.S.; inactive; U = -1.309, N.S.; other; U = 0.667, N.S.).

The distribution of adult syrphids between treatments.

1990

Table 1 summarises the species composition of the adults observed on each of the census dates during 1990. *E. balteatus* and *M. corollae* were the only syrphids with aphidophagous larvae which were recorded in sufficient numbers to allow statistical analysis of the data. One-way analysis of variance was used to compare the √ arc sine proportion of adults in the two headland treatments and the "green lane" plots. On 5 June there was no census of the "green lane" plots and a t-test was used compare the √ arc sine transformed proportion of the total number of observations which occurred in the plots of each of the two headland treatments.

On all census dates a significantly higher proportion of *E. balteatus* and *Metasyrphus* adults were recorded in the conservation headland plots (Table 1a). Fig. 3(b) shows the relationship between the mean floral area per plot($\log_{10}$) and the proportion of the total number of *E. balteatus* adults for all the census dates. Analysis of the relationship using Spearman's rank correlation produced a significant, positive r_s value (r_s = 0.763, P<.001, n= 30). Fig. 3(c) shows the relationship between the mean floral area and the proportion of *M. corollae* adults per plot. When data from all the census dates were combined, analysis using Spearman's rank correlation showed a significant positive relationship (r_s = 0.024, P<.005, n = 30). There was no significant relationship between mean floral area and the proportion of *Melanostoma* adults observed in a plot (r_s = -0.063, N.S., n = 30).

Fig. 6 shows the behaviour of *E. balteatus* adults in the ten headland plots. The five conservation headland plots and the five sprayed plots were used to calculate the mean proportion of observations in each behaviour category per treatment. Mann-Whitney U tests were used to compare the mean proportion of each of the four behaviours in the two treatments throughout the study. There was a significant difference in the proportion of *E. balteatus* adults which were observed feeding in the two treatments; a greater proportion of adults were recorded foraging in conservation headland plots than in the sprayed plots (U = 2. 807, P<.005). Conversely a greater proportion of the adults in the sprayed plots were inactive when compared to those in the conservation headland plots (U = -2.482, P<.05). The mean proportion of the two remaining behaviour categories were not significantly different between the two treatments (flight; U = -1.201, N.S.; other; U = 0.089, N.S.).

Fig. 7 shows the behaviour of *M.corollae* adults in the ten headland plots on 3 census days. The data was analysed using the procedure described for *E. balteatus*. There was no significant difference in the mean proportion of each behaviour in the two treatments (flight; U = 0.886, N.S.; forage; U = 1.77, N.S.; inactive; U = 0.664, N.S.; other; U = 0, N.S.).

Table 1. The species composition of syrphids calculated from counts made during the standard census walk on each of the four dates. N = total number of observations of adults of each species or genus; % = percentage of the total number of individuals of all species observed on that date.

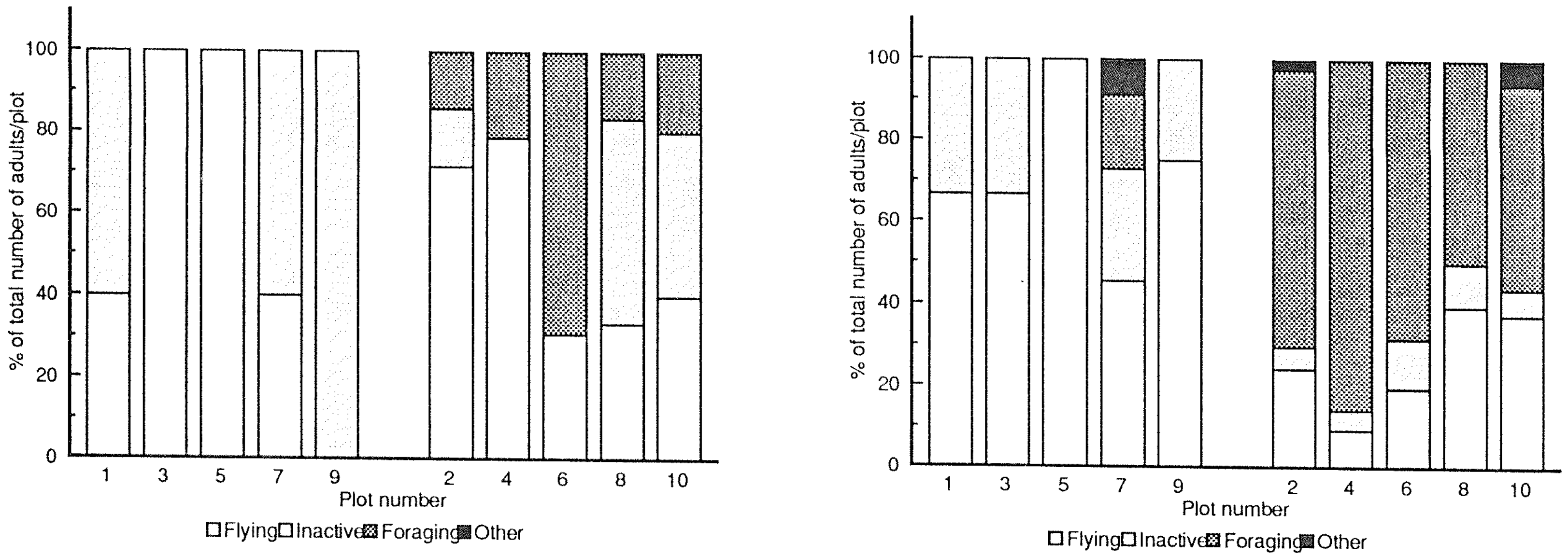
	Date							
	17 May		25 May		5 June		12 June	
Syrphid species	N	%	N	%	N	%	N	%
E. balteatus	13.0	14.6	90.0	81.8	203.0	76.9	157.0	53.0
P. manicatus	2.0	2.3	1.0	0.9	4.0	1.5	3.0	1.0
S. pipiens	9.0	10.1	1.0	0.9	0.0	0.0	0.0	0.0
P. albimanus	4.0	4.5	0.	0.	0.0	0.0	3.0	1.0
E. tenax	10.0	11.2	3.0	2.7	0.0	0.0	4.0	1.4
S. scripta	2.0	2.3	0.	0.	5.0	1.9	4.0	1.4
S. pyrastri	0.	0.	0.	0.	1.0	0.4	2.0	0.7
Melanostoma spp.	14.0	15.7	5.0	4.5	3.0	1.1	9.0	3.0
Metasyrphus spp.	18.0	20.2	5.0	4.5	47.0	17.8	102.0	34.5
Syrphus spp.	10.0	11.2	4.0	3.6	1.0	0.4	9.0	3.0
Others	7.0	7.7	1.0	0.9	0.0	0.0	3.0	1.0

Table 1(a). The distribution of *Episyrphus* and *Metasyrphus* adults between the two headland treatments and the adjacent green lane. One-way analysis of variance performed on the√arc sine transformed proportion of the daily total of adults of each genus. On 5 June a t-test was used to compare the√arc sine proportion of the total number of adults in the conservation and fully sprayed headland treatments.

	Date					
	25 May		5 June		12 June	
E. balteatus adults						
	Mean	F -ratio	Mean	t -value	.Mean	F -ratio
Conservation headland	20.069	5.720	24.247	-6.41	22.343	14.913
Fully sprayed headland	11.9662	<.05	9.922	<.001	7.697	<.001
"Green lane"	7.831	(d.f=2,12)	+	(d.f=8)	8.678	(d.f.=2,12)

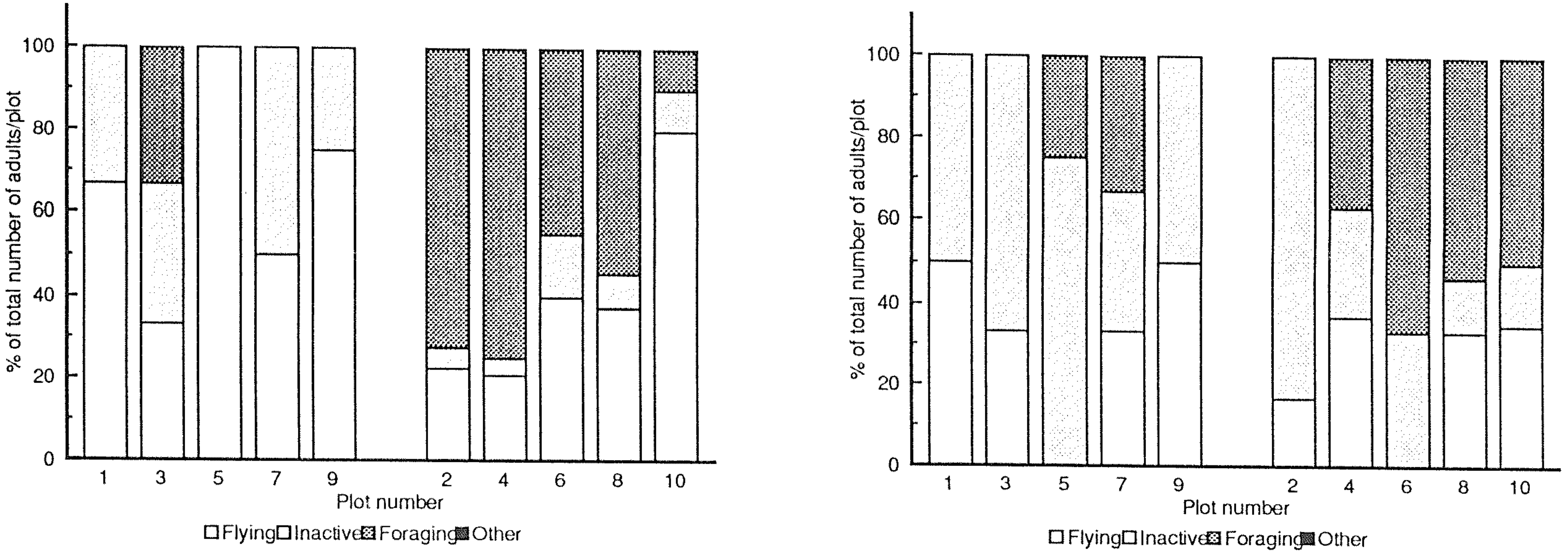
	24 June	
E. balteatus adults		
	Mean	F -ratio
Conservation headland	20.116	5.156
Fuly sprayed headland	10.461	<.05
"Green lane"	9.62	(d.f = 2,12)

	5 June		12 June	
M. corollae adults				
	Mean	t -value	Mean	F -ratio
Conservation headland	24.247	-6.41	22.334	11.335
Fully sprayed headland	9.922	<.001	8.519	<.005
"Green lane"		(d.f= 8)	7.047	(d.f = 2,12)



25 May

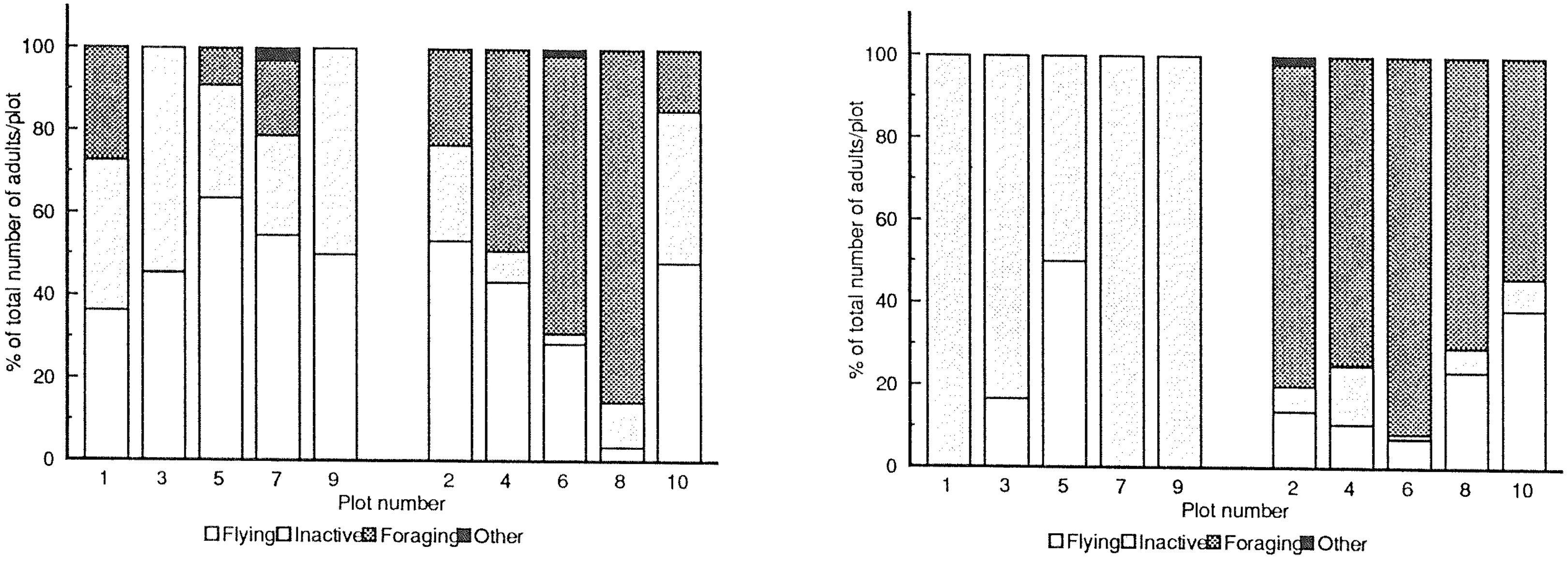
5 June



12 June

24 June

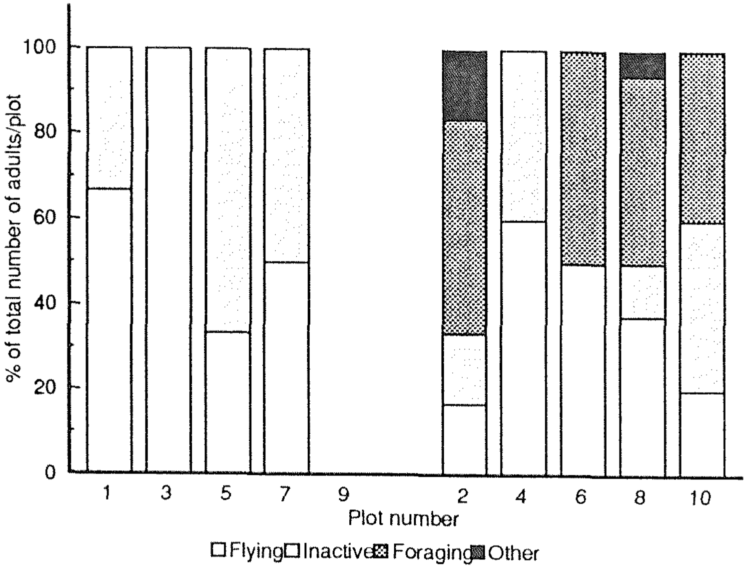
Fig. 6. The behaviour of E. balteatus adults in the ten headland plots on the census days in 1990. The total number of individuals in each plot was calculated from the census records. The bar segments represent the % of the total number of observations in each of the four behaviour categories per plot. 1,3,5,7,9 = fully sprayed treatment; 2,4,6,8,10 = conservation headland treatment.



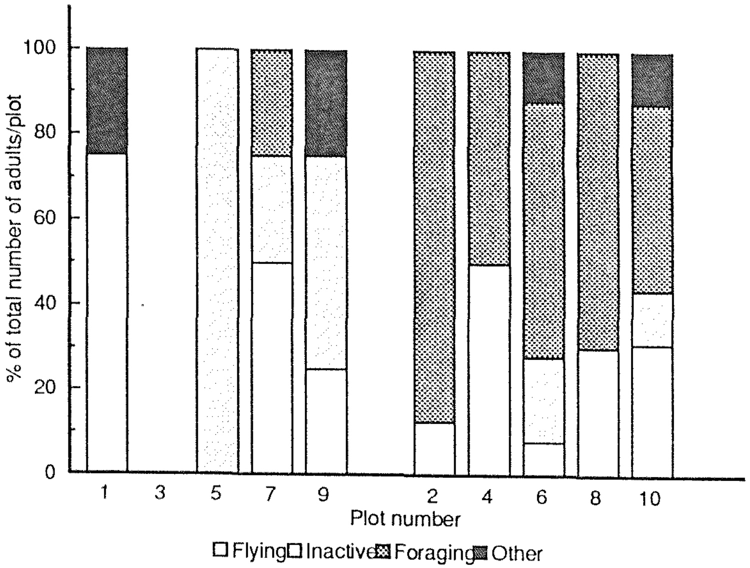
28 June

6 July

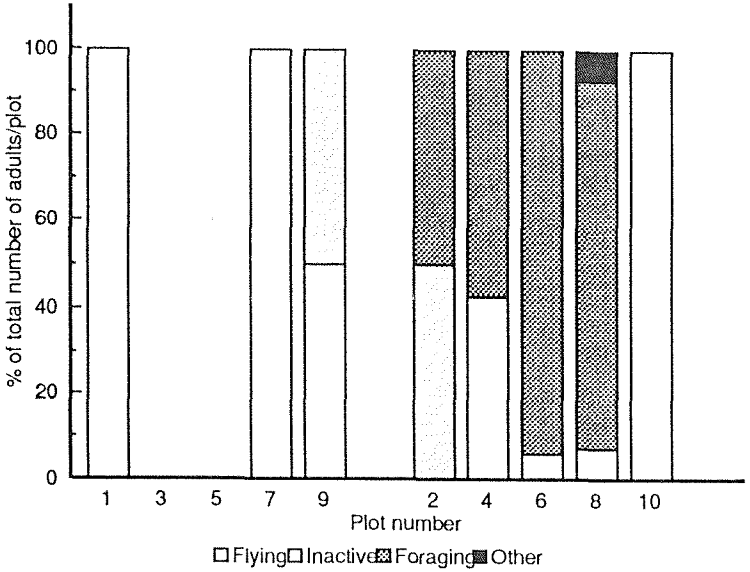
Fig. 6 (contd.). The behaviour of E. balteatus adults in the ten headland plots.



5 June



12 June



6 July

Fig. 7. The behaviour of M. corollae adults in the ten headland plots on the census days in 1990.
The total number of individuals in each plot was calculated from the census records. The bar segments represent the % of the total number of observations in each of the four behaviour categories per plot. The absence of a bar indicates that no flies were recorded in that plot during the census on that date.
1,3,5,7,9 = fully sprayed treatment; 2,4,6,8,10 = conservation headland treatment.

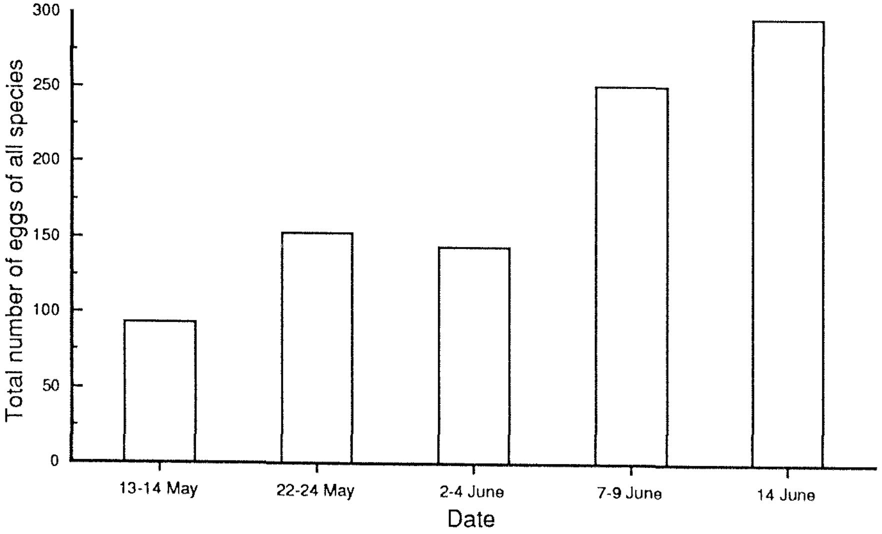


Fig.8(a). The total number of eggs collected during the five sampling periods.

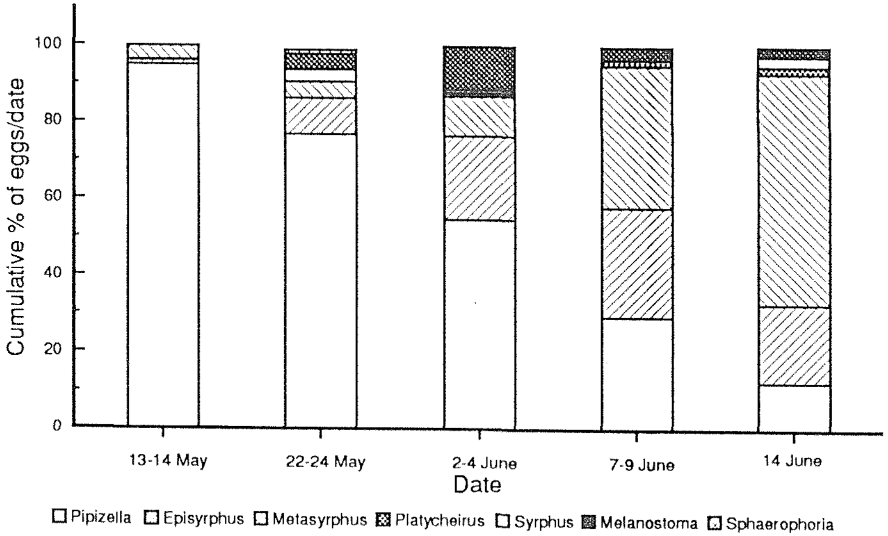


Fig.8(b). The composition of all eggs, identified to genus, during the five sampling periods.

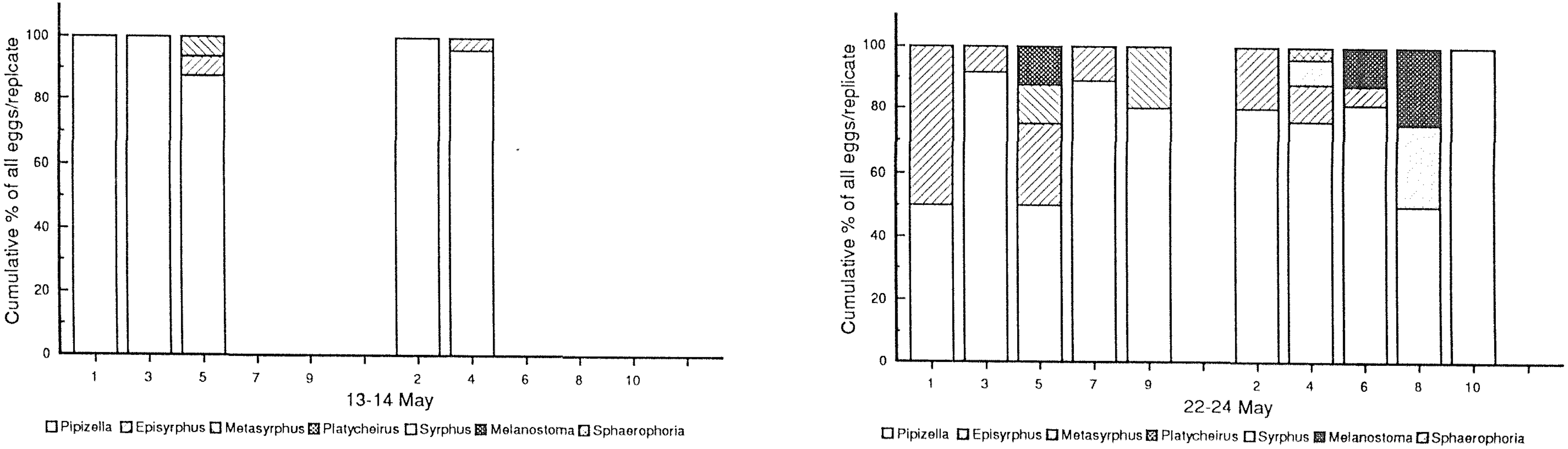


Fig.8(c). The distribution of eggs of seven syrphid genera between the replicates of the two treatments
1,3,5,7,9 = fully sprayed treatment; 2,4,6,8,10 = conservation headland treatment

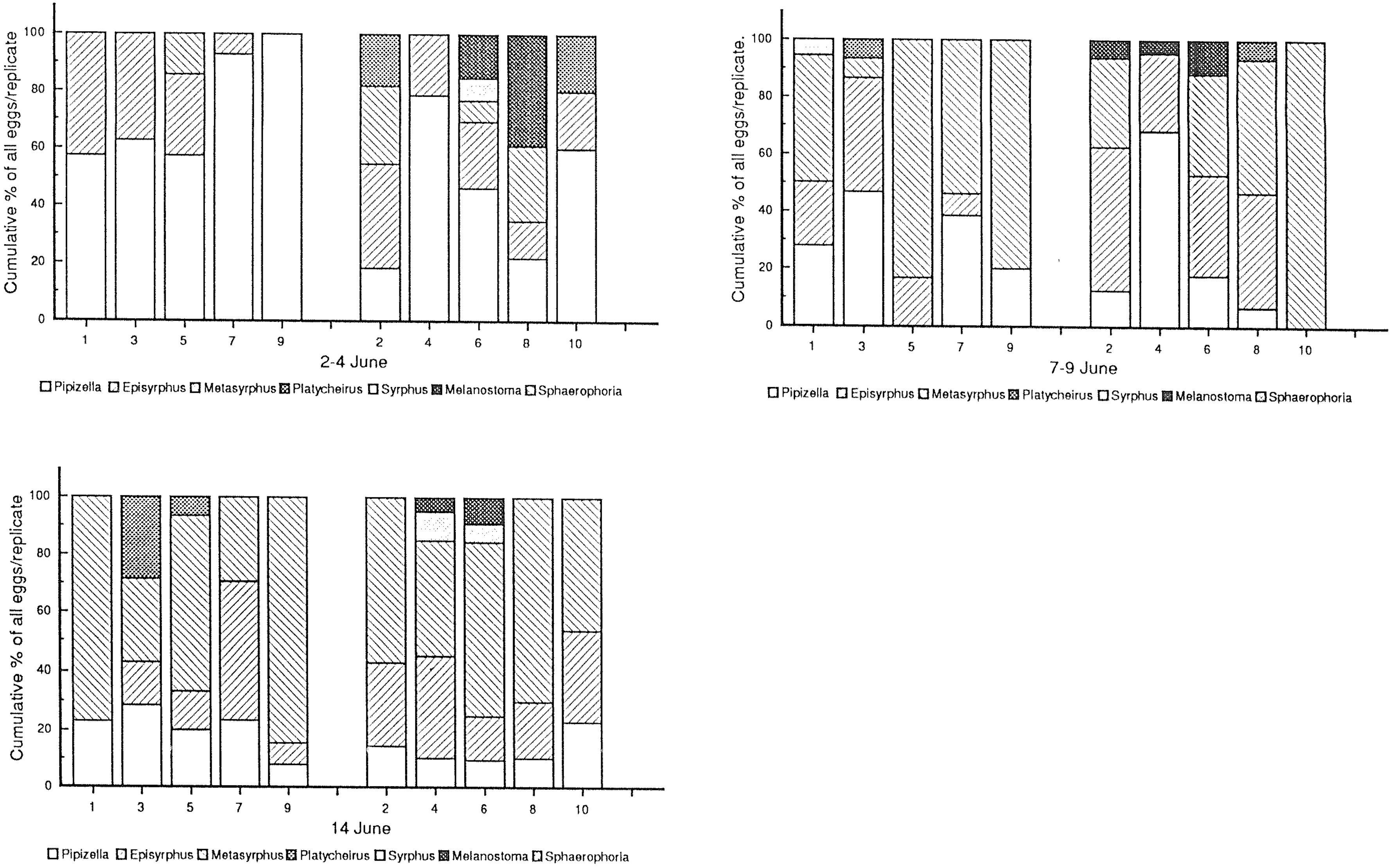


Fig. 8(c). The distribution of eggs of seven syrphid genera between the replicates of the two treatments.

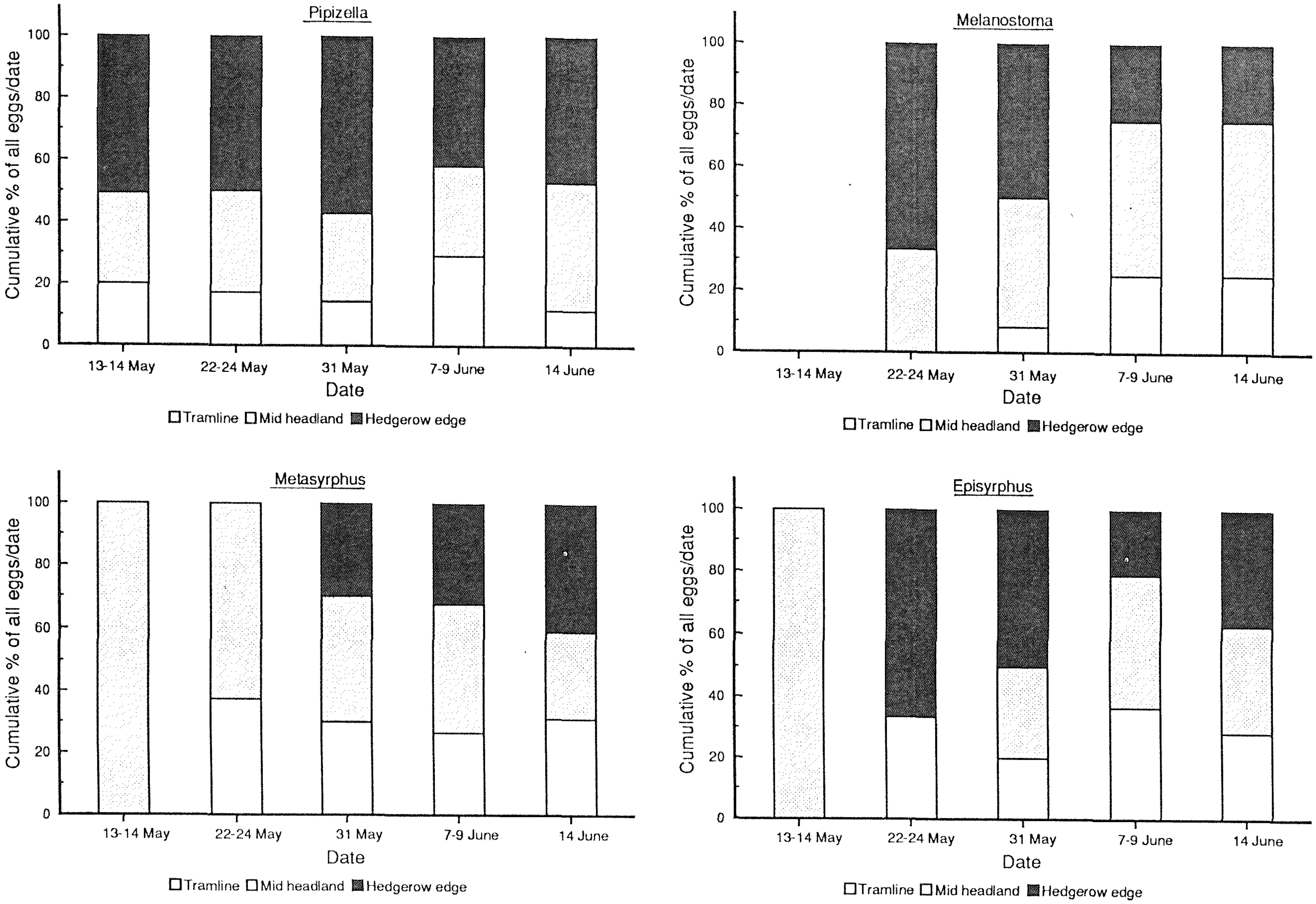


Fig.9. The distribution of Pipizella, Melanostoma, Metasyrphus and Episyrphus eggs between the three headland transects.

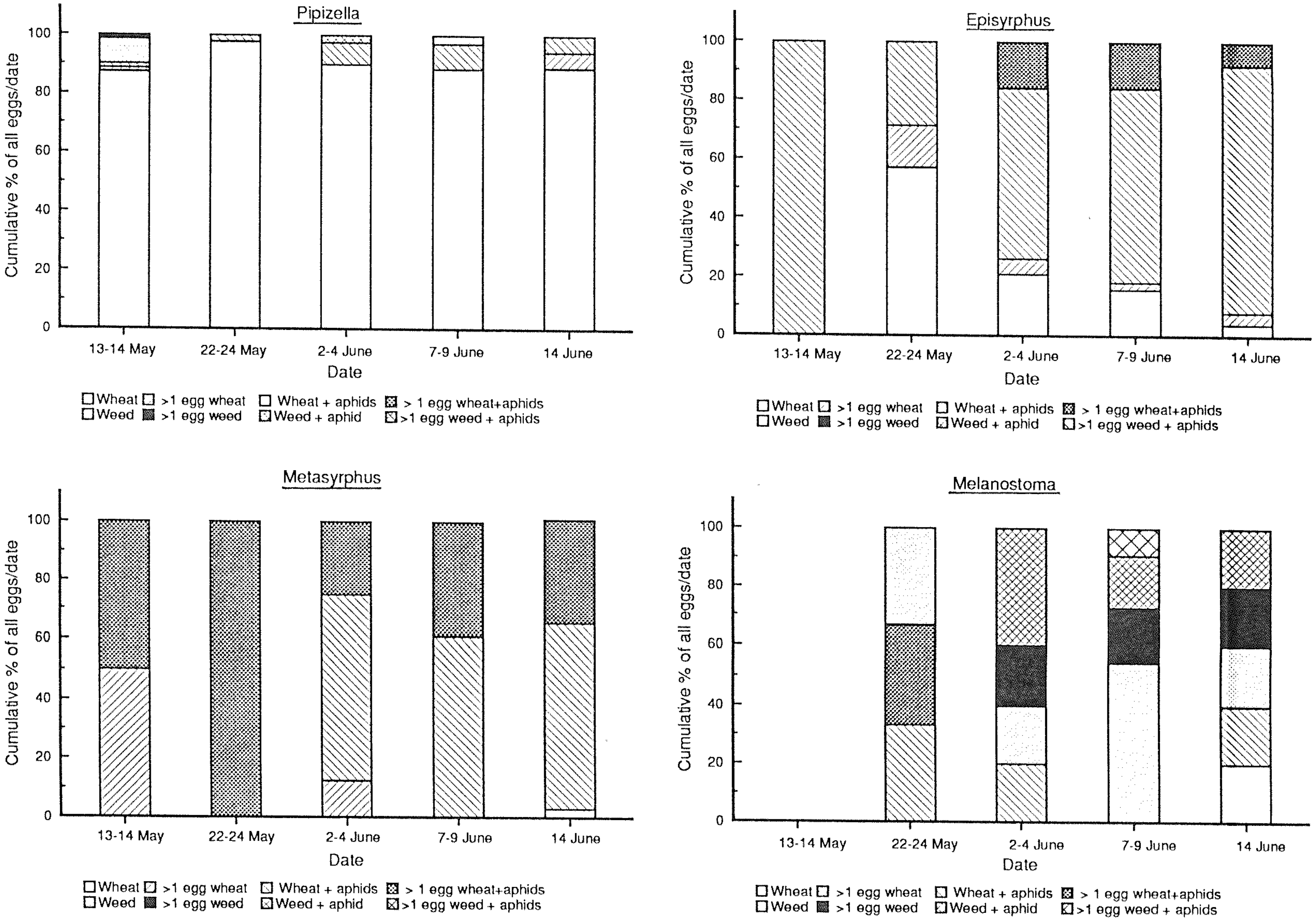


Fig. 10 The distribution of eggs of four syrphid genera between the crop and non-crop plants and according to the presence or absenceof aphids.

Headland variables 1989.

During 1989 the headland plots in Side Scammel were sampled during the periods 19-20 May, 30 May-1 June, 9-10 June and 15-16 June. The plots in Mesh Bottom were sampled during the periods 25-26 May, 5-6 June, 11-12 June, 17-18 June and 23-24 June.

On all the sampling dates there were significant differences in the rooted weed densities in the two treatments at Side Scammel (Mann-Whitney U; U = -4.279, P = < .005; U = -2.409, P<.05; U = 2.855, P<.005; U = -2.856, P<.005). Within individual treatments there were significant differences in weed density according to the position in the headland; the highest weed densities were recorded at the hedgerow edge (Friedman's two-way analysis by ranks; Table 2). On 19 May and 16 June there were significant differences in weed density among the conservation headland and sprayed plots respectively (Table 2).

From 21 June - mid July there were significant differences in the mean floral area in the two treatments on census days at Side Scammel (Mann-Whitney U; Table 3(a)). On 21 June there was significant within-treatment variation among the conservation headland plots (Friedman's two-way analysis by ranks; Table 3(b). At that time *Sinapsis arvensis* was in flower; the plants showed a contagious distribution which concentrated the majority of flowers in plot 2. During July there was no significant within-treatment variation among both the conservation headland and fully sprayed plots (Table 3a).

On 13 June the headland plots in Mesh Bottom were censussed. On this date there was no significant difference in floral area between the two treatments (Mann-Whitney U; U = -1.405, N.S.) The total number of aphids per wheat stem at Side Scammel was not significantly different between treatments on 19-20 May; after this date significantly higher aphid densities were recorded from the conservation headland plots; the variation between the treatments was significant above and beyond the variation within the treatments (nested ANOVA; Table 4).

The total number of eggs per aphid per $0.5m^2$ of cropped area, including eggs from non-crop plants, did not differ significantly between the two treatments during the study (Mann -Whitney U; U = -0.677, N.S.; U =0.897, N.S.; U = -0.788, N.S.; U = 0.501, N.S.). Within the conservation headland treatment there was a significant difference in the number of eggs per aphid among the plots during May. There were higher numbers of eggs per aphid in plot two which was also the weediest plot (Friedman's two way analysis by ranks; Table 6). When data from the six plots was pooled there was no correlation between the number of eggs per aphid and weed density (Table 7a). On 10 June the calculated r_s values for the relationship between the number of eggs per aphid and the number of wheat stems/ $0.5m^2$ approached significance at the 5% level (Table 8a).

There was no significant difference in weed density between the two treatments at Mesh Bottom on any of the sampling dates (Mann Whitney U; U = -1.573, N.S.; U = -0.6344; N.S.; U = -0.827; P=0.409; U = -1.881, N.S.; U = 0.557, N.S.). Analysis of data for the remaining headland variables (aphid density, egg density and the number of eggs per aphid) was limited to an examination of relationship between weed density and the number of eggs per aphid using Spearman's rank correlation in which data from all six plots was combined. During 25-26 May there was a significant positive relationship between the number

Table 2. The within-treatment variation in weed density, 1989.
Friedman's two-way analysis by ranks on weed density/0.5m^2 among (a) replicates and (b) transects of the conservation headland treatment and fully sprayed treatment.
(a) Site 1 (Side Scammel).

	Date			
Conservation headland plots	19 May	30 May	10 June	16 June
Plot	Average rank	Average rank	Average rank	Average rank
2	2.33	2.27	1.50	1.43
4	2.20	1.97	1.50	1.57
6	1.47	1.77	N.A	N.A
Test statistic	9.56	2.92	0.0	0.33
P	<.01	<.01	N.S.	N.S.
N	(45)	(45)	(45)	(45)

Sprayed headland plots

Plot	Average rank	Average rank	Average rank	Average rank
1	1.90	2.43	N.A	N.A
3	2.00	1.90	1.43	1.33
5	2.10	2.10	1.57	1.67
Test statistic	2.0	1.0	0.66	5.00
P	N.S	N.S.	N.S.	<.05
N	(45)	(45)	(45)	(45)

(b) Site 1 (Side Scammel).
Conservation headland plots

Transect	Average rank	Average rank	Average rank	Average rank
1	2.50	2.67	2.60	2.70
6	2.00	1.80	2.10	2.05
12	1.50	1.53	1.30	1.25
Test statistic	11.54	14.04	10.12	12.79
P	<.005	<.01	<.01	<.002
N	(30)	(30)	(30)	(30)

Sprayed headland plots

Transect	Average rank	Average rank	Average rank	Average rank
1	2.20	2.43	2.50	2.60
6	1.90	1.73	1.60	1.65
12	1.90	1.83	1.90	1.75
Test statistic	6.0	10.75	8.0	11.47
P	<.05	<.005	<.05	<.005
N	(30)	(30)	(30)	(30)

Table 3 (a). The between-treatment variation in mean floral area ($mm^2/0.5m^2$), 1989.
Mann-Whitney U Test on mean floral area in the conservation and sprayed headland plots at Side Scammel on the five sample dates.

			Date		
	13 June	21 June	12 July	19 July	26 July
Treatment	Average rank	Average rank	Average rank	Average rank	Average rank
Fully sprayed headland	33.54	38.63	40.00	40.37	43.37
Conservation headland	39.46	52.37	57.00	50.86	47.63
U	-1.41	3.49	3.26	3.22	1.56
P	N.S	<.005	<.002	<.002	N.S
N					

Table 3(b). The within-treatment variation in floral area.
Friedman's two-way analysis by ranks on floral area among plots and transects of the conservation and fully sprayed treatments.

Conservation headland plots

Plot	Average rank	Average rank	Average rank	Average rank	Average rank
2	2.21	2.37	2.17	2.23	1.97
4	2.04	2.00	1.97	2.03	2.03
6	1.75	1.63	1.87	1.73	2.00
Test statistic	2.95	7.33	1.40	4.22	0.13
P	N.S.	<.05	N.S.	N.S	N.S.
N					

Sprayed headland plots

Plot	Average rank	Average rank	Average rank	Average rank	Average rank
1	2.21	1.90	1.97	2.07	2.03
3	2.00	2.00	2.07	1.97	1.93
5	1.79	2.10	1.97	1.97	2.03
Test statistic	1.92	2.00	2.00	2.00	1.00
P	N.S.	N.S.	N.S.	N.S.	N.S.
N					

Within treatment variation according to transect.
Conservation headland transects.

Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	2.50	2.07	2.23	2.17	2.13
Mid headland	1.58	1.90	1.83	1.90	1.97
Tramline	1.58	2.03	1.93	1.93	1.90
Test statistic	9.54	2.00	2.69	1.46	1.63
P	<.01	N.S.	N.S.	N.S.	N.S.
N					

Table 3(b) contd. The within treatment variation in floral area, 1989.
Friedman's two-way analysis by ranks on floral area among plots and transects of the conservation and fully sprayed treatments.

Fully sprayed headland transects

Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	2.71	2.30	2.07	2.07	2.03
Mid headland	1.63	2.03	1.97	1.97	1.93
Tramline	1.67	1.67	1.97	1.97	2.03
U	13.15	4.92	2.00	2.0	1.00
P	<.005	N.S.	N.S.	N.S.	N.S.
N					

Table 4. The variation in aphid density/0.5m^2 among treatments, plots and transects within plots determined by a nested analysis of variance. The raw data was normalised using a log (n+1) transformation.

	Date							
	19 -20 May		30 May -1 June		9-10 June		15-16 June	
Source of variation	F_s	P	F_s	P	F_s	P	F_s	P
Among treatments	119.50	<.001	366.68	<.001	197.64	<.001	207.13	<.001
Among plots within treatments	1.72	N.S.	1.91	N.S.	1.49	N.S.	1.18	N.S.
Transects within plots	0.81	N.S.	2.17	<.05	1.85	N.S.	4.68	<.001
(d.f)	(1,1,8)		(1,2,6)		(1,1,8)		(1,1,8)	

Table 6. The within-treatment homogeneity of the number of eggs per aphid at Site 1 during 1989.
Friedman's two-way analysis by ranks on the number of eggs per aphid among (a) plots and (b) transects of the conservation and fully sprayed headland treatments.

	Date			
	19 May	30 May	10 June	16 June
(a)				
Conservation headland plots				
Plot	Average rank	Average rank	Average rank	Average rank
2	+	2.63	1.63	1.50
4	+	1.60	1.37	1.50
6	+	1.76	N.A.	N.A.
Test statistic		10.45	1.33	0
P		<.01	N.S.	N.S.
N				
(a)				
Fully sprayed headland plots.				
Plot	Average rank	Average rank	Average rank	Average rank
1	+	2.17	+	+
3	+	2.03	1.50	1.53
5	+	1.80	1.50	1.47
Test statistic		1.32	0.00	0.11
N		N.S.	N.S.	N.S.
(b) Conservation headland transects				
Transect	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	+	1.83	1.55	1.75
Mid headland	+	1.97	2.45	2.35
Tramline	+	2.20	2.00	1.90
Test statistic		1.24	4.63	3.12
P		N.S.	N.S.	N.S.
N				
Fully sprayed headland transects				
Transect	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	+	1.80	2.05	1.70
Mid headland	+	2.167	1.85	2.30
Tramline	+	2.03	2.10	2.00
Test statistic		1.35	0.47	2.77
P		N.S.	N.S.	N.S.

On dates marked + there ws insufficient data to allow statistical analysis.
N.A. indicates that no data was collected in that plot during the sampling period.

Table 7. Spearman's rank correlation between the number of eggs per aphid and weed density/0.5m^2 1989. On each date data from the conservation and fully sprayed plots were combined. The values represent the calculated r_s values and the corresponding significance level. N = sample size.

(a) Site one (Side Scammel)

	Date			
	19. May	30. May	10. June	16. June
r_s	-0.145	-0.024	-0.015	-0.237
P	N.S.	N.S	N.S.	N.S.
N	81	90	60	60

(b) Site two (Mesh Bottom)

	Date				
	26. May	5. June	10. June	16. June	24. June
r_s	0.299	0.117	0.116	0.184	0.537
P	<.05	N.S.	N.S.	N.S.	N.S.
N	74	45	69	40	45

Table 8. Spearman's rank correlation between the number of eggs per aphid and the density of wheat stems/0.5m^2 1989. On each date data from the conservation and fully sprayed plots were combined. The values represent the calculated r_s values and the corresponding significance level. N = sample size.

(a) Site one (Side Scammel)

	Date			
	19. May	30. May	10. June	16. June
r_s	0.168	0.131	0.252	0.135
P	N.S.	N.S.	0.053	N.S.
N	81	90	60	60

(b) Site two (Mesh Bottom)

	Date				
	26. May	5. June	10. June	16. June	24. June
r_s	-2.835	0.019	0.084	0.083	-0.508
P	<.05	N.S.	N.S.	N.S.	N.S.
N	74	45	69	40	45

Table 9. Spearman's rank correlation between the number of eggs per aphid and weed density/0.5m2 and wheat stem density; data from all dates and all plots combined. The values represent the calculated r_s values and the corresponding significance level. N = sample size.

	Site 1.		Site 2.	
	Weed.density	Wheat. density	Weed.density	Wheat. density
r_s	-0.011	0.083	0.159	0.083
P	N.S.	N.S.	<.05	N.S.
N	291	291	259	259

of eggs per aphid and weed density (Table 7a). There was no significant relationship between the two variables during the rest of the study. However, there was a significant negative relationship between the number of eggs per aphid and the number of wheat stems during 25-26 May (Table 8b). This represents an opposite trend to that recorded at Side Scammel later in the season. When data from all dates was combined there was no significant relationship between the number of eggs per aphid and weed density, or with the density of wheat stems at either Side Scammel or Mesh Bottom (Table 9).

Headland variables 1990.

On all the sampling dates there were significant differences between the rooted weed densities in the two treatments (Mann-Whitney U; Table 10a). Within individual treatments there were significant differences in weed density among plots (Friedman's two-way analysis by ranks; Table 11a; 13a and according to the transect; Table 12a; 14a).

The total floral area was significantly different between the two treatments on all six sampling dates (Table 10b). In the conservation headland treatment there were significant differences in floral area between the replicates after 7 June (Table 15a). On all the sampling dates there were significant differences in floral area according to the position in the headland (Table 15b). Floral area did not vary significantly between replicates or transects in the fully sprayed treatment (Table 15a,b).

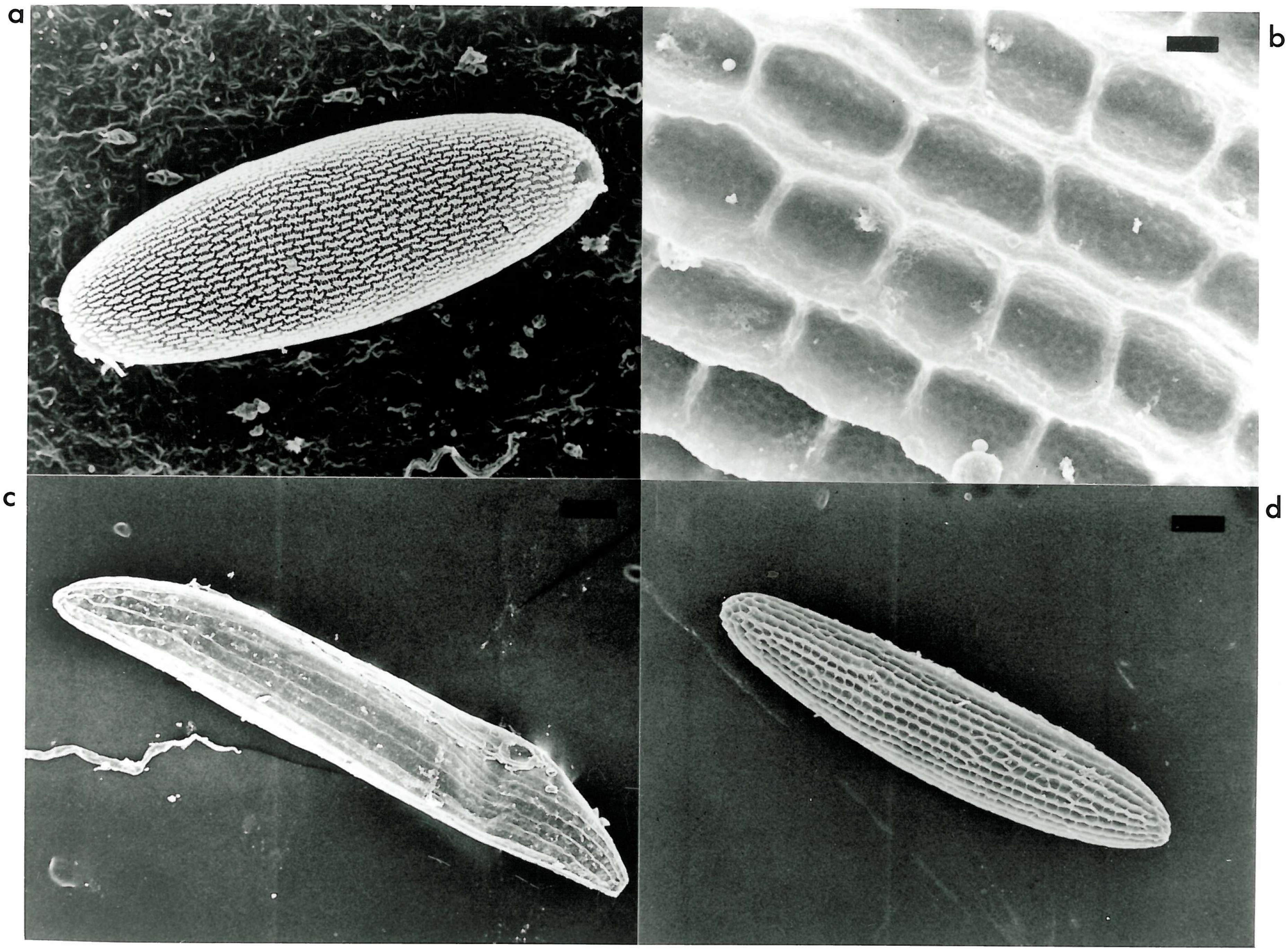
During all the sampling periods prior to 14 June, aphid density per $0.5m^2$, was significantly higher in the conservation headland treatment. The variation between the treatments was significant above and beyond the variation within the treatments (nested ANOVA on transformed data; Table 16). There was significant variation in aphid density among plots on all dates before 14 June (Table 16b). On 7-9 June and 14 June, 2.04% and 1.90% respectively of the total number of aphids in the conservation headland plots occurred on non crop-plants. The aphids comprised pest species, including *S. avenae*, *R. padi* and *M. dirhodum.* Analysis of the relationship between aphid density and weed density showed that after 24 May there was a significant positive correlation between the two variables (Spearman's rank correlation; $r_s = 0.144$, $P = 0.5$, $n = 180$; $r_s = 0.238$, $P<.005$, $n = 180$; $r_s = 0.019$, $P<.05$, $n = 165$).

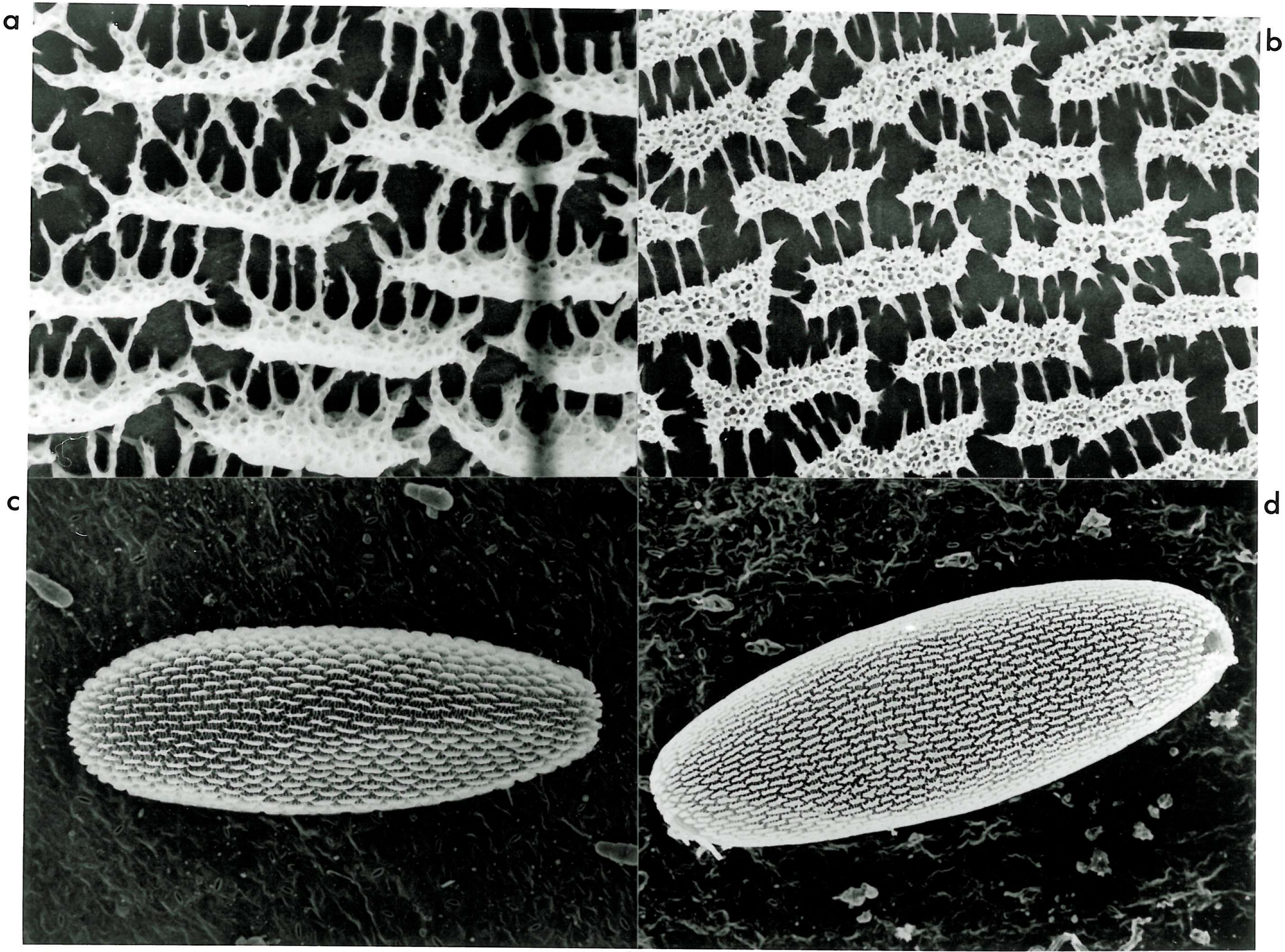
Syrphid eggs

Plates Ia to VIb are scanning electron micrographs of the eggs of eight genera. Plates Ia and IIa to VIb are micrographs of reference specimens; eggs of all the groups, with the exception of *Chrysotoxum cautum*, were recorded in the field. The identity of the eggs was determined from the adult females. Plates Ib, Ic and Id are of field collected specimens. It was not possible to identify the patterning in these plates to species because no *Pipizella* adults were collected in the field and therefore there were no reference specimens for comparison. In addition, the patterning of the exochorion of this genus has not been described in detail in the literature.

Key to S.E.M. plates

Page	Plate	Egg	Magnification
I	a	*E. balteatus*	x100
I	b	*Pipizella* spp. A	x1000
I	c	*Pipizella* spp. B	x100
I	d	*Pipizella* spp. A	x100
II	a	*M. luniger*	x1000
II	b	*E. balteatus*	x1000
II	c	*M. luniger*	x100
II	d	*E. balteatus*	x100
III	a	*Sph. scripta*	x1000
III	b	*M. corollae*	x1000
III	c	*Sph. scripta*	x100
III	d	*M. corollae*	X1000
IV	a	*S. vitripennis*	x80
IV	b	*S. ribesii*	x100
IV	c	*S. vitripennis*	x1000
IV	d	*S. ribesii*	x1000
V	a	*M. scalare*	x200
V	b	*P. peltatus*	x100
V	c	*M. scalare*	x1000
V	d	*P. peltatus*	x1000
VI	a	*C. cautum*	x100
VI	b	*C. cautum*	x1000


a
b
c
d



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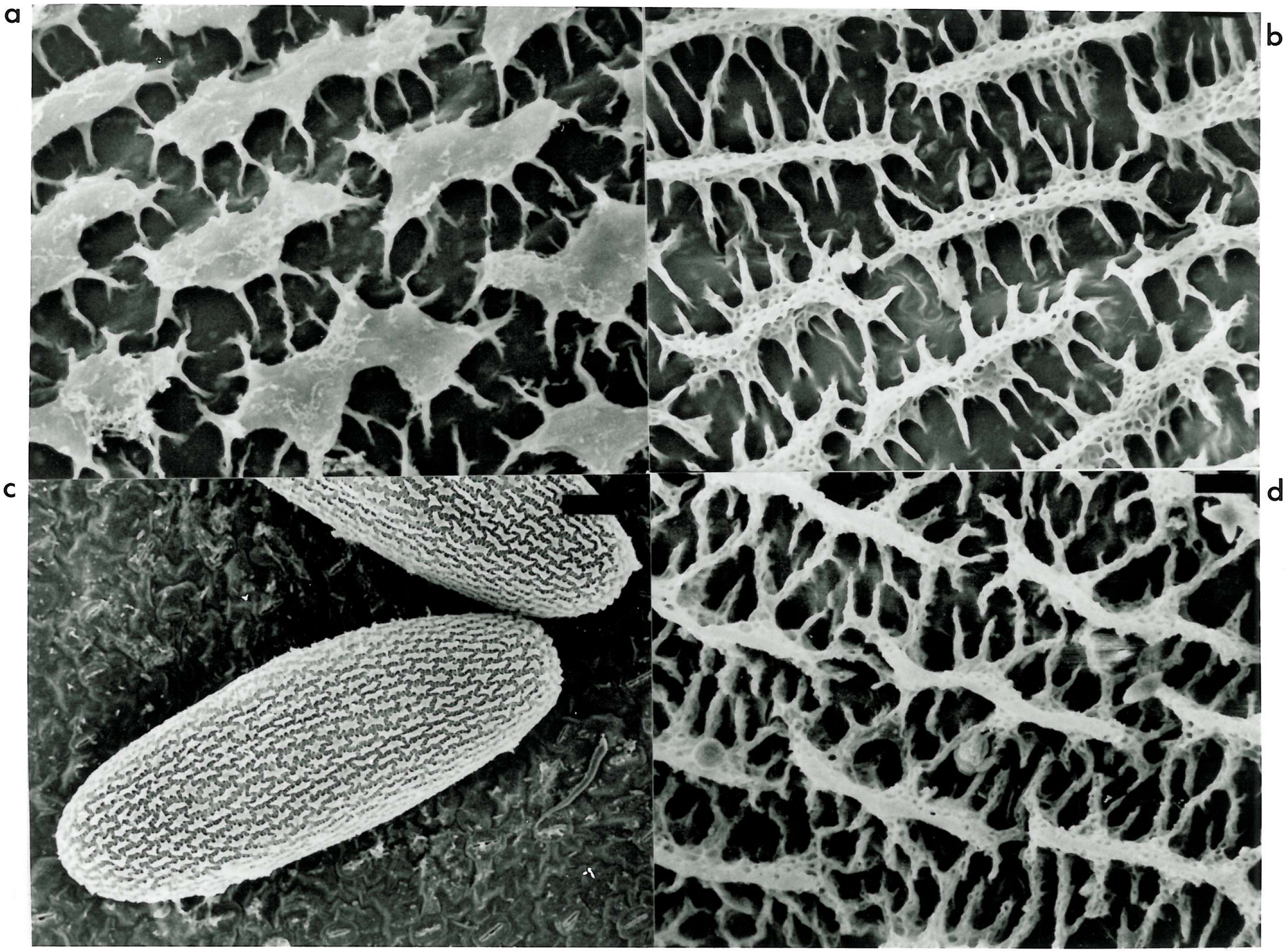

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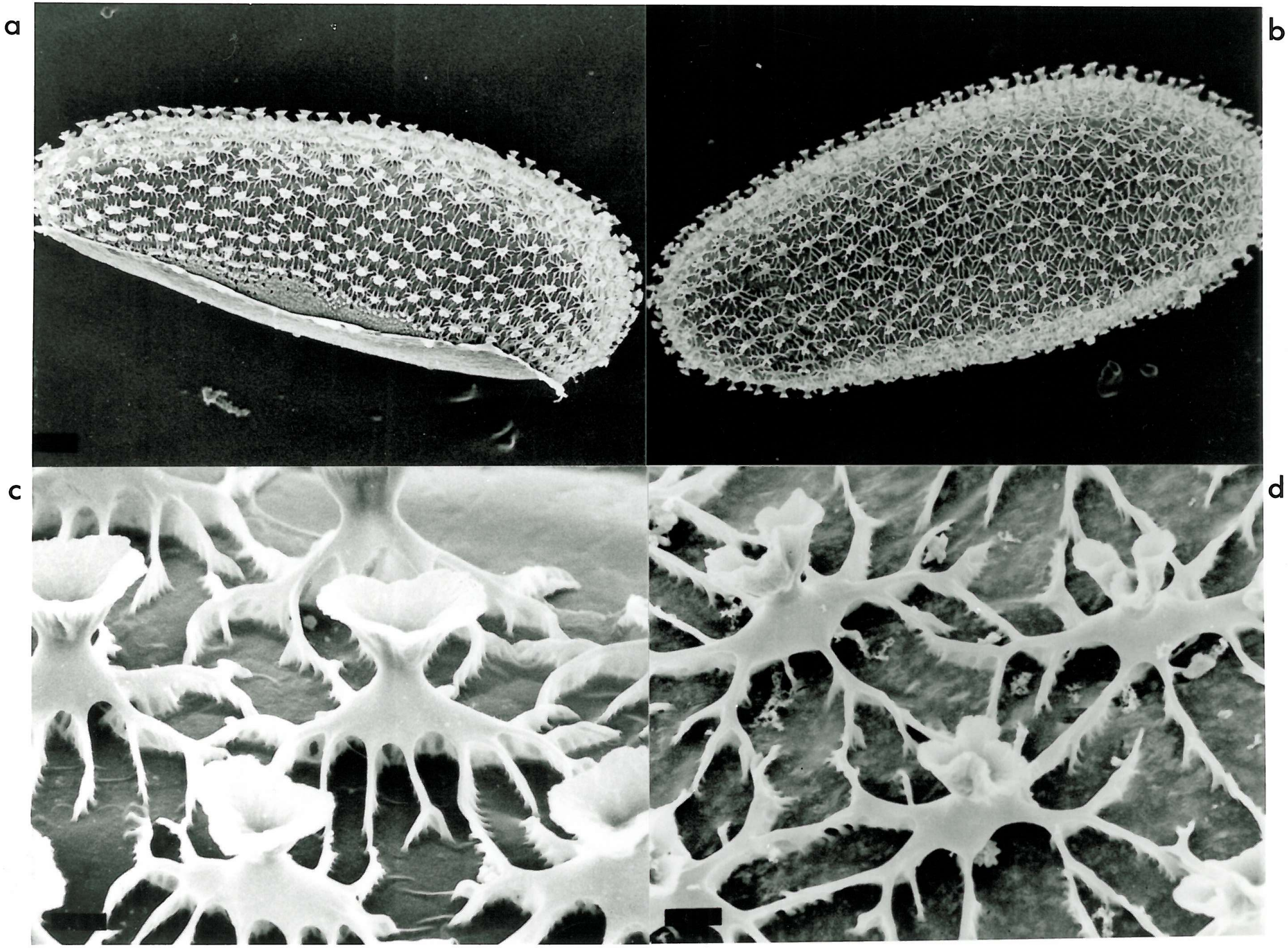

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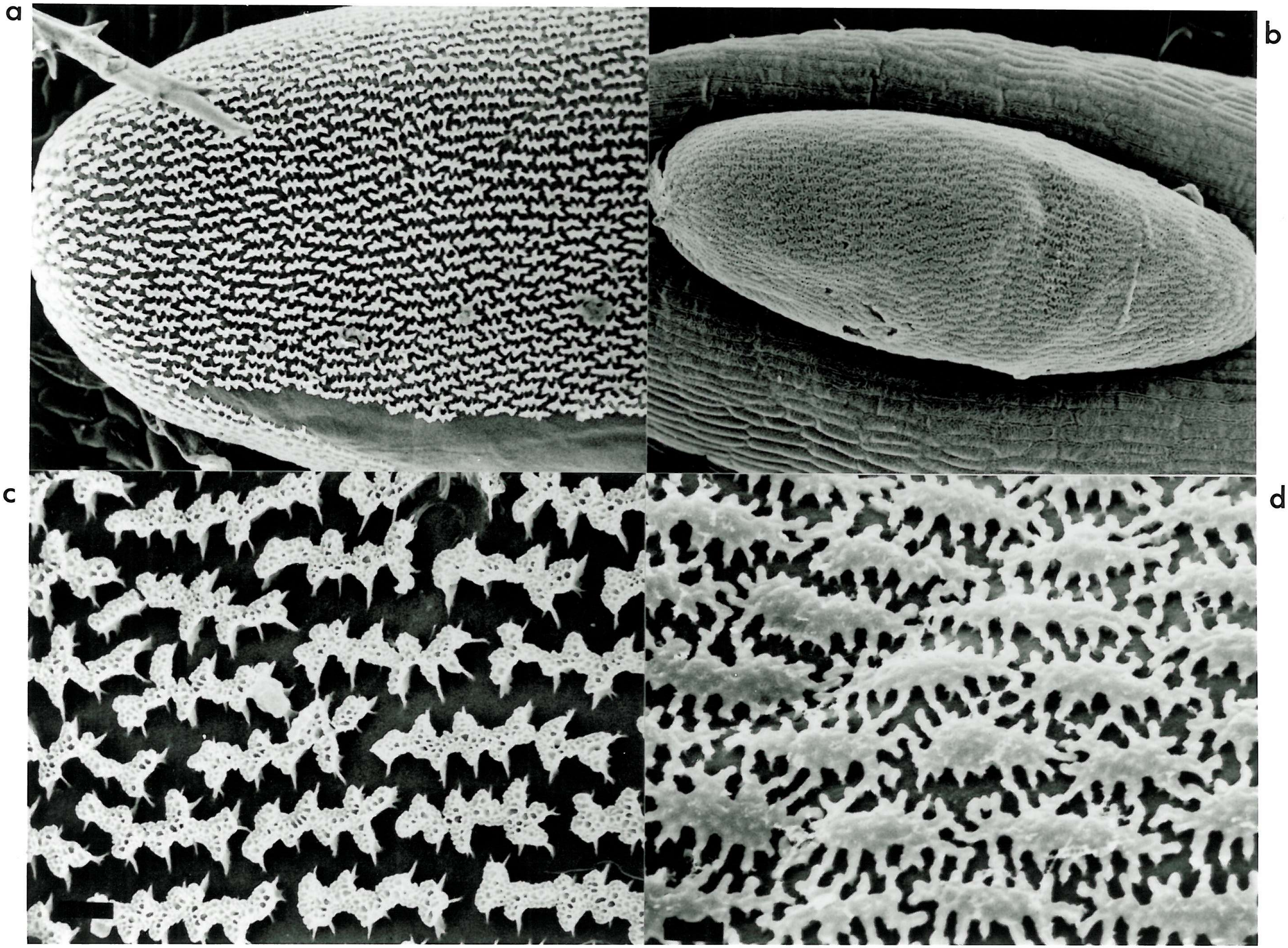
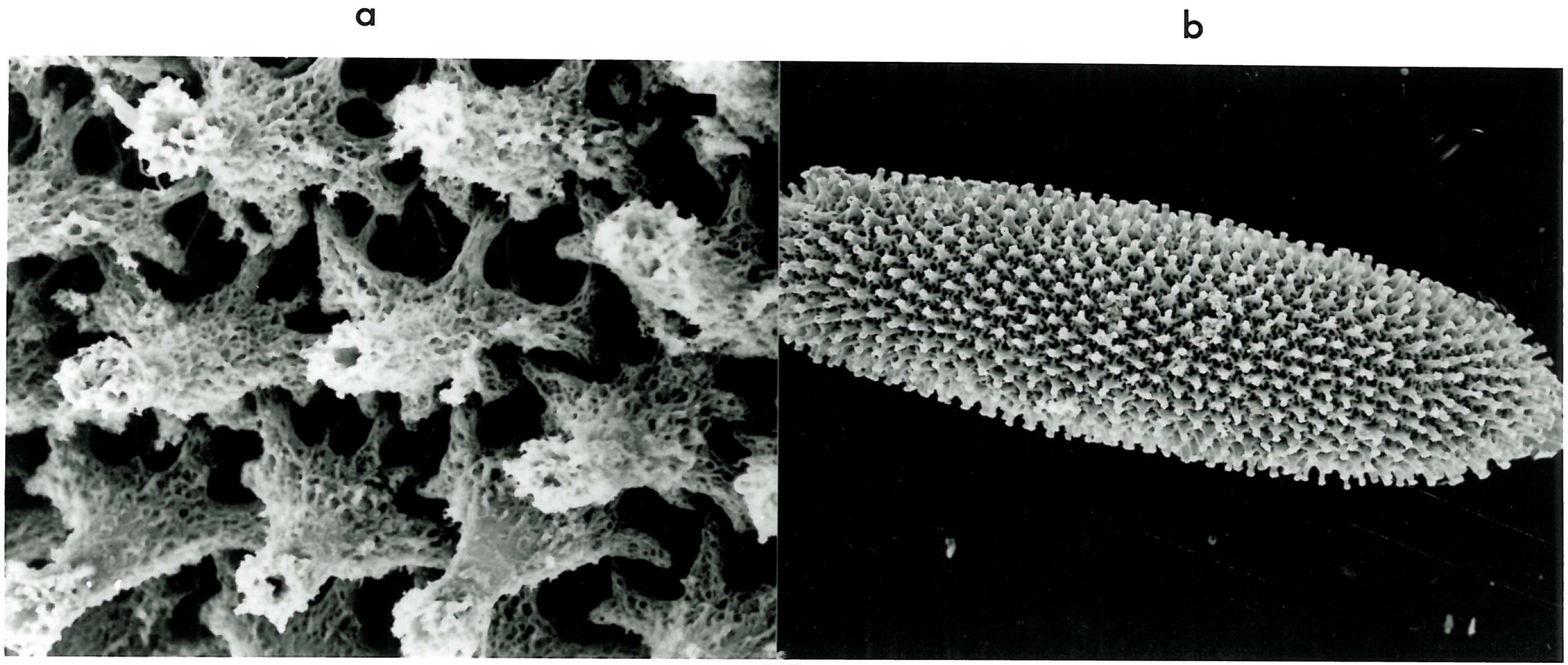


V



VI

Table 10. Mann-Whitney U test on (a)weed density/0.5m^2 (b)total weed cover/0.5m^2 (c)total number of *Episyrphus* eggs/0.5m^2 (d)total number of *Metasyrphus* eggs/0.5m^2 (e)total number of *Pipizella eggs/0.5m^2*, during the 5 sampling periods between 13 May-14 June.

	Date				
	13 - 14 May	22 - 24 May	2 4 June	7 9 June	14 June
Weed density/05m^2					
Treatment	Average rank	Average rank	Average rank	Average rank	Average rank
Conservation headland	141.714	124.717	126.139	126.289	117.387
Fully Sprayed headland	69.286	56.283	54.861	54.711	54.344
Test statistic	-9.205	-9.427	-9.760	-9.704	-9.205
P	<.001	<.001	<.001	<.001	<.001
(b)Total floral area mm_2/0.5m^2					
Treatment	Average. rank	Average rank	Average rank	Average rank	Average rank
Conservation headland	66.5	113.0	118.5	117.00	117.2
Fully sprayed headland	44.00	68.00	62.500	64.00	54.5
Test statistic	-5.643	-7.618	-8.787	-8.470	-9.894
P	<.001	<.001	<.001	<.001	<.001
(c)Total number of *Episyrphus* eggs/0.5m^2					
Treatment	Average rank	Average rank	Average rank	Average rank	Average rank
Conservation headland	52.500	90.994	90.500	94.656	85.833
Fully sprayed headland	53.330	90.006	90.500	86.344	80.639
Test statistic	0.797	-0.376	0.00	-1.880	-1.155
P	N.S.	N.S.	N.S.	N.S.	N.S.
(d)Total number of *Metasyrphus* eggs/0.5m^2					
Treatment	Average rank	Average. rank	Average rank	Average rank	Average rank
Conservation headland	53.75	89.500	93.011	87.944	81.82
Fully sprayed Headland	52.50	91.500	87.989	93.056	83.983
Test statistic	-1.205	1.410	-1.263	0.953	0.375
P	N.S.	N.S.	0.054	N.S.	N.S.
(e)Total number of *Pipizella* eggs/0.5m^2					
Treatment	Average rank	Average rank	Average rank	Average rank	Average rank
Conservation headland	52.976	95.383	91.594	92.967	82.367
Fully sprayed headland	53.016	85.617	89.406	88.033	83.528
Test statistic	0.004	-1.568	-0.380	-0.930	0.278
P	N.S.	N.S.	N.S.	N.S.	N.S.
(f)Total number of "aphidophagous" eggs per aphid/0.5m^2					
Treatment	Average rank	Average rank	Average rank	Average rank	Average rank
Conservation headland	49.333	87.856	97.533	94.839	91.540
Fully sprayed headland	55.44	93.144	83.467	86.161	75.883
Test statistic	1.566	0.909	-2.233	-1.187	-2.168
P	N.S.	N.S.	<.05	N.S.	<.05

Table 11. The within-treatment variation in headland variables.
Friedman's two-way analysis by ranks on weed density, aphid density and the number of identified syrphid eggs in the fully sprayed headland treatment on the five sampling dates.
Data was tested for homogenity among plots.

(a) Weed density/0.5m^2

	Date				
	13 -14 May	22- 24 May	2- 4 June	7- 9 June	14 June
Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
1	2.905	2.778	2.528	2.944	2.972
3	3.048	3.222	3.389	3.222	3.139
5	2.52	2.528	2.917	2.972	3.028
7	3.357	3.222	3.222	3.139	3.167
9	3.167	3.250	2.944	2.722	2.694
Test statistic	7.462	11.832	7.972	2.791	4.779
P	N.S.	<.05	N.S.	N.S.	N.S.

Total number of *Episyrphus* eggs/0.5m^2

Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
1		3.056	3.056	3.361	2.722
3		3.028	3.194	2.944	2.861
5		3.083	3.056	2.944	3.00
7		2.917	2.917	2.944	3.556
9		2.917	2.778	2.806	2.861
Test statistic	+	2.462	3.714	7.077	11.00
P		N.S.	N.S.	N.S.	<.05

Total number of *Metasyrphus* eggs/0.5m^2

Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
1		2.944	2.972	3.194	3.167
3		3.083	2.972	2.583	2.444
5		3.083	3.111	2.944	3.361
7		2.944	2.972	3.25	3.00
9		2.944	2.972	3.028	3.028
Test statistic	+	3.0	4.0	4.235	5.884
P		N.S.	N.S	N.S.	N.S.

Total number of *Pipizella* eggs/0.5m2

Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
1		3.528	2.944	3.0	3.00
3		3.134	3.028	3.278	2.972
5		2.750	2.972	2.583	2.972
7		3.222	3.194	3.417	3.222
9		2.361	2.861	2.722	2.833
Test statistic	+	12.046	1.0	10.656	2.125
P		<.05	N.S	<.05	N.S

On dates marked with + there was insufficient data to allow statitical analysis of the within treatment variation in the headland variables.

Table 12. The within-treatment variation of headland variables.
Friedman's two-way analysis by ranks on weed density and the number of identified syrphid eggs in the fully sprayed headland treatment on the five sampling dates.
Data was tested for homogenity among transects.

Date

(a) Weed density/0.5m^2

Transect	13- 14 May Average rank	22-24 May Average rank	2- 4 June Average. rank	7- 9 June Average rank	14 June Average rank
Hedgerow edge	2.686	2.567	2.567	2.583	2.5
Mid headland	1.657	1.717	1.717	1.717	1.75
Tramline	1.657	1.717	1.717	1.700	1.75
Test statistic	48.00	34.00	34.00	33.418	30.00
P	<.001	<.001	<.001	<.001	<.001

(b) Total number of *Episyrphus* eggs/0.5m^2

Transect	Average rank	Average rank	Average rank	Average. rank	Average rank
Hedgerow edge	1.976	1.95	1.967	2.033	2.033
Mid headland	2.048	2.00	2.067	2.033	1.983
Tramline	1.976	2.05	1.967	1.933	1.983
Test statistic	2.00	2.00	1.143	1.333	0.25
P	N.S.	N.S.	N.S.	N.S.	N.S.

(c) Total number of *Metasyrphus* eggs/0.5m^2

Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow	2.00	2.017	2.033	1.817	2.017
Mid land	2.00	1.967	1.983	2.100	2.017
Tramline	2.00	2.017	1.983	2.0833	1.967
Test statistic	1.00	1.0	2.0	3.569	0.092
P	N.S.	N.S.	N.S.	N.S.	N.S.

(c) Total number of *Pipizella* eggs/0.5m^2

Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow	2.381	2.217	2.283	2.150	2.167
Mid headland	1.976	1.917	1.867	1.950	1.967
Tramline	1.643	1.867	1.850	1.900	1.867
Test statistic	9.64	5.059	8.68	3.5	6.222
P	<.001	N.S.	<.05	N.S.	<.05

Table 13. The within-treatment variation in headland variables.
Friedman's two-way analysis by ranks on weed density and the number of identified syrphid eggs in the conservation headland treatment on the five sampling dates.
Data was tested for homogenity among plots.

	Date				
	13-14 May	22-24 May	2-4 June	7-9 June	14 June
(a) Weed density/0.5m^2					
Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
2	2.761	2.861	3.139	2.306	2.067
4	2.833	2.556	2.500	2.861	2.800
6	3.548	3.667	3.583	4.306	4.100
8	3.310	3.417	3.111	3.167	3.467
10	2.548	2.500	2.667	2.361	2.567
Test statistic	6.132	8.174	5.605	19.792	17.227
P	N.S.	N.S.	N.S.	<.001	<.001
(b) Number of *Episyrphus* eggs/0.5m^2					
Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
2		3.028	3.056	3.000	2.567
4		3.167	3.194	2.583	3.267
6		3.028	3.056	3.167	2.900
8		2.889	2.917	3.222	3.200
10		2.889	2.778	3.028	3.067
Test statistic	+	3.5	4.333	5.216	5.036
P		N.S.	N.S.	N.S.	N.S.
(c)Number of *Metasyrphus* eggs/0.5m^2					
Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
2		2.944	2.972	3.139	2.400
4		3.083	2.833	3.111	2.733
6		3.083	2.972	3.000	3.433
8		2.944	3.389	3.167	3.300
10		2.944	2.833	2.583	3.133
Test statistic	+	3.00	9.00	4.409	8.898
P		N.S.	N.S.	N.S.	N.S.
(d) Number of *Pipizella* eggs/0.5m^2					
Replicate	Average rank	Average rank	Average rank	Average rank	Average rank
2		2.861	2.639	3.028	2.733
4		3.417	3.056	3.444	2.900
6		3.083	3.278	2.833	3.067
8		3.111	3.278	2.611	3.067
10		2.528	2.750	3.083	3.233
Test statistic	+	4.681	9.00	6.468	3.467
P		N.S.	N.S.	N.S.	N.S

On dates marked + there was insufficient data to allow statistical analysis of the within treatment variation.

Table 14. The within-treatment variation in headland variables.
Friedman's two-way analysis by ranks on weed density and the number of identified syrphid eggs in the conservation headland treatment on the five sampling dates.
Data was tested for homogenity among transects.

			Date		
	13-14 May	22-24 May	2-4 June	7-9 June	14 June
(a) Weed density/0.5m^2					
Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	2.571	2.500	2.600	2.583	2.700
Mid headland	2.271	2.450	2.333	2.317	2.080
Tramline	1.157	1.050	1.067	1.100	1.220
Test statistic	39.151	43.168	42.761	38.479	29.699
P	<.001	<.001	<.001	<.001	<.001
(b) Total number of *Episyrphus* eggs/0.5m^2					
Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	21.500	1.933	1.967	2.017	2.080
Mid headland	21.500	2.083	2.117	2.033	1.940
Tramline	21.500	1.983	1.917	1.950	1.980
Test statistic	1.00	3.500	3.714	0.378	0.765
P	N.S.	N.S.	N.S.	N.S.	N.S.
(d) Total number of *Metasyrphus* eggs/0.5m^2					
Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	21.000	2.000	2.017	1.900	2.000
Mid headland	22.500	2.000	1.983	2.050	1.960
Tramline	21.000	2.000	2.000	2.050	2.040
Test statistic	2.00	1.00	0.125	1.636	0.20
P	N.S.	N.S.	N.S.	N.S.	N.S.
(e) Total number of *Pipizella* eggs/0.5m^2					
Transect	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	21.964	2.067	2.050	2.033	1.960
Mid headline	23.214	2.017	2.117	2.000	2.080
Tramline	19.321	1.917	1.833	1.967	1.960
Test statistic	1.011	0.737	2.678	0.170	1.00
P	N.S.	N.S.	N.S.	N.S.	N.S.

Table 15(a). Friedman's two-way analysis by ranks on total floral area/0.5m^2 among conservation headland and fully sprayed plots. (N= sample size).

		Date				
		13-14 May	22-24 May	2-4 June	7-9 June	14 June
		Average rank	Average rank	Average rank	Average rank	Average rank
Conservation headland						
Replicate	2	3.238	3.361	3.306	2.111	1.867
	4	2.929	2.527	2.167	2.944	2.067
	6	3.048	3.333	3.361	3.833	3.900
	8	2.595	2.500	3.389	3.556	4.333
	10	3.191	3.278	2.778	2.556	2.833
Test statistic		2.774	7.628	8.735	16.050	31.458
P		N.S.	N.S.	N.S.	<.005	<.005
N		(21)	(18)	(18)	(18)	(15)
Fully sprayed headland						
Replicate	1	3.000	3.000	3.000	3.000	3.000
	3	3.000	3.000	3.000	3.000	3.000
	5	3.000	3.000	3.000	3.000	3.000
	7	3.000	3.000	3.000	3.000	3.000
	9	3.000	3.000	3.000	3.000	3.000
Test statistic		1.000	1.000	3.000	3.000	3.000
P		N.S.	N.S.	N.S.	N.S.	N.S.
N		(21)	(18)	(18)	(18)	(18)

Table 15(b). Friedman's two-way analysis by ranks on total floral area/0.5m^2 among transects of the conservation headland and fully sprayed headland treatments. (N= sample size).

Conservation headland	Average rank	Average rank	Average rank	Average rank	Average rank
Hedgerow edge	2.429	2.200	2.433	2.350	2.360
Mid-headland	2.157	2.417	2.300	2.283	2.440
Tramline	1.414	1.383	1.267	1.367	1.200
Test statistic	26.233	21.816	26.691	21.314	24.517
P	<.001	<.001	<.001	<.001	<.001
N	(35)	(30)	(30)	(30)	(30)
Fully sprayed headland					
Hedgerow edge	2.000	2.000	2.000	2.000	2.000
Mid-headland	2.000	2.000	2.000	2.000	2.000
Tramline	2.000	2.000	2.000	2.000	2.000
Test statistic	1.000	1.000	1.000	1.000	1.000
P	N.S.	N.S.	N.S.	N.S.	N.S.
N	(35)	(30)	(30)	(30)	(30)

Table 16(a). The variation in aphid density/0.5m^2 among treatments, plots within treatments and transects within plots determined by nested analysis of variance. On dates marked with an * the raw data was transformed by taking the square root of aphid density. For the remaining dates the data was normalised using a log (n+1) transformation.

	Date											
	22-24 May *			2-4 June			7-9 June			14 June*		
Source of variation	Mean square	F_s	P	Mean square	F_s	P	Mean sqaure	F_s	P	Mean square	F_s	P
Among treatments	21.80.51	1313.80	<.001	359.71	3472.42	<.001	465.59	5276.75	<.001	10330.92	1458.51	<.001
Among plots within treatments	18.51	11.15	<.001	1.69	16.35	<.001	0.81	9.13	<.001	8.46	1.19	N.S.
Transects within plots	1.87	1.13	N.S.	0.9	0.89	N.S.	.07	0.80	N.S.	8.53	1.20	N.S.
(respective df's)	(1,4,20)			(1,4,20)			(1,4,20)			(1,4,20)		

(b) The variation in aphid density among conservation headland plots.
One-way analysis of variance was used to identify heterogenity among the plots. Homogeneous groups determined using Tukey's test, are represented by the same letter.

	22 -24 May		2-4 June		7 -9 June	
Plot	Mean	F-ratio	Mean	F -ratio	Mean	F -ratio
2	1.190 a	6.185	5.899 a	6.838	1.989 a	8.159
4	1.067 ab	<.001	6.178 a	<.001	1.596 ab	<.001
6	1.192 a	(4,94 df)	6.732 a	(4,88 df)	4.279 ab	(4,74 df)
8	1.059 ab		6.240 a		1.639 ab	
10	0.769 b		3.618 b		1.384 b	

(d) The variation in aphid density among fully sprayed plots.
One-way analysis of variance was used to identify heterogenity among the plots. Homogeneous groups determined by Tukey's test, are represented by the same letter, with a being the group with the highest aphid density.

Plot	Mean	F -ratio	Mean	F -ratio	Mean	F -ratio
1	3.720 a	6.315	5.217 a	10.371	1.609 a	4.570
3	3.886 a	<.001	5.833 a	<.001	1.357 b	<.05
5	3.767 a	(4,89 df)	5.483 a	(4,87 df)	1.512 ab	(4,88 df)
7	3.019 ab		6.562 a		1.692 a	
9	1.904 b		3.551 b		1.517 ab	

The distribution of identified eggs.

A total of 939 eggs were recorded during the period 11 May to 14 June. Fig. 8(b) shows the composition of the identified eggs which were collected during the study. The eggs were identified to genus. Fig.8(c) shows the distribution of the eggs of the seven commonly occurring genera between the ten headland plots. No eggs were recorded before the 11 May 1990. It is probable that eggs were present in the crop before this date but they occurred in such low numbers that they were not detected.

Eggs of the genus *Pipizella* accounted for greater than 50% of all the eggs during the period 13 May to 4 June. The remaining eggs comprised representatives of the genera *Episyrphus* and *Metasyrphus*; *Syrphus* and *Melanostoma* eggs were also recorded during four of the sampling periods. The distribution of the eggs of the three most commonly occurring genera did not differ significantly between the two treatments on any of the sampling dates (Mann Whitney U; Table 11c,d,e). Fig. 9 shows the distribution of the eggs according to their position in the headland plots. Analysis of the distribution of eggs within individual treatments showed that during three sampling periods (13-14 and 2-4 June and 14 June) there were significant differences in the number of *Pipizella* eggs recorded at the three positions within the sprayed plots, with higher numbers of eggs being recorded at the hedgerow edge (Table 14d). During the two remaining sampling periods there was a significant difference in the number of *Pipizella* recorded in the five fully sprayed plots; however, there was no constancy with regard to the replicate containing the highest number of eggs (Table 13d). In the conservation headland treatment there were significant differences in the number of *Pipizella* eggs between the replicates on 13-14 May (Table 11d). No differences in egg density between the hedgerow edge, mid headland and tramline were recorded (Table 12d).

The number of *Episyrphus* eggs recorded among the fully sprayed plots was significantly different on 14 June (Table 13b). Eggs belonging to the remaining group, *Metasyrphus* species, did not vary within the treatments on any of the sampling dates.

In Fig. 10 the eggs of the four most commonly occurring genera are classified according to the number laid, whether they were recorded on the crop or from non crop plants and whether they occurred in close proximity to aphid colonies. From the figure it can be seen that eggs belonging to the genus *Pipizella* tended to occur singly on wheat plants in the absence of aphids. *Metasyrphus* eggs invariably occurred on wheat plants, usually in close proximity to aphid colonies; there was often more than one egg per ear. *Episyrphus* eggs also invariably occurred on wheat plants; however, there tended to be a single egg laid in close proximity to aphid colonies. Analysis of the distribution of identified syrphid eggs with respect to aphid density showed that on two of the five sampling dates there was a significant positive relationship between the numbers of *E. balteatus* eggs and aphid density (Spearman's rank correlation; Table 17). *Metasyrphus* eggs also showed the same positive relationship on two of the sampling dates. However, the distribution of *Pipizella* eggs was not related to aphid density on any of the dates. Eggs of the remaining genera occurred in insufficient numbers to allow statistical analysis of the data.

Melanostoma eggs tended to occur on non-crop plants, with or without aphids. On the five sampling

Table 17. Spearman's rank correlation on the relationship between number of "aphidophagous" eggs per aphid/0.5m^2 and weed density/0.5m^2. For each of the five sampling periods data from the two treatments were combined. The values represent the calculated r_s values and the corresponding significance level. N = sample size.

	Date				
	13-14 May	22-24 May	2-4 June	7-9 June	14 June
r_s	.004	-.051	.161	.188	.155
P	N.S.	N.S.	<.05	<.05	0.054
N	105	173	178	180	165

Table 17(a). Spearman's rank correlation on the relationship between the total number of eggs/0.5m^2 and aphid density. The values represent the calculated r^s values for the three most commonly occuring groups of eggs. For each of the five sampling periods data from the two treatments were combined. N = sample size.

	Date				
	13-14 May	22-24 May	2-4 June	7-9 June	14 June
Episyrphus					
r_s	.160	.087	.178	.187	.138
P	N.S.	N.S.	N.S.	<.05	N.S.
Metasyrphus					
r_s	-.072	.092	.043	.264	.218
P	N.S.	N.S.	N.S.	<.001	N.S.
Pipizella					
r_s	.089	.069	.053	-.038	-.08
P	N.S.	N.S.	N.S.	N.S.	N.S.
N	105	180	180	180	165

dates the number of identified eggs which were recorded from weeds in the conservation headland treatment comprised 8.45, 4.57, 4.58, 2.04, 1.90 % of the total number of eggs respectively. During each period over 80% of these eggs were identified as belonging to the genus *Melanostoma*.

Eggs which were identified as belonging to genera known to have aphidophagous larvae were pooled for further analysis. This included all the commonly occurring eggs except those belonging to the genus *Pipizella*. The pooled value was used to calculate the number of "aphidophagous" eggs per aphid. On 31 May and 14 June there were significantly more aphidophagous eggs in the conservation headland treatment (Mann Whitney U; Table 10f). Analysis of the correlation between the number of aphidophagous eggs per aphid and weed density showed that during June there was a trend towards higher numbers of eggs per aphid in the weedier plots (Table 17). On both these dates there was a significant positive correlation between the number of aphidophagous eggs per aphid and aphid density (Spearman's rank correlation; $r_s = 0.2279$, $P<.005$; $r_s = 0.1732$, $P<.05$).

Analysis of the distribution of *Pipizella* eggs showed that during 22-24 May and 2-4 June there was a significant association between the presence of *Galium aparine* plants and the occurrence of *Pipizella* eggs ($\chi^2 = 13.161$, $P <.001$, d.f=1; $\chi^2 = 5.675$, $P <.05$, d.f=1).

Discussion

In both years there were significant differences in aphid density between the conservation and fully sprayed treatments; higher aphid densities were recorded from the conservation headland plots. The presence of aphids on the non-crop plants at the base of the crop was at least in part responsible for these differences. During the initial period of the study it might have been expected that higher densities of aphids would occur in the fully sprayed plots; the presence of weeds has been shown to reduce the attractiveness of the crop to immigrant alates resulting in lower rates of colonisation than in weed-free crops (Smith, 1976). In the present study weeds may not have been present in sufficient densities to effect a distinct difference in crop background between the two treatments.

The identification of the syrphid eggs collected during 1990 showed that *E. balteatus* and *Metasyrphus* species were numerically important. However, *Pipizella* eggs were also recorded in large numbers, especially during May. This is the first time that eggs of this genus have been recorded from arable crops. *Pipizella* adults were not recorded during the standard census walks. This may be due to the fact the flies are relatively small and inconspicuous. They have been recorded flying very low among short grass and above bare patches of earth, their erratic searching flight mimicking that of a small black wasp (Stubbs and Falk 1983).

On several dates there were higher numbers of *Pipizella* eggs recorded from the hedgerow edge than from the mid headland and tramline edge in the fully sprayed plots; this area contained the highest density of weeds. There were no differences in the numbers of *Pipizella* eggs among the transects in the conservation headland plots. These results suggest that the site of oviposition in this group was to some extent influenced by the presence of weeds in the crop. This might be associated with the observation that the flies fly low among short grasses (Stubbs and Falk 1983). The most commonly occurring member of the genus, *P. varipes* has been found to have "a particular liking for *Galium* flowers" although it can also be found on other low growing flowers (Stubbs and Falk, 1983). *Galium aparine* was one of the commonest arable weeds recorded from the hedgerow edge in this study. Analysis of the distribution of *Pipizella* eggs showed a significant association between the presence of this weed and the occurrence of eggs at the end of May and during early June. This association may explain the variation in the number of eggs among plots and transects of the fully sprayed treatment. The observed differences may have reflected the distribution of *G. aparine* plants although the plants were not oviposition sites; the majority of *Pipizella* eggs were recorded from wheat plants and grasses.

Pipizella larvae have been recorded utilising subterranean root aphids as prey. Dixon (1959) showed that *P. varipes* tended to select oviposition sites in the bases of stems of *Pastinaca sativa*. The roots of the plants were infested with *Anuraphis subterranea* just below soil level. Stubbs and Falk (1983) suggested an association between *P. virens* larvae and aphids on the roots of the umbellifer, *Anthriscus sylvestris*. In this study *Pipizella* eggs were recorded from wheat plants without subterranean aphid colonies; in addition there were no umbellifers within the immediate vicinity (< 5metres) of the oviposition sites.

The observation that *Pipizella* larvae probably only feed on root aphids suggests that their occurrence in large numbers within the headland has little significance for the biological control of cereal aphids by syrphids. In addition, it is probable that their occurrence in the crop is atypical; the presence of the adults in close proximity to arable land may have been due to the adjacent non-crop areas, in particular the wide shelterbelt which contained a range of herbaceous and woody plant species. A survey covering a wider range of fields and field margin types would clarify this point.

During 1989 there was no significant difference in the number of eggs per aphid between the two treatments during any of the sampling periods. However, there were significant differences among the conservation headland plots during 30 May-1 June; the highest numbers of eggs per aphid were recorded from the weediest plot. During this period there was no significant difference in aphid density among the conservation headland plots; therefore it seems unlikely that the higher number of eggs per aphids reflects a positive reproductive numerical response to aphid density by female flies.

During 2-4 June and 14 June 1990 higher numbers of aphidophagous eggs per aphid were recorded from the conservation headland treatment than the fully sprayed treatment. This may have been a result of a positive reproductive numerical response; since there were significantly higher aphid densities within these plots and a positive correlation between aphid density and the number of eggs per aphid was recorded. Both the number of *Episyrphus* and *Metasyrphus* eggs was positively correlated with aphid density during 7-9 June. In addition, the records of higher numbers of eggs per aphid in the conservation headland plots also coincided with a period when *Melanostoma* eggs were recorded predominantly from weed species, in particular corn poppy, *Papaver rhoeas*. These eggs also contributed to the higher levels of oviposition in conservation headland plots during early June, 1990.

Smith (1976) suggested that weeds may indirectly influence syrphid oviposition by altering plant density, height, contrast or colour of the background, thus affecting the optical attractiveness of the crop (Banks 1959, Dixon 1959, Peschken 1964, van Emden 1965). However, the results reported in this study may reflect a direct effect of the presence of weeds, as oviposition sites for phytozetic species, such as *Melanostoma*.

Smith (1969, 1976) showed that oviposition by *Melanostoma* species was usually much greater in plots of Brussels spouts containing weeds than in weed-free plots. In particular their eggs were very abundant on weeds and were frequently laid on aphid-free plants. Fig. 6 shows that from the beginning of June onwards the majority of *Melanostoma* eggs recorded in the present study occurred on non crop plants. Some of the *Melanostoma* eggs were laid on plants which were not infested with aphids; on hatching the larvae would be capable of moving to adjacent plants, including wheat plants, in search of aphid prey (Sol 1966).

The agronomic consequences and economic costs of adopting the conservation headlands technique have been described by Boatman and Sotherton (1988). The growth of weeds within the headlands is acceptable to farmers because of the reduced yields normally associated with these areas (Boatman and Sotherton, 1988). In addition, farmers receive benefits in terms of the enhanced game bird chick survival which is associated with this technique (Rands 1985,1986). The weed densities which occur in conservation headlands would be unacceptable in the rest of the crop because of the consequent interference with harvesting operations and the contamination of the grain, in addition to reductions in yield and grain quality. Therefore, the benefits in terms of enhanced syrphid oviposition, as a result of the presence of weeds such as *P. rhoeas*, are likely to remain restricted to conservation headlands.

More generally, although imperfect control of weeds has been shown to result in higher populations of natural enemies in a variety of crops (eg., cereals Speight & Lawton 1976, Vickerman 1974, Powell *et al* 1981, 1985, 1986) the absence of information about the effect of weed species on current and future crops (Orson 1990) means that it is unlikely that farmers will tolerate substantial densities of weeds within the crop. The perceived and real losses attributable to poor weed control will outweigh any benefits which might be gained from a reduction in insect pest colonisation and increases in predator densities or in levels of oviposition.

An alternative approach which may have potential for manipulating syrphid oviposition behaviour within spring crops is undersowing. The benefits of undersowing include the suppression of weeds and reductions in the level of pest populations. Dempster and Coaker (1974) showed that there were larger populations of predatory arthropods in Brussels sprouts undersown with white clover than in the same crop gown in bare ground. In addition there was reduced survival of *P. rapae* larvae in the undersown plots. Potts (1977) reported experiments in which predatory arthropods comprised nearly

43% of the insect fauna in an undersown cereal field compared with 28% under cereal monoculture. Studies on integrated management systems in arable farming in West Germany (El Titi, 1982) have shown that trefoil (*Medicago lupulina*) or red clover (*Trifolium pratense*) sown in wheat reduced the density of cereal aphids; in some years reductions to levels below the economic threshold were recorded (Wipperfuerth 1983 and Gross-Wichtrup 1984). Powell (unpublished) released the aphid *Metopolophium festucae* onto rye grass (undersown in wheat) containing larvae of the parasitoid *Aphidius uzbekistanicus*; as a result parasitoids were already established throughout the cereal fields by the time *S. avenae* colonised the cereals. *S. avenae* populations were smallest in the plots which had developed the largest *M. festucae* populations in the spring.

The potential for the use of undersowing as a technique to enhance syrphid oviposition will be determined by the plant-related factors which are important in stimulating the flies to oviposit. Smith (1976) has shown that although both *Platycheirus* species and *Melanostoma* species are phytozetic they show different oviposition responses. Oviposition by *Platycheirus* species was inconsistent; more eggs were recorded on sprouts than on weeds in July but the trend was reversed during August and September. *Melanostoma* eggs occurred on weeds in high numbers throughout the study; oviposition on weeds was principally on *Chenopodium album, R. raphanistrum* and *Sinapsis arvensis* (Smith 1976). In the present study *Melanostoma* eggs were recorded predominantly on *P. rhoeas*. These results indicate that plants from several different families are acceptable as oviposition sites for these flies. Further studies are required to supplement the work by Chandler (1968a,b); to examine in more detail the plant-related factors which are important in stimulating oviposition by different species of phytozetic syrphids. Such information would make it possible to identify appropriate non-crop plants which would be agronomically acceptable to farmers for undersowing in spring cereals and may also provide additional information on which non-crop plants occurring in winter cereals are likely to be suitable as oviposition sites for the flies. Since winter cereals predominate in the UK the latter information will be particularly important, especially with the current trend towards lower input agriculture (Unwin, 1990). An understanding of the potential benefits of the presence of non-crop plants in terms of enhanced natural enemy action may affect the calculation of economic thresholds for certain weed species within cereal crops.

The effectiveness of the larvae of *Melanostoma* and *Platycheirus* larvae as aphid predators has not been studied although Rotheray (1983) compared the feeding behaviour of *M. scalare* with that of the obligate aphidophage *S. ribesii*. For each instar *S. ribesii* had higher capture efficiencies and shorter handling times than *M. scalare*. He concluded that the larvae of facultatively aphidophagous species such as *M. scalare* are less efficient predators than obligate aphidophages. In addition, on the basis of field survey results and surveys of the literature he suggested that aphids may be relatively unimportant in the diet of such facultatively aphidophagous species. This is in contrast to the observations of Dean (1982) who recorded *Platycheirus* larvae (mainly *P. manicatus*) attacking aphids (mainly *Brachycaudus helichrysi*) on lower canopy weeds in cereal fields. More recently Rotheray and

Gilbert (1989) have suggested that the larvae of several *Platycheirus* and all *Melanostoma* species may be generalized predators in leaf litter; *P. manicatus* and *P. peltatus* may be facultatively aphidophagous while *P. scutatus* has an obligatory relationship with a wide range of ground layer aphids. The role of these species in cereal crops requires further investigation. It is possible that their role will be restricted to limiting the growth of aphid populations on non-crop plants in the base of the crop. In the present study a high proportion of these aphids were pest species; therefore, the larvae may have an affect on the total number of cereal aphids per unit area, in weedy crops.

In addition to stimulating oviposition by *Melanostoma* species the presence of non-crop plants may influence the numbers of *E. balteatus* and *Metasyrphus* larvae within the crop because although the females of these flies respond primarily to aphid related factors when ovipositing, Peschken (1964) has shown that dense plant stands are preferred for syrphid oviposition. Honek (1983) concluded that plant density is important in determining the abundance of syrphid larvae. However, in the present study it was not possible to detect a consistent relationship between the density of the crop and levels of oviposition.

Non-crop plants may also provide alternative prey, in the form of non-pest aphid species, this may reduce larval mortality due to starvation at times when the main pest species are at low densities. In addition, it has been suggested that in at least one species the reproductive output of females is influenced by the nutritional status of their larvae (Cornelius and Barlow, 1980). Therefore, the adoption of appropriate vegetation management strategies has the potential to effect the control of aphid populations via several routes.

Although the weed densities which occur in conservation headlands would be unacceptable to the farmer elsewhere in the field, the restriction of flowering non-crop plants to the headlands of cereal fields may still have a beneficial effect on aphid predation by attracting adult flies into the area.

During 1989 there was no significant difference in the proportion of *E. balteatus* adults in conservation headland and fully sprayed plots. However, in 1990 the much higher number of infloresences in the conservation headland plots than in the sprayed plots resulted in a significant difference in the proportion of both *E. balteatus* and *M. corollae* adults in the two treatments. This suggests that it is possible to effect a local redistribution of syrphid adults through the provision of pollen and nectar supplies. Adult syrphids were retained in areas of high inflorescence density as a result of their foraging behaviour. The absence of a significant difference in the proportion of *Melanostoma* adults in the two treatments during 1990 further supports this suggestion; these flies have been recorded feeding on the pollen of grasses and plantains; therefore their distribution will be less influenced by the presence of flowers of broadleaved weeds in the conservation headland plots. The failure to detect a distinct difference between the proportions of *E. balteatus* adults in the two treatments in 1989, when the numbers of infloresences in conservation headland plots was low, indicates the importance of the density of inflorescences in effecting the redistribution of flies, at least on the small scale studied here.

Because of the significant variation in abundance of syrphids such as *E. balteatus* between years it was not possible to compare the number of adults observed per unit time in 1989 and 1990. As a result it was not possible to examine whether the higher density of infloresences in 1990 influenced the total number of syrphids per unit area at the site. Similarly it is not possible to quantify the scale of adult redistribution.

Assuming gravid female syrphids oviposit in the vicinity of their feeding sites, the attraction of syrphids to an area by the provision of pollen and nectar supplies and their subsequent retention within the area could result in a higher level of oviposition than in adjacent areas with lower levels of resource availability. Kühner (1988) and Molthan (1989) have studied the density and diversity of syrphid species in floristically different field margins; a greater diversity and higher numbers of syrphids were recorded from the most floristically diverse sites. These authors have not reported the relative levels of oviposition at the various sites. Chambers (1991) studied syrphid oviposition in fields with a range of margin types; he could find no obvious effect of any particular type of field margin on oviposition in the headland. Personal observations of the movement of marked adult *E. balteatus* (Chapter seven) suggest the effects of the presence of high densities of inflorescences in a field margin are unlikely to be restricted to the immediate vicinity of the field margin. Therefore, in the future it may be appropriate to change the spatial scale on which the relationship between the presence of pollen and nectar sources and syrphid oviposition is examined. Landscape-scale experiments, with widely separated farms as replicates may be needed to show the effects of cultural practices on mobile species such as syrphids (Bugg, 1990).

CHAPTER FOUR
THE DISTRIBUTION OF SYRPHID EGGS IN RELATION TO APHID DENSITY

Introduction

A range of syrphid species occur as larvae in cereal crops including members of the genera *Metasyrphus*, *Platycheirus*, *Syrphus*, *Melanostoma*, *Sphaerophoria*, *Scaeva* and *Episyrphus* (Dean, 1974; Laska and Stary, 1980; Adams, 1984; Honek, 1983; Chambers, Sunderland, Stacey & Wyatt, 1986). Species composition varies with time and according to geographical location. However, *E. balteatus* and *M. corollae* are the most commonly recorded species on arable land in Great Britain (Dean, 1982; Chambers *et al.*, 1986); *E. balteatus* has also been recorded as the predominant syrphid species in winter wheat in Germany (Poehling, 1988; Tenhumberg and Poehling, 1991).

Several components affect the overall effectiveness of syrphids as aphid predators; these include the temporal and spatial coincidence of the larvae and their prey and the response of syrphid larvae and adults to increasing aphid densities. Larvae may show a functional response to aphid density in which the number of aphids consumed increases with increasing aphid density. In addition, adult flies may show a numerical response to aphid density which effects an increase in the density of larvae at higher aphid densities.

The numerical response of female syrphids to aphid density has two components: (1) the aggregation of female flies in aphid infested crops and their retention in areas of higher aphid density (aggregative numerical response) (2) larger numbers of eggs laid at higher aphid densities (reproductive numerical response).

Tenhumberg and Poehling (1991) studied the response of syrphid larvae to aphid density; heavier larvae and pupae were recorded from cages with higher aphid densities indicating increased feeding activity (functional response) in these cages.

Because the distribution and abundance of syrphid eggs in relation to aphid density has implications for the effectiveness of syrphids as biological control agents, the relationship between syrphid oviposition and aphid density has been extensively studied. Banks (1953) showed that there was a positive correlation between the numbers of syrphid eggs laid on a bean (*Vicia faba*) shoot and the number of aphids (*Aphis fabae*) present, although very heavy infestations were avoided (cited in Chandler (1968)). Dixon (1959) examined the association of syrphid eggs with colonies of *Acyrthosiphon spartii* on broom (*Sarothamnus scoparius*); more eggs were laid in larger colonies. Chandler (1968b) examined the response of adults of individual syrphid species to the size of aphid populations within field cages. *Syrphus* species, *Scaeva pyrastri* and *Platycheirus albimanus* laid more eggs with increasing aphid infestation per plant up to a maximum beyond which the numbers laid decreased. The aphid density at which flies laid the maximum number of eggs varied with species; *S. ribesii* laid most eggs on plants with approximately 2000 aphids while the "optimum" aphid density for *P. scutatus* was about 1000 aphids per plant. *P. peltatus* and *P. manicatus* did not show a clear oviposition response to aphid density and laid many eggs on uninfested plants. Chandler (1968a) has described these two species as phytozetic; plant-related factors are important in affecting oviposition in these species.

Sanders (1979) recorded both an aggregative and numerical reproductive response to aphid density; there were more visits and larger numbers of eggs per female in larger aphid colonies. Ito and Iwao (1977) studied the response of *E. balteatus* females to differing densities of *Myzus persicae* on cabbage plants. The number of eggs laid was highest on the most heavily infested plant; more eggs were recorded from heavily infested leaves within the plant. However, the mean number of eggs per aphid decreased with increasing aphid density. Hajek & Dahlsten (1988) studied the impact of natural enemies on the population dynamics of two species of aphid (*Callipterinella calliptera, Euceraphis betulae*) occurring on white birch; both coccinellids and syrphids demonstrated a numerical response to aphid density. However, comparison of the slopes of responses by coccinellids and syrphids showed that the syrphid response was much "weaker" than that of the coccinellid. During the study natural enemies failed to prevent the development of large aphid populations. Mills (1982) studied predation of the lime aphid (*Eucallipterous tillae*) by the coccinellid *Adalia bipunctata*; both the aggregative and reproductive numerical responses were asymptotic. Chambers (1991) examined oviposition by syrphids in relation to the density and distribution of cereal aphids in winter wheat; he showed a numerical response to aphid density between fields. There was no indication of an asymptote in the reproductive numerical response of syrphids to aphid density. However, the gradient was less than unity; Chambers suggested that this may have been a result of the limited egg complement of female flies. During two of the three years of Chamber's study, cereal aphids were not a problem for farmers in the study area; observations suggested that aphid-specific predators, including syrphids and hymenopterous parasites, and fungal pathogens were important in limiting the growth of the aphid populations (Chambers *et al.*, 1986).

The present study was carried out on a different spatial scale to that of Chambers (1990); the oviposition response of syrphids to aphid density was studied between plots within a single field rather than between fields as studied by Chambers. In addition, artificial infestation of wheat within field cages was used to produce discrete patches of aphids within the field; reflecting the situation during the initial colonisation of cereals when aphids are recorded in discrete patches within a field (Dean, 1973). Because of the lack of a quantitative method for trapping adult syrphids it was not possible to examine the response of female syrphids to patches of aphid density. However, by recording the aphid density and numbers of eggs at the different sites within the field it was possible to determine whether the flies showed a reproductive numerical response to aphid density.

Materials and methods

Layout of Field Trial

The trial was conducted during the summer of 1988 in a 25 ha field of winter wheat, c.v. Avalon, at the Leckford Estate, Hampshire.

Twenty - five one metre^3 field cages were erected in a 5x5 randomised block design within the field (Fig. 1). The cages within one row were separated from their nearest neighbour by five metres. The first row of five cages was 1m from the nearest field margin; the next four rows were 36, 71, 106 and 144m from the margin, respectively. The four field margins differed in floral composition; the margin adjacent to the field cages comprised a 1m wide field fallow strip which had been colonised by a range of annual arable weeds. Two of the remaining field margins consisted of post and wire fence, while the third was a bank, 50cm high and 1.5m wide. The floral composition of these three margins was similar; grasses predominated although *Galium aparine* and *Lamium album* were also present on the bank.

During mid May twenty of the field cages were covered with Tygan mesh (1mm^2) covers to exclude predators. Aphid densities within the cages were manipulated by the addition of laboratory-reared and field-collected aphids. The remaining cages were left uncovered and there was no augmentation of aphid numbers.

Aphid Augmentation

To obtain a range of aphid densities among the cages within each row, laboratory cultured and field collected *S. avenae* were added to the cages to augment the existing field populations. Five treatments were randomly allocated among the cages within a row. The treatments were (1) naturally infested: no cage cover and no aphids added to the cages; (2) low : the field cages were covered but no aphids were added to the cage; (3) medium I : the field cages were covered and aphids added on a single date; (4) medium II : the field cages were covered and aphids were added on two dates; (5) high : the field cages were covered and aphids added on four dates.

Green morphs of *S.avenae* maintained in continuous culture on barley seedlings c.v. Sonia at 20°c, LD 16:8 were introduced into the twenty covered field cages on 22 May 1988, (G.S. 43) when the indigenous aphid population was negligible. Subsequent inoculations occurred at three day intervals; aphids obtained from field populations were used added on these dates.

Aphid Counts

On 17 June 1988 (G.S. 60) the field cage covers were removed and the initial aphid densities recorded. Thereafter, the aphid density on each of twenty - five marked stems per field cage was recorded weekly. Aphids were counted *in situ* and identified to species and instar (1-3, 4, adult). Counts continued until 17 July 1988, by which time aphid numbers had declined to very low levels.

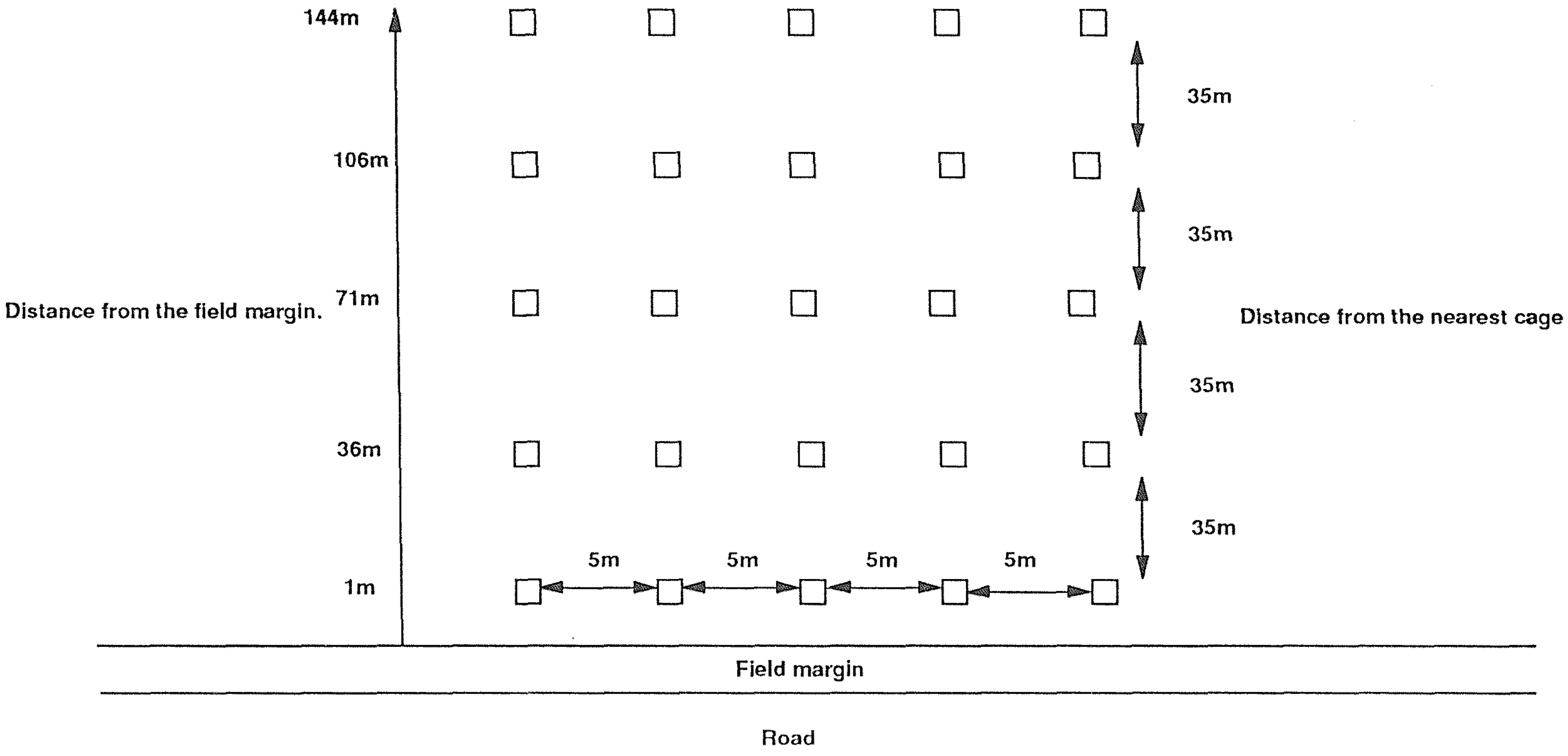


Fig 1. The arrangement of the twenty-five field cages (not to scale).

Syrphid Egg Counts

On each of the weekly sampling dates the twenty - five infested stems were examined for syrphid eggs. A further twenty-five marked, uninfested stems were also examined for eggs. The stems remained uninfested due the continual removal of aphids during the study.

For each syrphid egg observed the aphid density and proximity of the egg to the nearest aphid colony was recorded.

Crop Growth Stage

Crop growth stage, according to Zadoks *et al.* (1974), was recorded on each sampling occasion after examining one randomly chosen stem per field cage.

Results

Syrphid oviposition had already begun within the field prior to the removal of the field cage covers. Peak oviposition occurred during the week 21-27 June 1988.

The manipulation of aphid density by inoculation with the lab. reared and field collected aphids failed to produce a significant difference in aphid density among the treatments during the study (two-way analysis of variance on log transformed data; Table 1), although the calculated F-ratio approached significance on 17 June.

Spearman's rank correlation was used to investigate the relationship between mean aphid density/25 stems and the number of syrphid eggs/25 stems. Because of the large time intervals between sampling, linear interpolation was used to calculate the aphid densities on dates between the two sampling periods. Estimates of aphid density two days prior to the actual sampling date were used in the analysis. On all the dates there was no significant positive relationship between the number of eggs and aphid density, although the values did approach significance at the 5% level during the period 24-25 June (17-18 June $r_s = 0.257$, N.S.; 24-25 June $r_s = 0.380$, $P = 0.063$; 1-2 July $r_s = 0.308$, N.S.; 10-11 July $r_s = 0.246$, N.S.; n= 25). However, when data from all dates was pooled there was a significant positive relationship between the number of eggs per cage and mean aphid density (Spearman's rank correlation; $r_s = 0.350$, $P<.001$, n= 100; Fig.2).

There was no significant relationship between the number of eggs per aphid and aphid density during individual sampling periods (Spearman's rank correlation; $r_s = -0.239$, P = N.S.; $r_s = 0.365$, N.S.; $r_s = 0.236$, N.S.; $r_s = 0.183$, N.S.). When all dates were pooled there was a significant positive relationship ($r_s = 0.2215$, $P<.05$, n=97).

Where five or more syrphid eggs were recorded from separate stems in a single cage the mean percentage composition of aphid instars on uninfested stems was compared with that for stems with eggs, using a Kolmogorov-Smirnov test. Instars were categorised as first-third instars, fourth alate, fourth apterous, apterous adults and adult alates. On the four date/cage combinations where there was sufficient data to allow analysis there was no significant difference in colony composition between the stems with eggs and stems without eggs (D = 0.2, N.S.; D = 0.4, N.S.; D = 0.2, N.S.; D = 0.2, N.S.).

Table 1. The variation in aphid density among treatments and rows on the five sampling dates determined by two-way analysis of variance. Data was transformed using log(n+1) transformation.

17 June

Source of variation	Mean square	d.f.	F-ratio	P
Main	0.446	8	2.129	0.094
Rows	0.081	4	0.384	0.817
Treatment	0.814	4	3.875	0.022

24 June

Source of variation	Mean square	d.f.	F-ratio	P
Main	0.293	8	0.868	0.562
Rows	0.073	4	0.215	0.926
Treatment	0.514	4	1.520	0.243

1 July

Source of variation	Mean square	d.f.	F-ratio	P
Main	0.434	8	1.520	0.226
Rows	0.396	4	1.388	0.283
Treatment	0.472	4	1.653	0.210

July 10

Source of variation	Mean square	d.f.	F-ratio	P
Main	0.349	8	1.816	0.147
Rows	0.459	4	2.386	0.095
Treatment	0.239	4	1.246	0.331

July 17

Source of variation	Mean square	d.f.	F-ratio	P
Main	0.134	8	0.134	0.083
Rows	0.167	4	0.167	0.063
Treatment	0.101	4	0.101	0.204

The variation in aphid density log(n+1) among cages and treatments; homogeneous groups determined by Tukey's test, are followed by the same letter.

17 June

Treatment	Mean	Row	Mean
low	0.747 a	4	0.970 a
nat. infested	1.031 ab	3	1.002 a
med. I	1.046 ab	1	1.035 a
med. II	1.140 ab	2	1.043 a
high	1.204 b	5	1.117 a

24 June

Treatment	Mean	Row	Mean
low	0.683 a	1	0.861 a
nat.infested	0.981 a	4	0.898 a
med. I	0.983 a	3	0.932 a
high	0.991 a	5	0.981 a
med. II	1.016 a	2	0.982 a

Table 1 (contd.). The variation in aphid density log(n+1) among cages and treatments; homogeneous groups determined by Tukey's test, are followed by the same letter.

1 July

Treatment	Mean	Row	Mean
low	0.574 a	1	0.575 a
high	0.659 a	4	0.700 a
med. II	0.814 a	5	0.782 a
nat. infested	0.858 a	3	0.864 a
med. I	0.879 a	2	0.864 a

10 July

Treatment	Mean	Row	Mean
high	0.441 a	1	0.439 a
low	0.574 a	5	0.509 a
med. II	0.642 a	4	0.589 a
nat. infested	0.663 a	2	0.682 a
med. I	0.667 a	3	0.768 a

July 17

Treatment	Mean	Row	Mean
high	0.575 a	5	0.177
nat. infested	0.267 a	1	0.234
med. II	0.287 a	4	0.239
med. I	0.303 a	2	0.283
low.	0.306 a	3	0.389

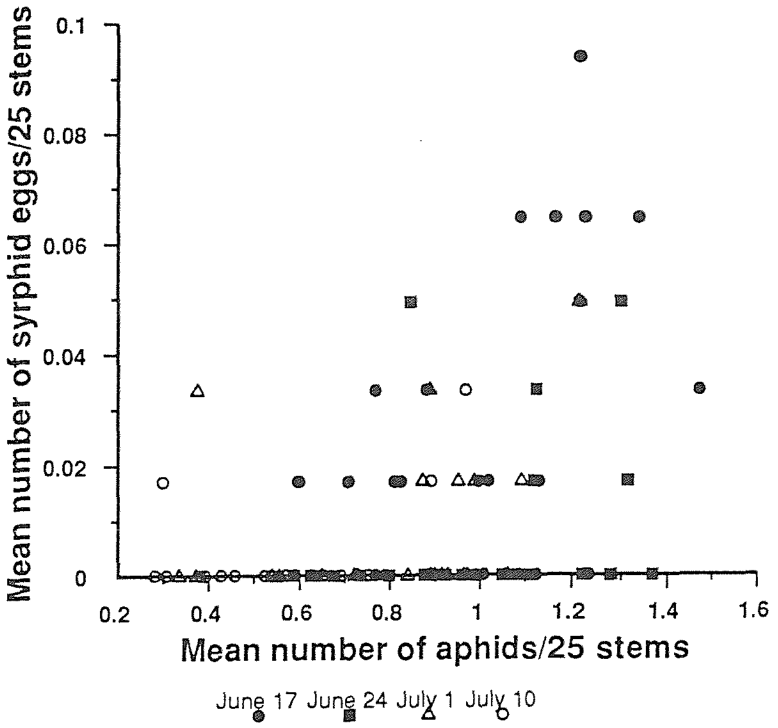


Fig. 2. The relationship between the number of syrphid eggs and aphid density.

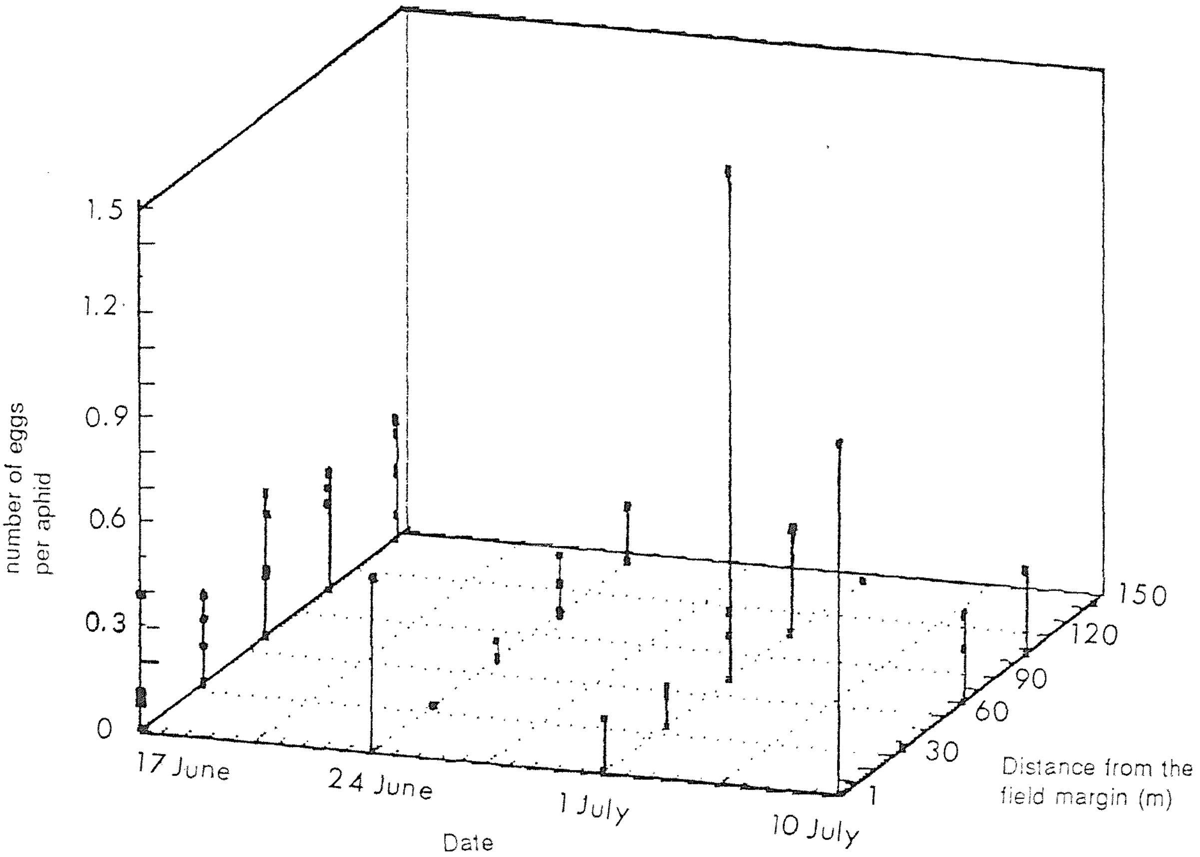


Fig. 3. The number of eggs per aphid at each position within the field on the sampling dates, 1988.

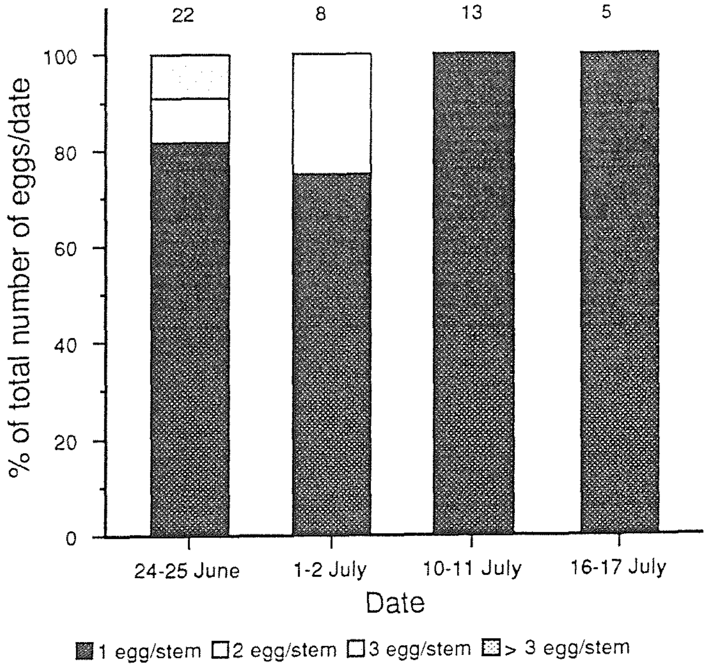


Fig. 4. The distribution of syrphid eggs according to the number of eggs per stem. Bar segments represent the number of eggs per stem, expressed as a percentage of the total number of eggs per date. Values in brackets represent the total number of eggs collected during each period.

Analysis of the distribution of the syrphid eggs among the five distances showed that there was no significant relationship between the number of eggs per aphid and distance on any of the dates (17-18 June r_s = 0.179, N.S.; 24-25 June r_s = 0.118, N.S; 1-2 July r_s = -0.048, N.S.; 10-11 July r_s = -0.092, N.S.; N= 25; Fig.3).

Examination of the distribution of all eggs according to the number of eggs per shoot showed that the majority of eggs were found singly (Fig.4); the modal value for the distance between an egg and the nearest aphid colony was <1mm.

Discussion

The results from the present study show that when data from all the sampling dates is pooled there is a significant positive correlation between the number of syrphid eggs and aphid density. These results agree with previous studies of syrphid oviposition behaviour which have shown a positive relationship between the number of syrphid eggs and cereal aphid density (Storck-Weyhermuller, 1987; Rautapää, 1976; Chambers, 1991). The significant positive relationship between the number of eggs per aphid and aphid density recorded when data from all dates was pooled was probably effected by the phenology of the flies and reflected a coincident increase in the number of gravid females and aphid density; rather than a differential response to aphid density with time.

When individual dates were treated separately it was not possible to detect a relationship between oviposition and aphid density. This may have been a result of the failure of aphid augmentation to establish significantly different aphid densities among the field cages; if a wider range of densities had existed among the cages on the individual dates a numerical response may have been detected. The observation that the majority of eggs occurred on infested stems, in close proximity to aphid colonies suggests that the eggs were laid by aphidozetic species (Chandler, (1968a). Therefore, the absence of a detectable numerical response on the individual dates cannot be attributed to oviposition by phytozetic species, which do not show a density dependant oviposition response to aphid density and often lay on uninfested plants (Chandler, 1968a).

Kan and Sasakawa (1986) studied syrphid oviposition on Japanese Maple (*Acer palmatum*) in response to two species of maple aphid (*Periphyllus californiensis* and *Yamatocallis tokyoensis*. Peak oviposition occurred in early spring before aphid population growth had begun. In mid April when the maple trees were heavily infested with maple aphids *E. balteatus* eggs were often found on other plants (vetch; *Vicia angustifolia*) infested with "small, young colonies " of other aphid species(*Megoura crassicauda*, *Acyrthosiphon pisum* and *Acyrthosiphon kondoi*). Kan (1988) suggested that the observed patterns of oviposition reflected the selection of colonies at particular developmental stages by the flies. She explained the observed patterns of behaviour in terms of the qualitative and quantitative value of the various types of colony. By ovipositing in small young colonies females ensured that newly hatched larvae would be able to find at least one young aphid nymph, to start successfully its larval development (Kan, 1989). If the females oviposited at the older, larger colonies newly emerged larvae would risk starvation because of the lack of young nymphs and/or by the dispersal of fourth instar nymphs and adults. *E. balteatus* females were able to discriminate between winged and wingless-aphid models and Kan (1986) suggested that aphid wings may be a repellent factor in ovipositional selection by females of this species. In the present study there was no significant difference in the percentage instar composition of the aphid colonies on stems with syrphid eggs and adjacent stems without eggs; eggs were recorded from colonies containing adult alates and apterous and alatiform fourth instars. However, at the time when eggs were recorded adults and fourth instars represented a small percentage of the aphids within individual colonies both on stems with and without eggs. During the remainder of the study predation of aphids by natural enemies, including syrphid larvae, prevented the colonies from reaching a stage in which fourth instars and adults comprised a high proportion of the aphids within a colony. Therefore, it was not possible to assess the oviposition response of syrphids to the age structure of *S. avenae* colonies.

Dean (1973) described the dynamics of *Sitobion avenae* colonies on barley; in the early stages of crop invasion third and fourth instar nymphs and apterous adults were the first forms of *S. avenae* to be found. Aphids of all ages moved to and from marked tillers; adult aphids remained in one place on a tiller for less than two days. This observation suggests that the use linear interpolation to estimate aphid density probably produced inaccurate estimates of the aphid density at the time of oviposition. In addition to the assumed movement of aphids there was an observable effect of the action of predators on the aphid colonies; syrphid eggs were recorded from ears which were not infested with live aphids but which showed the remains (aphid casts) of a colony. These eggs were not included in the analysis; however, it is probable that in many less obvious cases the action of predators resulted in an underestimation of the actual aphid density at the time of oviposition. In addition, there was no sampling of aphid density outside the field cages; there may have been significantly higher aphid densities (and numbers of eggs) in these areas. Therefore, the failure to detect an reproductive numerical response on individual dates during the study may have resulted from the experimental method. Kan's observations of the age structure of aphid colonies and the selection of oviposition sites by syrphids indicate that the relationship between aphid density and syrphid oviposition may be more complex than previously considered; it may be appropriate to re-examine the relationship between syrphid oviposition and cereal aphids in more detail. The selection of aphid colonies with a particular age structure has implications for the effectiveness of syrphids as cereal aphid predators. The selection of small, young colonies has the potential to affect the eventual aphid population peak.

During the present study adult syrphids of several species were observed foraging in the field margin adjacent to the experimental area containing the field cages. The margin represented an "oasis" of pollen and nectar supplies; the boundaries of surrounding fields contained grasses and very few flowering weeds. However, there was no significant relationship between the distance from the nearest field margin and the number of eggs per aphid. The final row of cages were 144m from the margin; the results show that it was not possible to detect an effect of the presence of flowers on the level of oviposition within this spatial scale. The predominant species at the site were *E. balteatus* and *M. corollae*; both immature and gravid females were recorded foraging in the field margin. The effect of field margin manipulation on syrphid oviposition is discussed in more detail in the next chapter.

During the present study no attempt was made to quantify the effect of the observed patterns of oviposition on the aphid population. In addition because other predatory groups were not sampled during the study it was not possible to quantify the relative importance of syrphid larvae as aphid predators during the study. Infact no published study has done this; only that of Winder (1990) modelled a complete predatory "guild", in that case the polyphagous groups.

CHAPTER FIVE

THE DISTRIBUTION OF SYRPHID EGGS IN RELATION TO THE DISTANCE FROM THE NEAREST FIELD MARGIN

Introduction

The influence of non-crop habitats on pest incidence and the numbers of beneficial insects within agricultural crops has been the subject of extensive study. Non-crop habitats may influence natural enemy efficacy within crops by providing shelter, overwintering sites, alternative prey at times of prey scarcity and pollen and nectar sources for adult feeding. For example, Solomon (1981) has reported the predatory flower bugs *Anthocoris nemorous* and *A. nemoralis* overwintering on shelterbelts of alder (*Alnus glutinosa*) and willows (*Salix caprea* and hybrids); the bugs subsequently dispersed into adjacent pear orchards where they predated aphids and mites. Banks (1955) showed the importance of the aphid *Microlophium evansi* on nettles as prey for post-overwintering coccinellid populations before they moved into agricultural crops. Powell (1986) reviewed six examples from the literature where workers had attributed increased parasitism on crops to the presence of nectar producing plants outside the crops and gave eight examples where increased parasitism was related to the presence of alternative prey

Several studies have examined the distribution of syrphid adults and/or eggs between crops and the adjacent non-crop habitats; some of the studies examined the provision of adult food sources while others assessed the importance of shelter on the observed distribution patterns. The studies have been conducted on a range of spatial scales.

Bowden and Dean (1977) used suction traps to assess the distribution of hymenopterous parasites and predators, including syrphids, in and near a hedgerow; the pattern of distribution appeared to be determined primarily by the comparative richness of the vegetation surrounding the trapping sites. The presence of a rich and diverse adult food source was apparently strong enough to attract and hold small insects such as parasitic Hymenoptera even in strong winds.

Several authors have studied the composition of syrphid communities associated with different types of field margin. The structure and floral composition of naturally occurring field margins can affect the density and diversity of syrphid species. Kühner (1988) compared three floristically different field margins: higher numbers of syrphids were recorded from the most floristically diverse site. Similarly, Molthan (1989) studied three types of naturally occurring field margin and showed that the highest syrphid density and most homogeneous community structure was recorded from the most floristically diverse margin.

Pollard (1971) compared the levels of syrphid oviposition in two areas of farmland, which differed in their habitat composition. Adult syrphids were more abundant at sites with higher densities of flowering weeds; there was no evidence that syrphid species which were not restricted to woodland habitats, oviposited more abundantly in the area of diverse habitats than in the mainly arable area. However, examination of the patterns of oviposition for individual species showed that two species (*Leucozona lucorum* and *Baccha obscuripennis*) laid in the woodland site and close to the shelter of the adjacent hedge; there was a marked reduction in the number of eggs laid at increasing distances from the hedge.

Syrphus eligans laid eggs abundantly in the hedge but no eggs were recorded 5m from the hedge. Of these species only individuals of *L. lucorum* were recorded from the predominantly arable site. In contrast, analysis of the distribution of *E. balteatus* and *P.peltatus* eggs showed that the eggs tended to occur in open habitats; eggs and adults of these species occurred at both sites. Pollard concluded that the diversity of habitats outside the crop made no difference to syrphid predation on *B. brassicae* when compared with the largely arable area.

van Emden (1965) planted flowers along parts of two edges of a Brussels sprout crop; significantly more syrphid eggs were laid on the crop near these flowers than elsewhere. This difference was associated with a 65-70% predation mortality of *B. brassicae* near these flowers, compared with under 50% at other edges and the centre.

Chandler (1968a) examined oviposition by syrphids in small replicated plots of Brussels sprouts; buckets of flowers (*Senecio jacobea*) were added to several of the plots. Chandler was unable to show any effect of the presence of the flowers on the oviposition of aphidophagous syrphids. As a result he suggested that the increased oviposition by syrphids on Brussels sprouts close to flowers recorded by van Emden may have been a shelter effect.

In recent years manipulation of field margin composition to enhance the syrphid oviposition within crops has involved the sowing of single-species stands. Klinger (1987) recorded higher numbers of adult syrphids in the vicinity of winter wheat plots with margin strips sown with *Phacelia tanacetifolia* or *Sinapsis alba* than in wheat plots without margin strips. Although a tendency to reduce infestations by cereal aphids was observed it was not significant. Sengonca and Frings (1988) reported that although syrphid adults were recorded in higher numbers in sugar beet plots with *P. tanacetifolia* margin strips than in control plots without *P. tanacetifolia*, the density of syrphid eggs was highest in control plots where aphid (*Aphis fabae*) density was highest.

The aim of the present study was to examine the composition and distribution of syrphid eggs and adults within a field in relation to the distance from the nearest field margin. The margins comprised naturally occurring, unmanipulated non-crop plants. In addition none of the margins contained shrubs or woody vegetation, therefore any observed effects were likely to be a result of the floral composition of the margins and not a shelter/shading effect.

Materials and methods

Layout of field trial

The experiment was conducted during the period June to 3 July, 1990, in a 38 hectare field of winter-wheat on an 8 km^2 mixed arable/ livestock farm on the Hampshire-Dorset border (see Fig.1)

The experimental design consisted of 25 one metre^3 field cages arranged according to Fig. 1a. The experiment was primarily designed to investigate the effects of pesticide use on populations of non-target invertebrates (see Duffield, 1991). The field cages were erected at 1, 40, 70, 135 and 200m from the nearest boundary, with five replicates of each distance. The field outside the cages was treated with

Fig. 1 The Study Farm

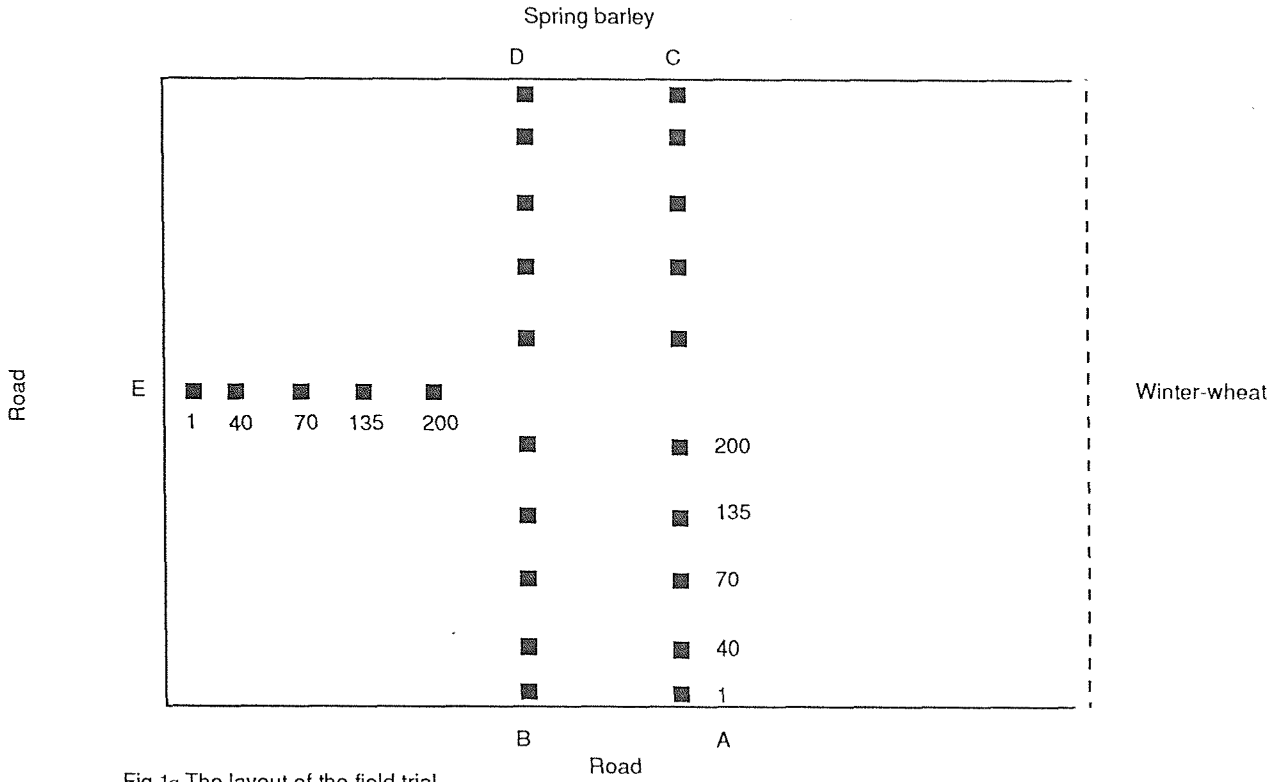


Fig.1a The layout of the field trial.

Each ▨ represents a 1m field cage. The numbers represent the distance from the nearest field margin. The letters indicate the five different transects. The solid line represents a field margin; - - represents the edge of the experimental area where no physical boundary was present.

dimethoate (Rogor E) at 340g ai/ha in 220 l water at pressure of 1.8bars and a ground speed of 10 kph with a tractor-mounted 24m hydraulic boom. This procedure had the effect of concentrating the majority of aphids and therefore, syrphid oviposition within the field cages. The field was sprayed on 12 June. During spraying the boom was switched off to produce a 1m insecticide free strip around each cage. The cages were covered with a Tygan (1mm^2 mesh) cover; a layer of polythene was also placed over the Tygan cover to minimise contamination of the crop within the cage by the pesticide.

Aphid counts

The field cage covers were used to exclude predators and promote the development of aphid colonies within the field cage. Existing aphid populations were augmented with *Sitobion avenae*, collected from the field, during late May 1990.

On 14 June (G.S. 71) the field cage covers were removed and the aphid densities recorded. In each cage the aphid density on 20 randomly selected stems was recorded. In addition, 20 randomly selected stems in the sprayed field adjacent to cage were examined for aphids. Each stem was also examined for syrphid eggs. For each syrphid egg recorded the corresponding aphid density and position of the egg on the wheat plant were recorded. The eggs were removed from the plant using a moistened paintbrush and were transferred to 70% alcohol. The preserved eggs were subsequently identified using a combination of light and scanning electron microscopy (see Chapter three).

On most occasions it was not possible to sample all the field cages on a single date; the sampling period usually extended over several days. For analysis, counts from adjacent dates were pooled to provide a complete data set for all the cages.

During the period 7 - 12 July "barley baits" were used to examine the distribution of syrphid oviposition. The baits consisted of barley seedlings c.v. Sonia, infested with green morphs of *Sitobion avenae* which were obtained from a continuous culture maintained at 20°C, LD 16:8. The seedlings were grown in John Innes No. 2 compost in 12cm diameter pots at 16 °C, LD 16:8. On 7 July, 25 baits were placed on the soil surface in the field, one bait adjacent to each of the 25 field cages.

The period 7 -12 July coincided with a period of very hot, dry weather. Under these conditions the barley seedlings wilted rapidly and were inefficient as baits for syrphid oviposition. After repeating the experiment, with seedlings of different ages, over several days the experiment was abandoned on 12 July.

Crop growth stage

Crop growth stage, according to Tottman and Broad (1987) was assessed on each sampling date, by examining 20 randomly selected stems.

The spatial distribution of syrphid adults

25cm^2 sticky yellow traps were used to catch adult syrphids. The traps were placed at the base of the crop, adjacent to the field cage. The traps were changed every 72 hours; the identity and sex of the syrphids was recorded. In addition a subjective assessment of the amount of pollen in the gut of female flies was also recorded.

Field margin floral composition.

Ten randomly-allocated 0.5m^2 quadrats were used to quantify the species composition of plants in the margins of the study field. The data was collected on 11 July; it was not necessary to sample repeatedly the field margin vegetation because there was little variation in the relative floral abundance at this time.

Results

Composition and distribution of syrphid eggs.

Fig. 2 shows the composition of the identified syrphid eggs collected during three sampling periods from 22 June - 3 July. The majority of the eggs belonged to the genera *Metasyrphus* and *Episyrphus*. There were two *Syrphus* eggs collected on 25 June, one egg belonging to the genus *Sphaerophoria* collected on 22 June and a single *Syrphus* egg collected on 28 June. In the first week of July aphid numbers on the crop had declined to very low levels and barley baits were used to examine the spatial distribution of syrphid eggs in the crop. However, because of the adverse effect of the hot weather on the (see above) baits the experiment was abandoned. No syrphid eggs were recorded from the baits; therefore, no egg data was available after 3 July. Because of the low numbers of eggs belonging to other genera only data referring to *Episyrphus* and *Metasyrphus* eggs was analysed.

The spatial distribution of all syrphid eggs within the field is shown in Fig. 2a. Fig 3a shows the spatial distribution of *Episyrphus* and *Metasyrphus* eggs within the field. The numbers of identified syrphid eggs recorded from each field cage were analysed using Friedman's two way analysis by ranks. There were no significant differences in the number of *Metasyrphus* or *Episyrphus* eggs between the five distances (*E. balteatus* M=1.614, N.S.; M= 6.857, N.S.; M=6.4, N.S.), (*M. corollae* M=2.027, N.S.; M=3.277, N.S.; M=7.396, N.S.) or the four transects (*E. balteatus* M=3.310, N.S.; M=6.857, N.S.; M=2.4, N.S.), (*M. corollae* M=6.5, N.S.; M=6.321, N.S.; M=1.5; N.S.) during the three sampling periods (Table 1). Fig. 3b shows the distribution of *Episyrphus* and *Metasyrphus* eggs on the wheat plants according to their position and presence or absence of aphids.

Aphid density

There was no significant difference in mean aphid density in relation to distance (Friedman's two-way analysis by ranks; M=2.303, N.S.; M=5.12, N.S.; M=7.556, N.S.) or transect(M=8.96, N.S.; M=3.273, N.S.; M=7.556, N.S.) during the three sampling periods. Similarly, there was no significant difference in the number of eggs per aphid (all syrphid genera combined) between transects (M=7.259, N.S.; M=7.6, N.S.; M=3.855, N.S.) or distances(M=2.6506, N.S; M=2.506, N.S.; M=3.826, N.S.). There was no significant positive correlation between the number of *E. balteatus* or *M. corollae* eggs and aphid density during the

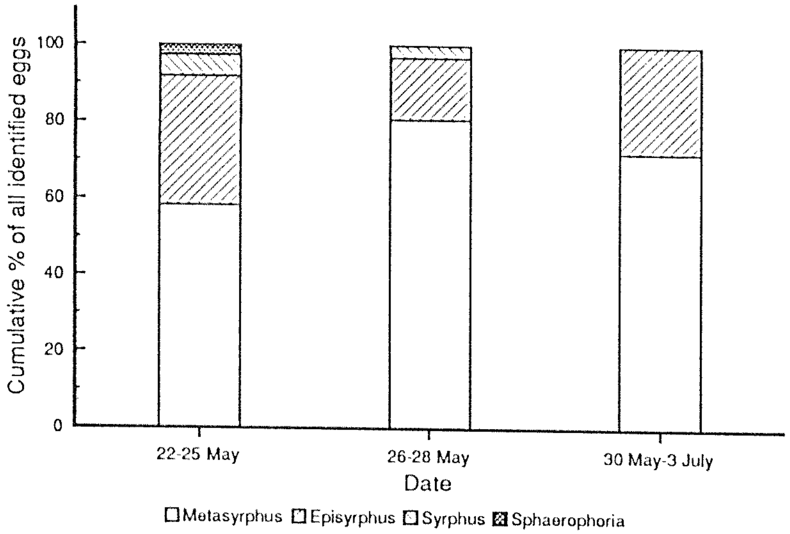


Fig. 2. The composition of identified syrphid eggs during the three sampling periods 22 June - 3 July.

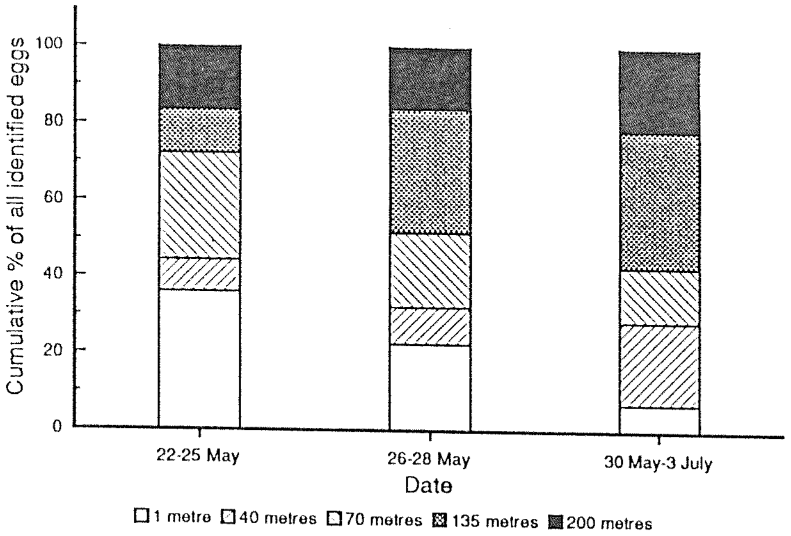


Fig. 2(a). The distribution of identified syrphid eggs within the field.
The bar segments represent the distance from the nearest field margin.

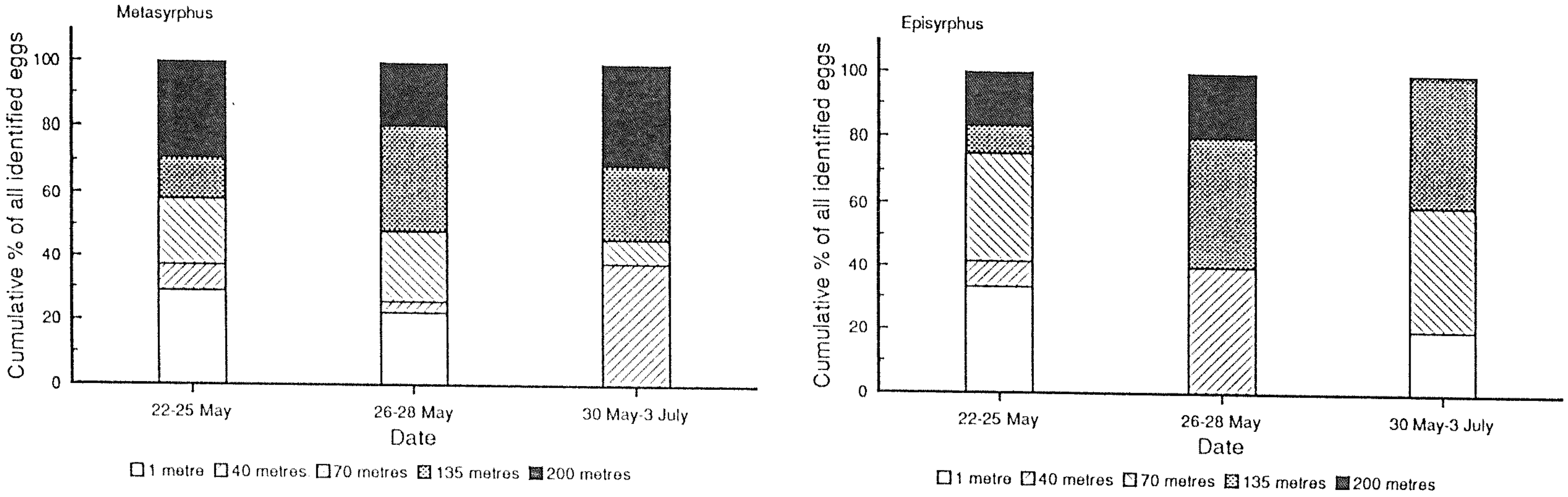


Fig.3a.The distribution of Metasyrphus and Episyrphus eggs within the field. The bar segments represent the distance from the nearest field margin.

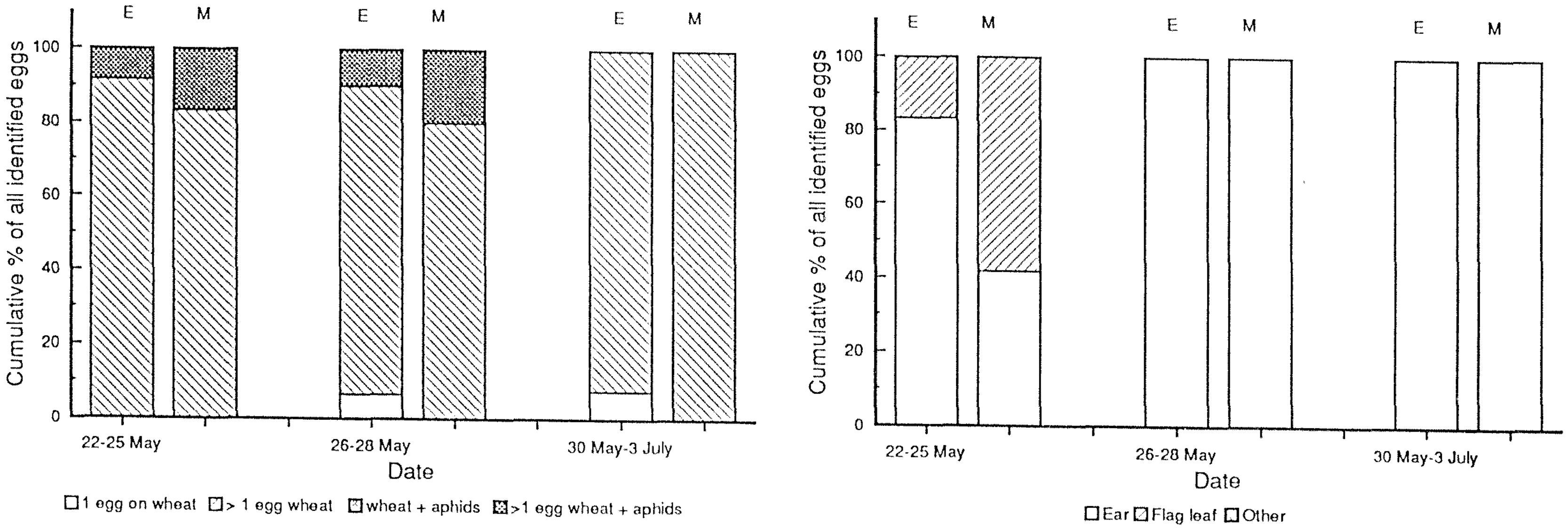


Fig. 3(b). The distribution of Metasyrphus and Episyrphus eggs according to(i) the presence or absence of aphids (ii) the position of the egg on the crop.
E = *Episyrphus*; M = *Metasyrphus*

Table 1. The variation in aphid density, number of eggs per aphid and total number of *Episyrphus* and *Metasyrphus* eggs with distance and according to transect. Friedman's two-way analysis by ranks; the calculated values represent the average rank of the treatment values.

Mean aphid density

Distance	22-24 June	26-28 June	30 June-3 July
1	2.6	2.6	2.3
40	3.8	3.4	3.2
70	3.3	2.6	2.6
135	2.7	4.2	4.6
200	2.6	2.2	2.3
M	2.303	5.12	7.556
P	N.S	N.S.	N.S.

Transect	22-24 June	26-28 June	30 June -3 July
1	1.8	2.1	2.8
2	3.2	3.2	3.8
3	4.0	3.6	2.1
4	4.0	3.5	4.2
5	2.0	2.6	2.1
M	8.96	3.273	7.556
P	N.S	N.S.	N.S.

Eggs/aphid

Distance	22-24 June	26-28 June	30 June-3 July
1	3.2	2.4	3.1
40	2.6	2.5	2.3
70	3.5	3.4	3.1
135	2.3	3.6	2.9
200	3.4	3.1	
M	2.651	2.505	3.826
P	N.S.	N.S.	N.S.

Transect	22-24 June	26-28 June	30 June -3 July
1	4.3	3.6	3.3
2	2.7	4.0	3.4
3	3.4	1.6	3.4
4	2.4	3.1	2.6
5	2.2	2.7	2.3
M	7.259	7.6	3.85
P	N.S.	N.S.	N.S.

Episyrphus eggs

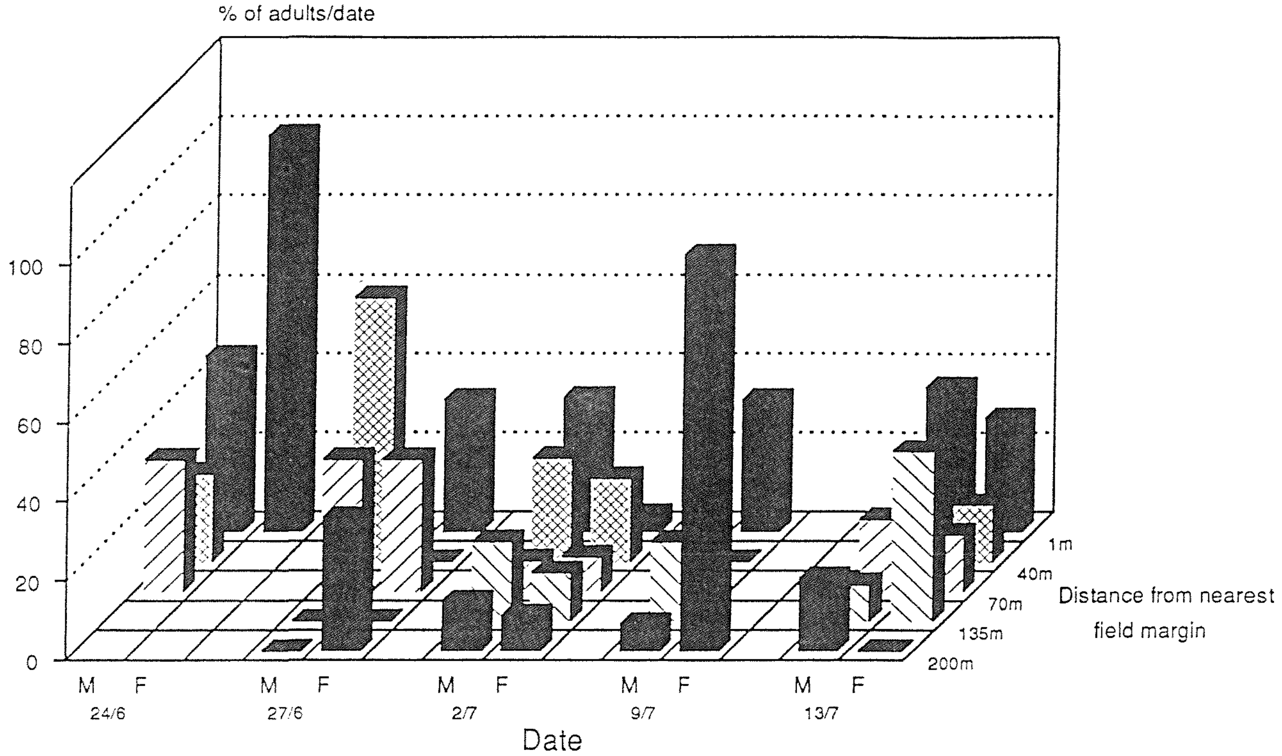
Distance	22-24 June	26-28 June	30 June-3 July
1	2.9	2.6	3.2
40	2.8	3.2	2.7
70	3.6	2.6	2.7
135	2.8	3.5	3.7
200	2.9	3.1	2.7
M	1.614	3.444	6.4
P	N.S.	N.S.	N.S.

Transect	22-24 June	26-28 June	30 June-3 July
1	3.5	2.6	3.2
2	3.2	3.2	3.2
3	3.3	2.6	3.2
4	2.7	3.5	2.7
5	2.3	3.1	2.7
M	3.310	3.444	2.4
P	N.S.	N.S.	N.S.

Metasyrphus eggs

Distance	22-24 June	26-28 June	30 June-3 July
1	3.1	3.2	2.3
40	2.5	2.2	3.7
70	3.5	2.8	2.3
135	2.6	3.8	3.0
200	3.3	3.0	3.7
M	2.027	3.277	7.396
P	N.S	N.S.	N.S.

Transect	22-24 June	26-28 June	30 June-3 July
1	4.2	3.7	2.8
2	2.7	3.9	3.3
3	3.3	2.0	3.3
4	2.4	2.5	2.8
5	2.4	2.9	2.8
M	6.5	6.321	1.5
P	N.S	N.S.	N.S.



The spatial distribution of E. balteatus adults. The values represent the % of the total number of adults of each sex caught on sticky yellow traps.
M = male; F = female.

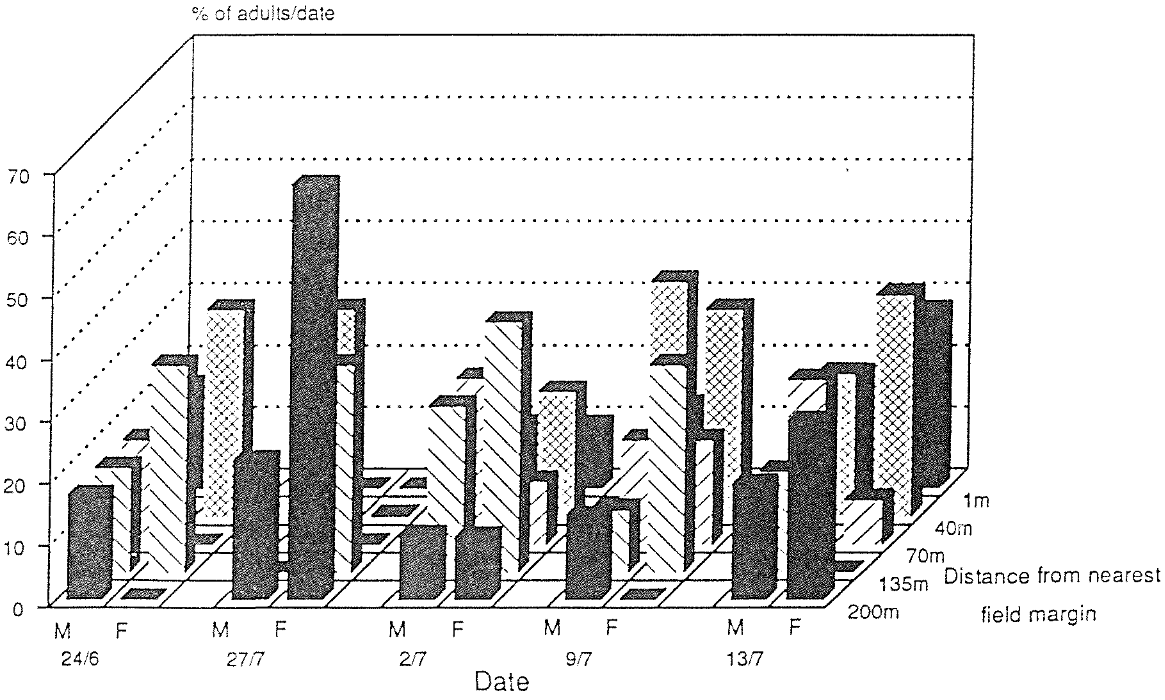
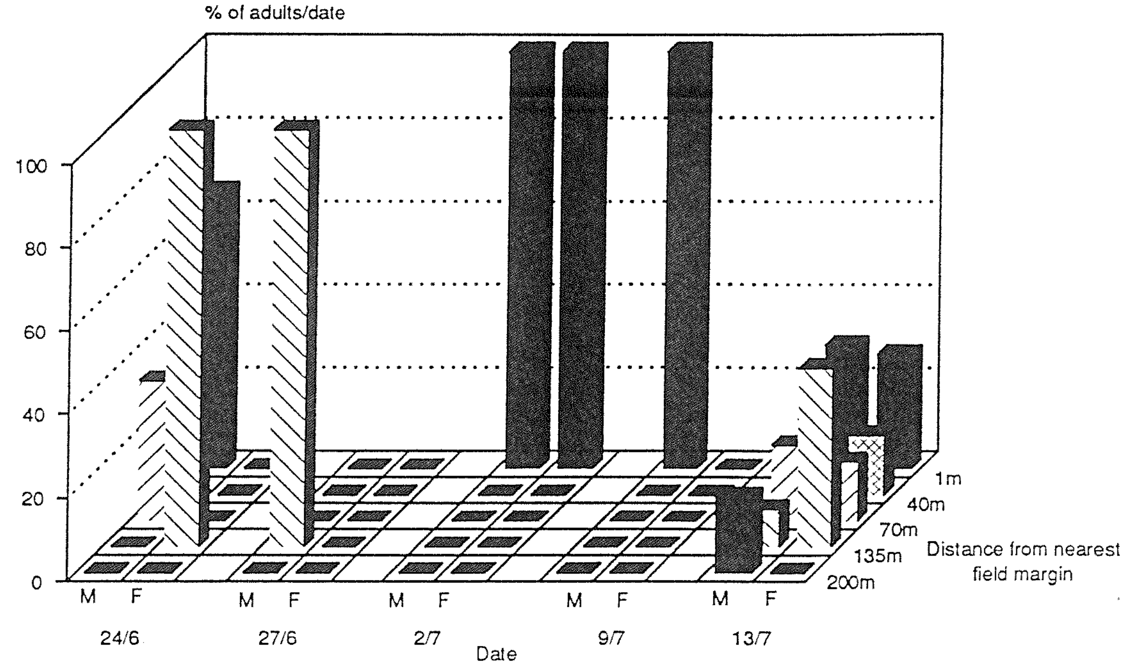


Fig.4
The spatial distribution of M.corollae adults. The values represent the % of the total number of adults of each sex which were caught on yellow sticky traps.

M = male; F = female.



The spatial distribution of Syrphus spp. adults. The values represent the % of the total number of adults of each sex caught on sticky yellow traps.
M = males; F = females

Table 2.
Results from the floral vegetation survey of the three field margins surounding the study field. The margins are identified by the letter of the adjacent field cage(s), (see Fig 1.). Unless otherwise stated all values refer to numbers per 0.5m^2 (n=10).

Margin	Mean rooted plant density	Mean number of flowerheads	% of quadrats containing grass species				% species composition of of all flowerheads						
			A.s	A.e	L.p	D.g	P.r	M.p	C.n	A.m	L.c	P.s	F.n
D/C	0.9 + 1.1	2.7 + 4.67	70	10	40	0	18.52	81.48	0	0	0	0	0
E	2.4 + 0.70	12.3 + 14.08	0	40	20	0	17.74	59.68	4.03	0.81	6.45	5.65	4.03
A/B	1.1 + 1.20	8.3 + 14.64	20	90	40	10	23.17	76.83	0	0	0	0	0

Grass species

A.s	*Agrostis* spp.
A.e.	*Arrhenatherum elatius*
L.p	*Lolium perenne*
D.g	*Dactylis glomerata*

Flowering weeds

P.r	*Papaver rhoeas*
M.p	*Matricaria perforata*
C.n	*Centaurea nigra*
A.m	*Achillea millefolium*
L.c	*Lapsana communis*
P.s	*Pastinaca sativa*
M.a	*Myostis arvensis*

study although the values for *E. balteatus* did approach significance at the 5% level on the 26 June (Spearman's rank correlation coefficient: *E. balteatus*; 22 June r_s = -0.079, N.S.; 26 June r_s = 0.37, P = 0.067; 30 June r_s = 0.28 N.S. n= 24. *M. corollae*; 22 June r_s =-0.26, N.S.; 26 June r_s = 0.19 N.S.; 30 June r_s = -0.11, N.S. n=24). When data from individual sampling periods were combined there was a significant positive relationship between the number of *Episyrphus* eggs and the number of *Metasyrphus* eggs per cage (Spearman's rank correlation; r_s = 0.293, P<.05, n = 75).

Distribution of adult syrphids

In the case of *E. balteatus* and *M. corollae* there was a tendency for males to be caught in higher numbers than females. This might have been a result of males emerging before the females and therefore being present in larger numbers. However, the trend persisted throughout the trapping period and therefore may have represented a differential attractiveness of the traps to males and females of these species. Because of the limited number of traps used during the study it was not possible to test for statistical differences in the percentage of the total number of individuals of each species at each of the five distances. Fig. 4 shows the spatial distribution of the adults of three commonly occurring species; the values represent the percenatge of the total number of flies which were caught on yellow traps at the five distances.

Composition of field margins

Table 2 summarises the quadrat data from the three margins which surrounded the study field. Margin E (see Fig.1a) had the highest mean number of flowerheads/0.5m^2; margin D/C was the least floristically diverse margin and grass species predominated here at the time of the study.

Discussion

E. balteatus and *Metasyrphus* eggs were predominant during the study. When data from all the dates was pooled there was a significant positive relationship between the numbers of *Metasyrphus* and *E. balteatus* eggs; this suggests that the females of these two genera were responding to similar stimuli when selecting oviposition sites. During the study there were no aphids in the majority of the 38 ha field as a result of the insecticide application; in this context the presence of eggs in the field cages is significant. It indicates that *Metasyrphus* and *E. balteatus* females respond to aphid patches, comprising aphid densities of 3 aphids per stem/cage (22 June; G.S. 73). If this response were to occur early in the season during the initial phase of aphid population growth syrphids could have a significant impact on the rate of population growth and the eventual aphid peak. For example, Entwistle and Dixon (1990) introduced *S. avenae* into areas within a field of winter wheat during early May when the indigenous population was negligible. Aphid numbers in the areas increased for the first three weeks of the study and then declined for four weeks. The authors concluded that the establishment of syrphid larvae in these areas was responsible for the observed decline in aphid population growth.

In the present study the absence of eggs belonging to genera other than *Episyrphus* and *Metasyrphus* may have been the result of several factors. Firstly, the study was undertaken during a short period at the end of June and early July. This may have represented a period when there were low numbers of individuals of many species due to the phenology of the flies. Pollard (1971) described the voltinism of several syrphid species. *M. mellinum, P. peltatus, P. manicatus* and *P. clypeatus* were bivoltine with the generations being dissimilar in size. Examination of the data presented by Pollard suggested that *E. balteatus, M. mellinum* and *Metasyrphus* and *Syrphus* were the only syrphids likely to be present in any number during late June and early July. Pollard (1971) also recorded the numbers of syrphid eggs during his study; *E. balteatus* and *Syrphus* eggs predominated during late June and early July. In the present study adults of *Syrphus* species were not recorded in large numbers until 13 July. By this time the collection of syrphid eggs from the field had ceased.

Neither *Melanostoma* adults nor eggs were recorded in significant numbers during the study. The colour of the traps may have been responsible for the failure to trap adults of this genus. Hickman (pers comm.) recorded higher numbers of *Melanostoma* adults in blue water traps than in yellow water traps. The efficiency of the traps in catching adults of all species may have also been influenced by the reproductive condition and nutritional status of the flies; Schneider (1948) showed that syrphid females are attracted to yellow traps when food-seeking rather than when searching for oviposition sites.

The design of the experiment may have contributed to the failure to collect any eggs belonging to the genus *Melanostoma*. The design was selective for species in which aphid related factors are important in stimulating oviposition since the main sampling areas were the cages which contained the aphid infested wheat plants. The two *Melanostoma* species and most of the *Platycheirus* species are known to be phytozetic: plant-related factors are more important than aphid-related factors in stimulating oviposition. Therefore, the technique of using aphid infested baits or areas of crop to assess the level of oviposition within the crop (or between crops and habitat types) may underestimate the contribution made by these species.

During the present study *E. balteatus* and *Metasyrphus* eggs were collected from cages throughout the field; there was no significant difference in the number of eggs per aphid at the five distances. This agrees with the work of Chambers (1990) who was unable to find a correlation between the number of eggs and the distance from the nearest field margin or the size of the field; *E. balteatus* and *M. corollae* were the predominant syrphid species in the study.

Several authors have studied the flower visiting patterns of syrphids in an attempt to identify which species are important to the flies as pollen and nectar sources. Ruppert and Klingauf (1988) recorded the number of syrphid visitors per 15 minutes to a range of weeds and ornamental and field-bank plants. Cowgill (1988) compared the distribution of flower visits by syrphids with the abundance of flower species in the habitat to identify which flowers were used selectively. Several species of flower, identified as being important to the flies, occurred in one of the three field margins (c) of the present study. The remaining two boundaries (a-b and d-e) comprised grasses; *Melanostoma* and *Platycheirus* species have been recorded foraging on Gramineae (van der Goot and Grabandt, 1970; Pollard, 1971). However, Gramineae are not important pollen sources for *E. balteatus* and *M. corollae*. The failure to detect a difference in the number of eggs between the three transects indicates that the presence of the flowers in margin c did not result in higher numbers of eggs in the vicinity of the margin. Syrphids were observed foraging in the margin however, the sex and reproductive status of the observed adults was not quantified. It is assumed that gravid females require amino acids available from pollen to mature successive batches of eggs (Gilbert, 1986) however, the relationship between the site of feeding and the site of oviposition is uncertain. In a study by Dixon (1959) peak syrphid oviposition coincided with the flowering of broom; most of the syrphids occurring in the study area were immigrants which had completed their development elsewhere. It is unclear whether the syrphids were attracted to the area by the adult food source or whether they were present because of an aggregative numerical response by female flies. Smith (1976) failed to find a relationship between higher catches of *Sphaerophoria* females and the levels of oviposition. Van Emden (1963) and Pollard (1967) have both suggested that it is immature, not mature, female parasitoids which are attracted to flowers; however, gravid syrphid females of several syrphid species have been observed foraging on pollen (personal observation; Hickman pers. comm.). The failure to detect an edge effect may have been the result of the low densities of flowers in the margin c; resource availability at the site may have been insufficient to cause the retention of gravid females in the vicinity of the margin.

The observations of the distribution of adult syrphids between plots containing flowers and plots without flowers discussed in Chapter three indicate that it is possible to bring about at least a small scale redistribution of individuals of some syrphid species. If gravid females remain and oviposit in the vicinity of the field margin in which they have been foraging there may be an increase in the level of oviposition within the area. However, the mobility of females searching for oviposition sites (Chambers, 1991) suggests that it is unlikely that the effect of field boundary manipulation will be restricted to the immediate vicinity of the margin.

Klinger (1987) and Sengonca and Frings (1988) manipulated flower density in field margins by sowing *Sinapsis alba* and *P. tanacetifolia*. Higher numbers of syrphid adults were recorded in the margins containing *S. arvensis* and *P. tanacetifolia* than in unmanipulated margins. However, the authors recorded that aphid density was the most important factor in determining the distribution of syrphid eggs. Further studies are required to examine the spatial relationships between adult feeding sites and oviposition sites. A preliminary study to assess the use of marking techniques to study movement and habitat use by adult *E. balteatus* is described in Chapter seven.

CHAPTER SIX

THE PHENOLOGY, RELATIVE ABUNDANCE AND ACTIVITY OF COMMONLY OCCURRING SYRPHIDS ON FARMLAND.

This chapter is essentially descriptive and consists of a discussion of the observations made during the standard census walks in the headland of Side Scammel during 1989 and 1990. The chapter is divided into two parts. In the first part the phenology, species composition and relative abundance of syrphids at the site during the two sampling periods is described and the observed patterns are compared with several previous studies. In the second part the observed patterns of activity are discussed in relation to microclimatic factors.

PHENOLOGY, SPECIES COMPOSITION AND RELATIVE ABUNDANCE.

Introduction

It is an obvious phenomenon of nature that not all species occur in all habitats, but rather that most species seem to show some kind of selectivity of habitat (Gilbert, 1981). Studies of the diversity of syrphid species occurring in a range of habitat types agree with this observation. Pollard (1971) and Gilbert (1981) recorded the abundance and species composition of syrphids during transects of woodland and farmland and woodland and urban garden sites respectively. In both studies there was a complement of species which occurred exclusively in the woodland sites. In Gilbert's study these included *Brachyopa, Criorhina, Baccha* and *Chrysotoxum cautum* while Pollard recorded four species which were caught only in woodland (*Platycheirus tarsalis, Pyrophaena rosarum, Syrphus cinctella* and *S. eligans*); a further four species were caught only in the wood and adjacent hedgerow (*Baccha obscuripennis, Syrphus auricollis, S. diaphanus* and *Syrphus grossulariae*).

Gilbert (1981) suggested that habitat selection by syrphids might be governed by the availability of larval food. He observed an increase in the percentage of species whose larvae live in rot-holes as the study area became more wooded while the sites with standing water had relatively greater numbers of species whose larvae feed on aquatic debris and decay. The relative abundance of syrphids at a particular site will be affected by the seasonal reproductive cycle (voltinism) of the flies, the degree of specialization of the larvae and the relative abundance of larval prey.

Pollard (1971) recorded the number of generations per year of several commonly occurring syrphid species; *M. mellinum, P. peltatus, P. manicatus* and *P. clypeatus* were bivoltine. The two generations were different in size: in *M. mellinum* and *P. clypeatus* the second generation was larger than the first whereas in *P. peltatus* the reverse was true. These patterns were also recorded in Norway

(Nielsen, 1971) and Germany (Claussen, 1980). Pollard recorded extended phenological curves for *Syrphus ribesii*, *S. vitripennis* and *E. balteatus*. However, Goedlin (1974), Schneider (1948) and Grosser and Klapperstuck (1977) recorded *E. balteatus* as polyvoltine, suggesting that this species may exhibit a clinal pattern of phenological adaptation from polyvoltinism in the southern part of its range to univoltinism in the north.

Owen and Gilbert (1989) examined the relationships between both abundance and variability in abundance and features of the life-history of syrphids, using data collected from a suburban garden over a fifteen year period. In particular they examined whether larval feeding type, habitat or degree of specialisation influenced the population size and its variability. They concluded that specialization in either habitat or prey type led to low relative abundance. Species with specialized predatory larvae were least abundant, moderately specialised species had intermediate levels of abundance while polyphagous species had high levels of abundance. Species which feed in leaf litter or that are found in many types of aphid colonies had higher average abundances than those restricted to herb, arboreal or gall/subterranean aphids while syrphids whose larvae live in tree rot-holes or in social insects' nests were less abundant than those living in situations of general decay.

Contrary to the situation with the level of abundance, there were few differences in stability between the various groups however, species with generalist and narrow specialist larvae had less stable populations than moderate specialists. Adult feeding guilds did not differ in stability and no differences were found in the abundance of species with different adult foods.

The observations of syrphids in the present study are restricted to several months over a two year period; therefore they provide an incomplete record of the syrphids associated with area. However, they do provide information on the timing of appearance and relative abundance of syrphids in early summer which is the important period in terms of the control of aphid population growth.

Materials and methods

The study area and standard census walk were described in Chapter three so only a brief summary is provided here.

The south-facing headland of Side Scammel was censused in 1989 and 1990. During both years the headland was divided into alternate blocks, of conservation and fully sprayed headland, along its length. The margin of Side Scammel consisted of an approximately 10m wide shelterbelt containing beech, *Fagus sylvatica*, Yew *Taxus* spp., sycamore *Acer pseudoplatanus* and bramble, *Rubus fruticosus*.

During 1989 censuses took place at approximately weekly intervals from 25 May to 26 July inclusive. Censuses began at 04.30 G.M.T.; each census lasted approximately 90 minutes. It was usually possible to complete five standard census walks in a single day. During 1990 censuses took place at approximately weekly intervals from 24 April to 10 July. On each date there was a single census which usually began at 07.00 GMT. The censuses in 1989 had shown that syrphid activity reached a peak in mid morning, after which activity declined, presumably due to the high temperatures recorded around mid-day and in the early afternoon. Censuses were not carried out on cold, wet days; therefore, the recorded changes in the abundance of flies are not a result of adverse weather conditions on particular census days.

During each census a set route along the headland was walked at a constant speed. Adult syrphids encountered during the census were identified to species and the behaviour at the time of first siting was recorded onto a microcassette tape recorder. Each observation had a corresponding recording of the time of day, cloud cover, wind speed, temperature and relative humidity. The starting point for the standard census was randomly allocated. The standard census walk techniques is described in more detail in Chapter three.

The number of species recorded during the census is a non-linear function of the time spent observing; therefore, it was not possible to correct for the differences in census duration between years. As a result, care must be used when comparing the species composition of syrphids at the site between the two years.

Results

Table 1 shows the percentage species composition of syrphids during 1989 and 1990; the data is represented graphically in Fig.1. When data from the period 25 May to 12 July was pooled there was no significant difference in the species composition between years (Kolmogorov-Smirnov goodness of fit test; D =0.364; N.S. n=12; Fig.2).

Figs. 3-6 show the number of individuals observed per census hour, on each of the sampling dates in 1989 and 1990, for eight commonly occurring species. Because of the different times of day at which the censuses were carried out and the different census durations between dates and years the calculated values for the numbers observed per hour are not directly comparable; however, the figures show the changing trends in the number of individuals of each species with time in each of the two years.

Fig. 3 shows that *E. balteatus* was recorded throughout the sampling period, although individuals were recorded in low numbers during late April and early May. The trends recorded were consistent between the two sampling years. *M. scalare* was consistently one of the most abundant species during late April and early May 1990 and was also recorded during July 1989. It was not possible to differentiate between males of *Syrphus vitripennis* and *Syrphus ribesii* in the field; therefore all the data was pooled to produce a phenological curve for *Syrphus* species. Low numbers of

Table 1 The percentage species composition of syrphids on each of the sampling dates during (a) 1989 (b) 1990.

Species	25 May	13 June	21 June	12 July	19 July	26 July
E. balteatus	61.7	34.1	70.6	58.2	27.7	4.4
M. corollae	10.3	9.1	6.3	28.6	37.9	15.4
Melanostoma spp.	9.1	10.1	2.5	5.6	5.3	15.4
Syrphus spp.	1.6	3.4	8.4	2.0	0.5	1.6
P. manicatus	2.8	3.8	0	0	4.9	6.0
P. albimanus	2.8	9.1	1.7	0.5	0.5	0
R. campestris	0.4	0	0	0	0	0
C. cautum	2.8	2.4	0	0	0	0
S. pipiens	5.1	8.2	7.6	3.1	13.6	50.
L. lucorum	1.2	1.0	0	0	0	0
Er. arbustorum	1.2	0	0	0	0	0
Er. nemorum	0.4	0.5	0	0	0	0
Er.tenax	0.8	12.5	0.8	0	0.5	0.5
Sp. scripta	0	1.0	0.4	1.5	9.2	15.4
Sc. pyrastri	0	1.0	0	0	0	0
V. pellucens	0	0.5	0	0.5	0	0
P. peltatus	0	0	0	0	0	1.1
H. pendulus	0	0.5	0	0	0	0
N	253	208	238	392	206	182
Census duration (mins)	540	440	440	450	540	450

Species	24 April	30 April	5 May	17 May	25 May	12 June	24 June	3 July	10 July
E. balteatus	0	2.3	2.6	14.6	81.8	53.0	68.6	82.6	53.7
M. corollae	16.1	2.3	2.6	20.2	4.5	34.5	5.9	0.9	11.3
Melanostoma spp.	9.7	20.9	28.2	15.7	4.5	3.0	5.3	0	1.7
Syrphus spp.	21.0	27.9	28.2	11.2	3.6	3.0	4.1	8.1	14.0
P. manicatus	3.2	16.3	0	2.2	0.9	1.0	0	0	0
P. albimanus	25.8	16.3	0	4.5	0	1.0	0	1.0	1.5
R. campestris	4.8	0	0	2.2	0	0	0	0	0
C. cautum	0	0	0	1.1	0	0	0	0	0
S. pipiens	0	2.3	10.3	10.1	0.9	0	0.6	3.8	9.6
L. lucorum	1.6	2.3	0	2.2	0.9	0	0	0	0
Er. arbustorum	6.5	0	5.1	0	0	0.3	0	0.7	0.2
Er. nemorum	0	0	0	2.2	0	0	0	0	0
Er. tenax	8.1	0	2.6	11.2	2.7	1.4	0.6	1.4	2.5
Sp. scripta	3.2	9.3	12.8	2.2	0	1.4	14.8	2.5	5.4
Sc. pyrastri	0	0	0	0	0	0.7	0	0	0
V. pellucens	0	0	7.7	0	0	0	0	0	0.2
P. peltatus	0	0	0	0	0	0.7	0	0	0
N	62	43	39	89	110	296	169	1030	816
Census duration (mins)	200	170	190	190	180	175	115	100	100

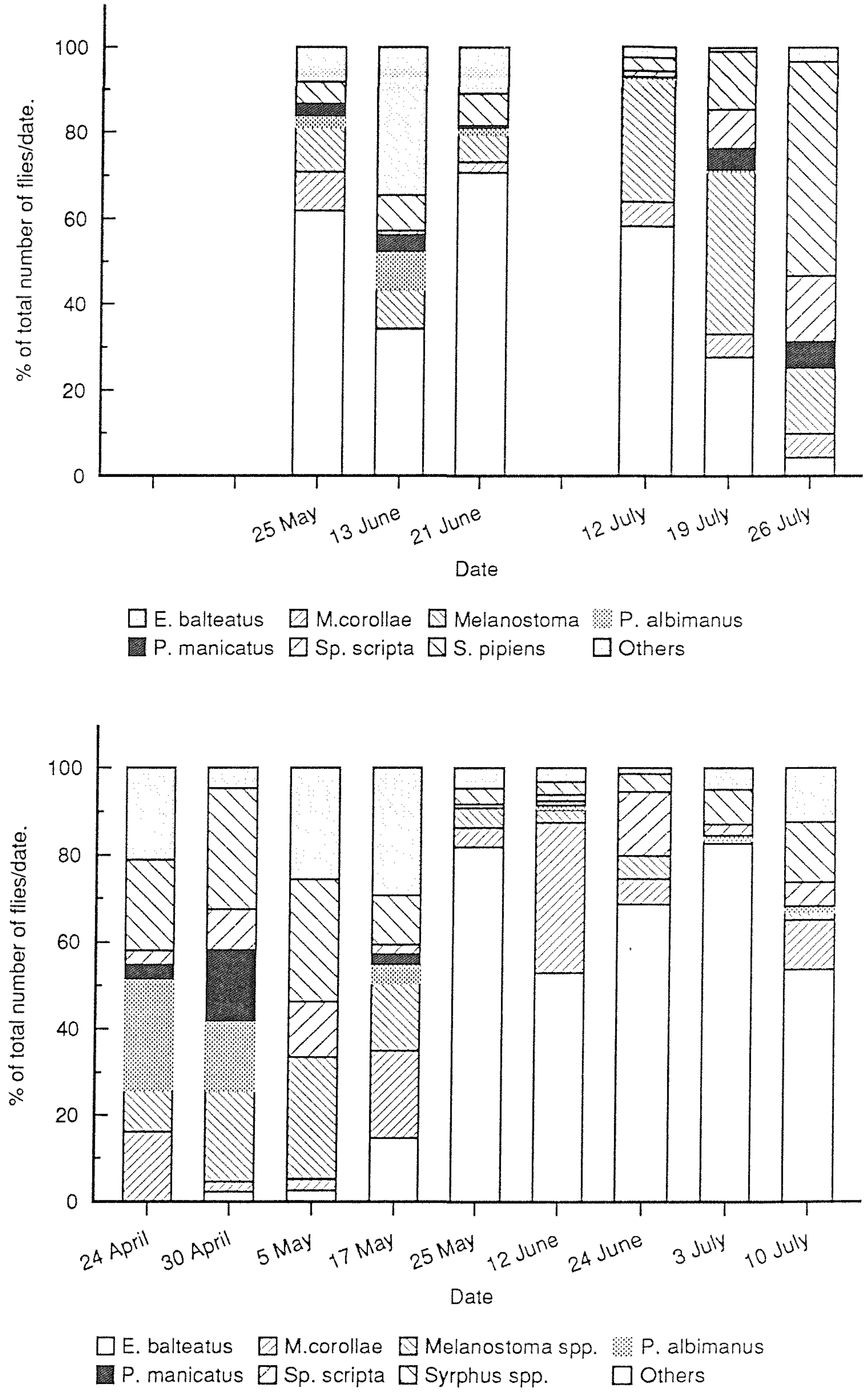


Fig.1 Comparison of the relative abundance of syrphid species observed in the headland of Side Scammel during 1989 and 1990.

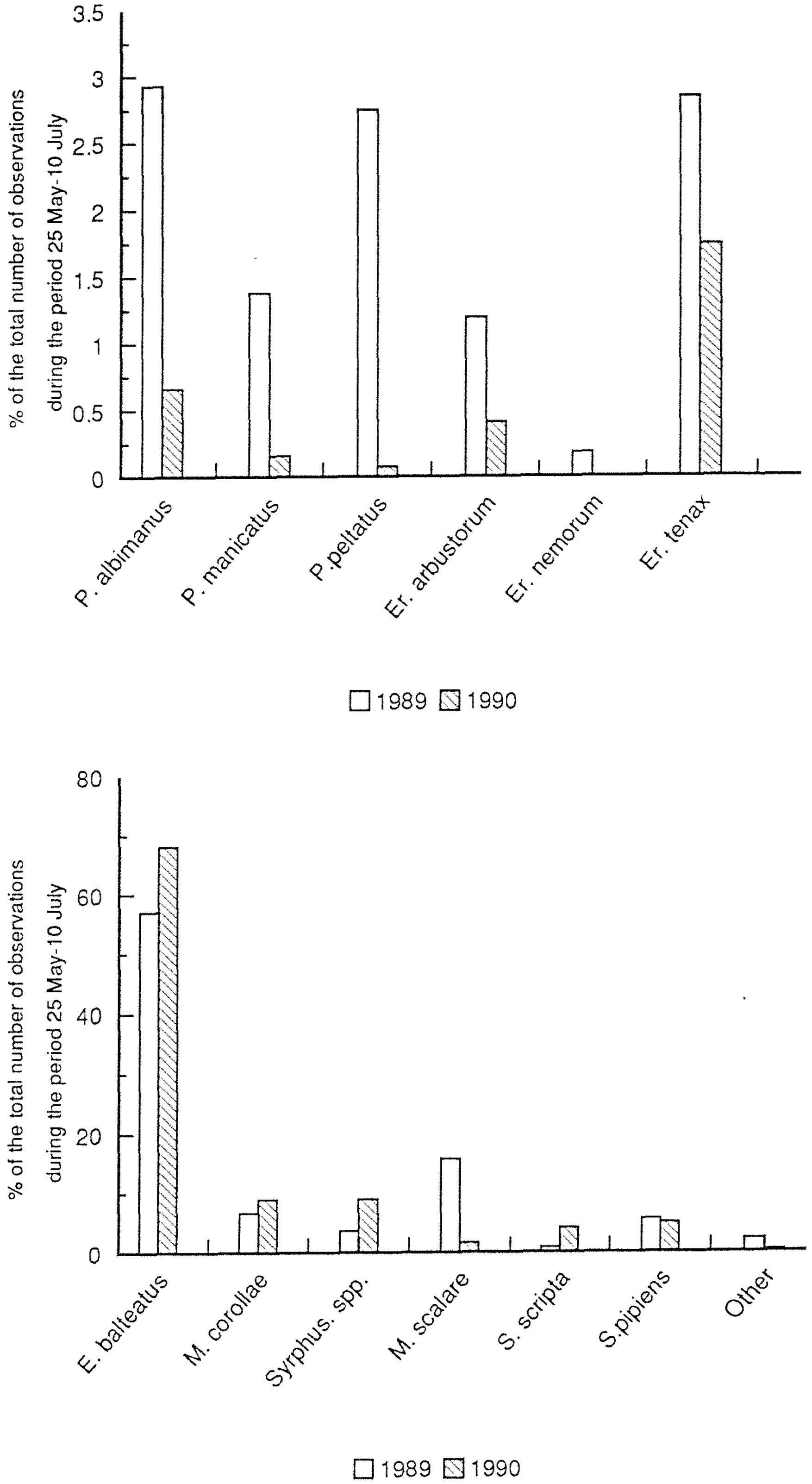


Fig.2. Comparison of the species composition and relative abundance of flies during the period 25 May-10 July 1989 and 1990

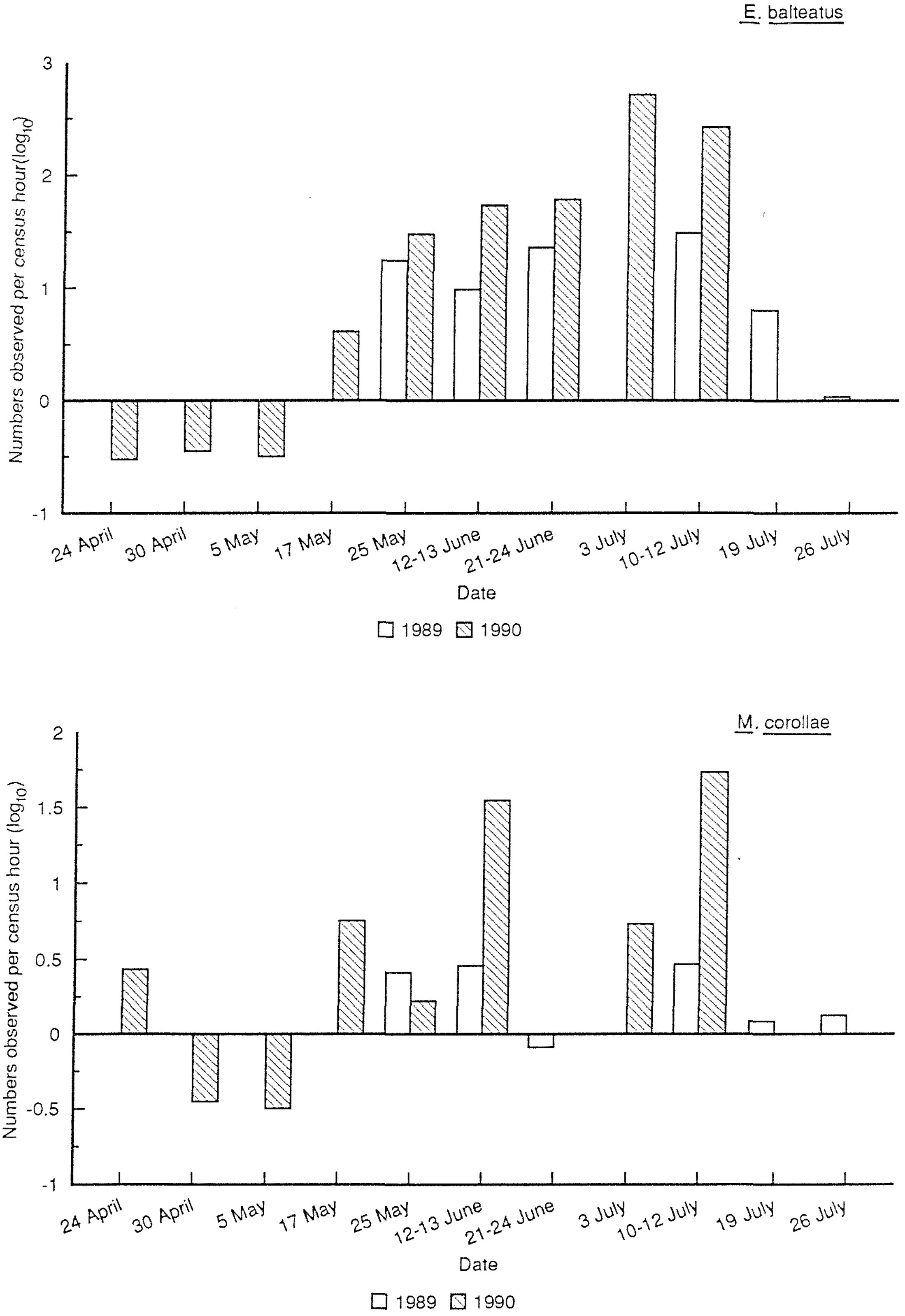


Fig. 3. The numbers of E. balteatus and M. corollae observed per census hour on census dates during 1989 and 1990.

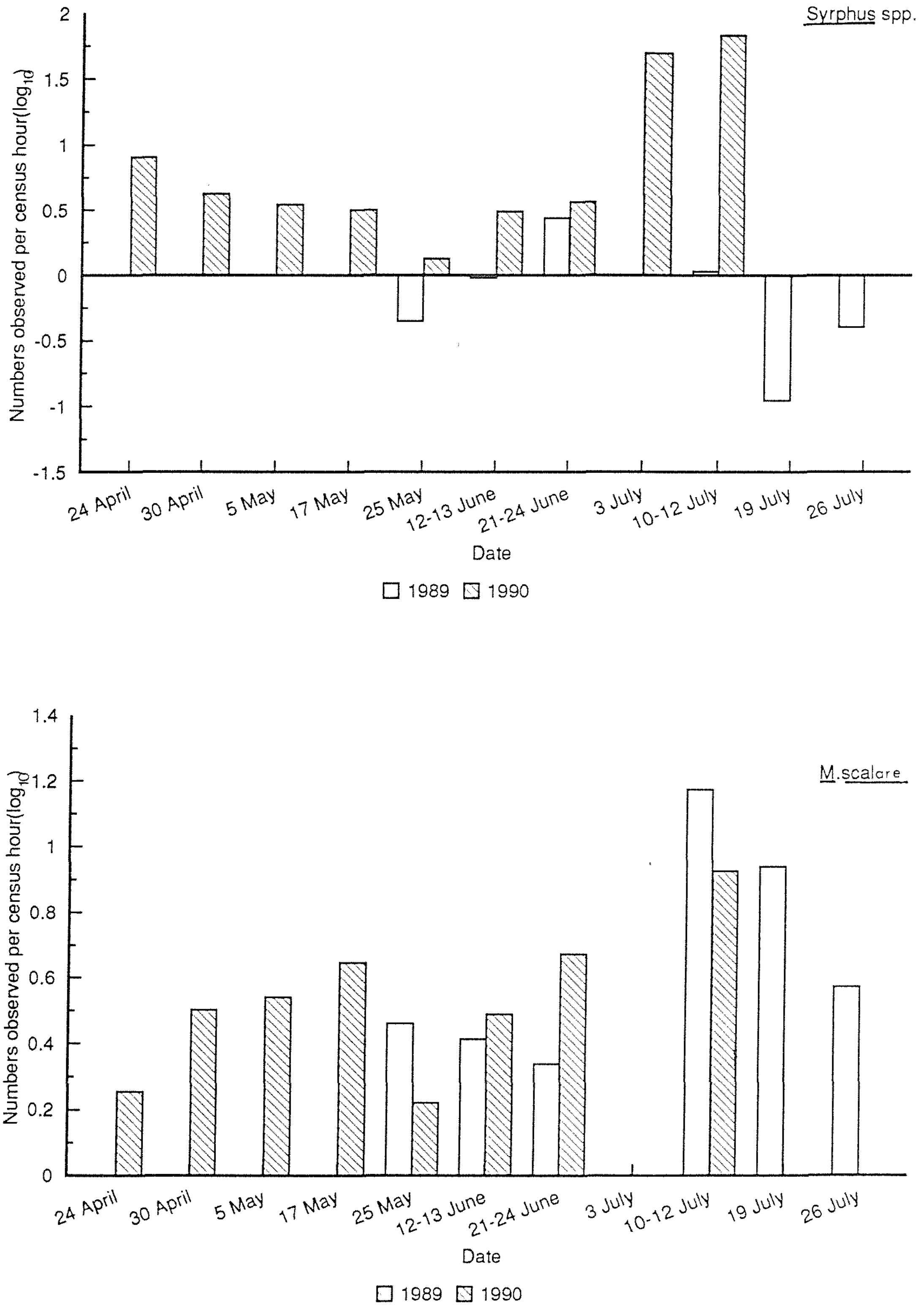


Fig.4. The numbers of Syrphus spp. and M. scalare observed per census hour on census dates in 1989 and 1990.

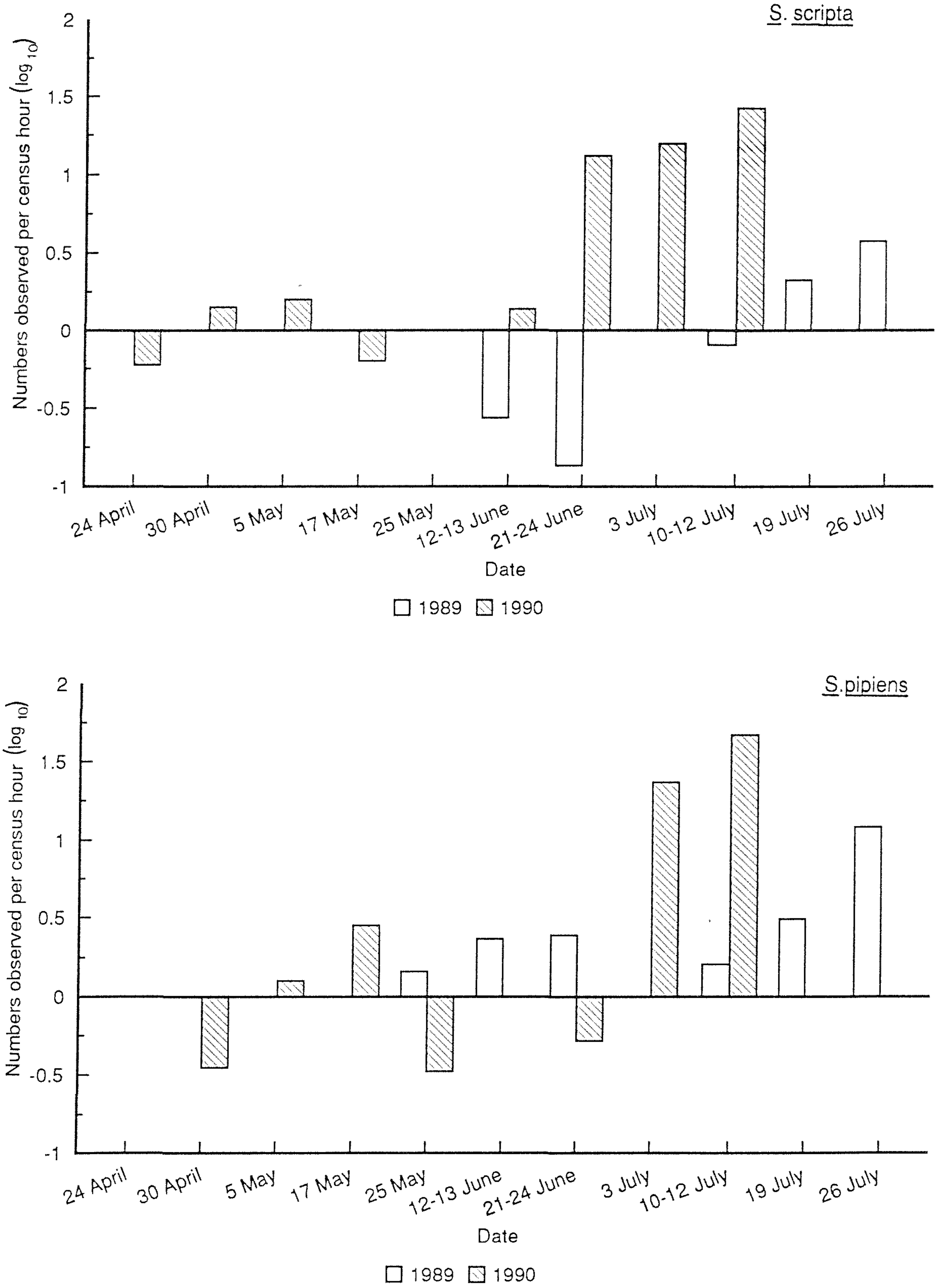


Fig. 5. The numbers of S. scripta and S. pipiens observed per census hour on the census dates in 1989 and 1990.

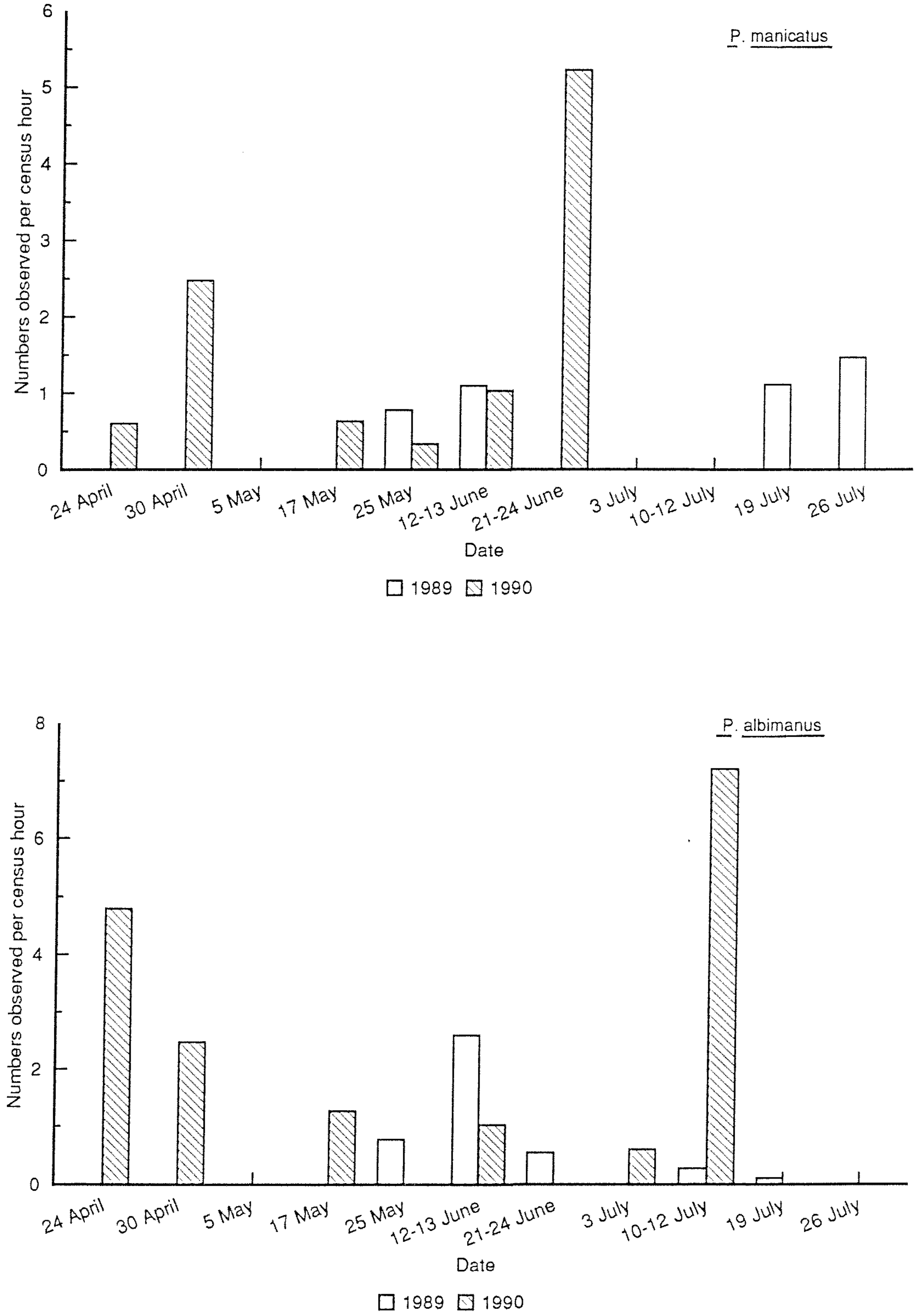


Fig.6. The numbers of P. manicatus and P. albimanus observed per census hour on census dates during 1989 and 1990.

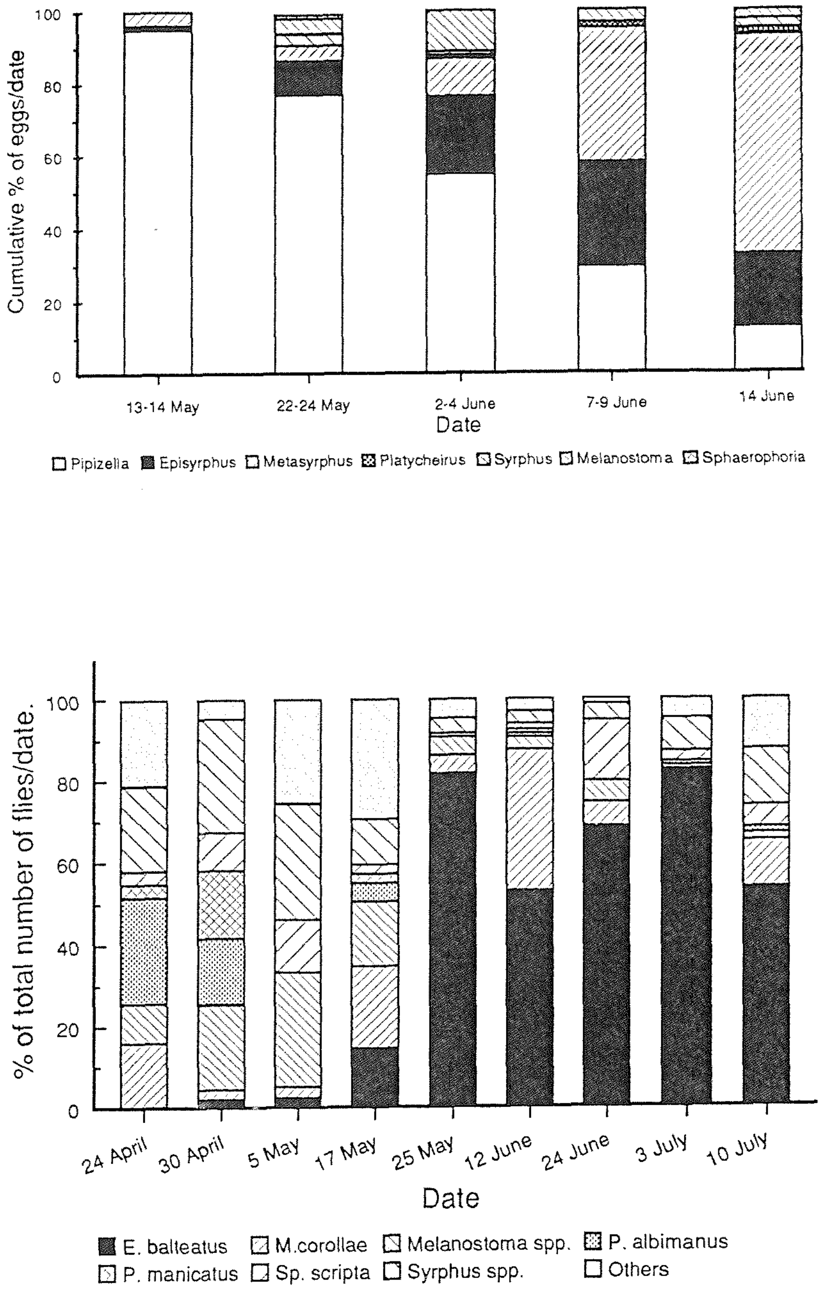


Fig.7 Comparison of the percentage composition of indentiied syrphid eggs and syrphid adults in the headland of Side Scammel, 1990.

individuals were recorded in 1989; individuals were relatively more abundant in 1990 and were recorded from late April to mid-July. With *M. corollae* there appeared to be a lull in the numbers of individuals observed during late June and early July in both years. Both *S. pipiens* and *S. scripta* showed trends towards higher numbers of individuals being recorded during early July. With the remaining two species, *P. manicatus* and *P. albimanus*, it was not possible to detect a consistent trend between the years; both species occurred intermittently throughout the sampling periods.

Fig. 7 shows the composition of adult syrphids recorded during the standard census walks of the headland in 1990 and the composition of identified eggs collected from the headland during the same period.

Discussion

The phenologies of the commonly occurring syrphids recorded in the present study are broadly similar to those described by Pollard (1971). He recorded *E. balteatus* and *M. scalare* occurring throughout the period from May to late September. Peaks in the numbers of mature *M. scalare* females occurred during late May- mid June and mid September. The timing of the appearance of mature *E. balteatus* females differed between the two years of his study. Low numbers of mature *E. balteatus* females were recorded during May, June and July in the first year while in the second year the mature females were not recorded until late June. The large numbers of *E. balteatus* individuals during August and early September were immature females and males.

During the present study it was usually not possible to differentiate between mature and immature females during the standard census walks. However, the identified syrphid eggs collected from the headland in 1990 can be used to estimate the timing of the appearance of mature females within the crop. *E. balteatus* adults were recorded in low numbers throughout April and early May; however eggs of this species were first recorded in the second week of May; at this time aphid densities ranged from 0-1.1 aphids per 20 stems (G.S. 47). *M. scalare* adults were relatively more abundant than *E. balteatus* adults during late April and early May. However, *Melanostoma* eggs were not recorded until the period 22-24 May; the eggs were most abundant during the first week in June. *Metasyrphus* eggs were most abundant during mid June; the collection and identification of eggs did not continue after this period, therefore it was not possible to examine whether the lull in the number of *M. corollae* adults recorded during late June and early July was associated with a reduction in the relative abundance of *Metasyrphus* eggs in the crop at this time. In Pollard's study *Syrphus* eggs were the most commonly recorded eggs on aphid- infested Brussels sprout baits in an arable crop during late May. In the present study *Syrphus* adults were recorded throughout the sampling period in 1990; however, their eggs never represented a significant proportion of the total number of eggs recorded on any date.

Dean (1982) recorded the occurrence of syrphid adults within a field of winter wheat using sticky traps; there were peaks in the abundance during early June and early August with a lull in the number of flies trapped during early July. This can be explained by the observation that *Platycheirus* species were the most commonly recorded syrphids on the sticky traps during the study. Pollard (1971) showed that the commonly occurring members of this genus are bivoltine, the first generation of flies being recorded in June and the second during August.

Dean (1982) also recorded the occurrence of different syrphid life-stages within the crop. Syrphid eggs were recorded during the last week in May until the end of July. Syrphid larvae were first recorded during the second week in June; at this time there were 63 aphids per 100 stems. The maximum number of syrphid larvae occurred during early July. However this was too late to have an impact on the aphid population peak. This is in contrast to the observations of Chambers and Adams (1986) who calculated that syrphid larvae had the potential to halt aphid increases in four of the six field populations of cereal aphids which they studied.

The majority of larvae collected from wheat during Dean's study were identified as *E. balteatus*. These observations, in addition to those in the present study indicate that although adults of several species may occur in the vicinity of the crop it is *E. balteatus* (and *Metasyrphus*) eggs and larvae which are most abundant in the crop. The failure to detect significant numbers of *Melanostoma* eggs and *Platycheirus* larvae, despite the relative abundance of the adults may be a result of the oviposition behaviour of these species. That is, plant related factors are relatively more important than aphid-related factors in stimulating oviposition in both genera.

Pollard (1971) recorded differences in the timing of the appearance of mature females of several species between the two years. For example, mature *P. clypeatus* females occurred several weeks earlier in the second year than in the first. *E. balteatus* females showed the most pronounced variation between years, appearing a month later in the second year than in the first. In the present study syrphid eggs recorded in 1989 were not identified. Therefore, it was not possible to compare the timing of the onset of oviposition between the years. Similarly because no censuses were carried out prior to 25 May in 1989, it is not possible to compare the timing of the appearance of *E.balteatus* adults between years. In addition to differences in the timing of the appearance of flies between years, differences in the appearance of flies between regions, within a single year have also been recorded. For example, Poehling, Tenhumberg and Groger (1991) recorded a time lag of several weeks between the appearance of *E. balteatus* adults in winter-wheat crops in southern and northern Germany.

Table 2 compares the percentage composition of syrphids in the present study with previous studies of the composition of syrphids occurring in a range of habitats. In the majority of studies *E. balteatus* was the most abundant species while the relative abundance of the remaining species varied between the studies. *Met. corollae, M. mellinum, Platycheirus clypeatus, P. manicatus,*

Table2 The percentage species composition of syrphids recorded during this study and comparisons with other studies (modified from Gilbert 1981).

Species	1	2	3	4	5	6	7	8	9
Cheilosia pagna	0.3	0.2	1.6	0	0	1.1	0	0	0
E. balteatus	31.7	30.4	21.6	31.1	31.4	4.4	9.0	46.5	66.5
Er. arbustorum	4.1	0.3	1.7			4.9		0.9	0.6
Er. tenax	6.3	1.1	0.8			1.2		2.2	1.7
H. pendulus	0.3	0.3	1.8	0	0	2.2	0	0.1	0
Melanostoma spp.	8.8	19.2	12	34.6	22.1	11.6	22.6	18.8	2.3
M. corollae	13.6	7.4	0.4	2.6	1.4	1.6	1.6	6.3	8.4
Pi. austri	0	0	0	0	0	0	0	0	0
P. albimanus	8.0	2.9	3.9	1.9	1.2	0.8	11.8	2.2	1.3
P. clypeatus	1.4	5.7		5.6	4.0	5.3	9.3	0	0
P. manicatus	0.2	0.1	16.3	2.3	8.0	0.8	0.8	2.4	0.5
P. peltatus	0.7	0.7	4.7	3.0	10.2	1.0	1.4	0.1	0.1
R. campestris			1.0			2.2		0.1	0.1
Syrphus spp.	10.9	21.9	9.5	5.8	1.1	0.8	0.7	2.9	9.8
S. pipiens	6.6	4.7	1.0			3.7	20.5	12.1	4.4
Sp. scripta	1.9	0.4	0.2	0.1	4.8	0.6		3.8	3.8
Xylota segnis	0.1	0.1	6.0	0	0	0.7	0	0	0
N	4478	3314	1580	3806	2263	10857	2611	1479	3639

References

1= Botanic Garden, Cambridge 1979-1980 (Gilbert, 1981)
2= Fellows Garden, Cambridge 1979-1980 (Gilbert, 1981)
3= Hayley Wood, Cambridge 1979 (Gilbert, 1981)
4= Monk's Wood, Huntingdon 1969 (Pollard, 1971)
5= Monk's Wood, Huntingdon 1970 (Pollard, 1971)
6= Schleswig (Claussen, 1980)
7= Aphidophagous spp. in crops (Banks, 1959)
8= The present study: Side Scammel (25 May-26 July, 1989)
9= The present study: Side Scammel (24 April-10 July, 1990).

and *Sphaerophoria scripta* have all been categorised as predominantly open ground species (Pollard, 1971). However, with the possible exception of *M. corollae* there was no apparent trend for these species to contribute a greater percentage of the total number of adult flies in the more open habitats (Botanic garden and aphidophagous spp. in crops). *P. manicatus* was relatively more abundant in wooded areas; this is consistent with the suggestion that the availability of larval food determines habitat selection by syrphids. Gilbert (1981) recorded an increase in the proportion of the community occupied by facultatively aphidophagous species (such as *P. manicatus*) as the study area became more wooded. In the present study the shelterbelt adjacent to the headland may have influenced the species composition of syrphids. The shelterbelt provided a leaf litter layer which has been recorded as a larval habitat for facultatively aphidophagous species (Rotheray and Gilbert, 1989) and it also contained herbaceous plants; *Sphaerophoria* larvae have been recorded foraging on aphids associated with herbaceous plants (Watts, 1983).

The differences in the relative abundance of *S. pipiens* between years in the present study were affected by the species composition of non-crop plants in the headland. During 1989, mayweed, *Matricaria perforata* and fool's parsley, *Aethusa cynapium* were the dominant plant species in areas of the headland where the density of wheat shoots was low. Female *S. pipiens* foraged on these low-growing plants while male flies hovered in the immediate vicinity of the flowers, mating with the females as they fed. In 1990 these low-growing flower species were less common and both male and female *S. pipiens* were recorded in low numbers.

Table 2 also shows that the relative abundance of *Syrphus* species varied between years in both the present study and that of Pollard. In addition, *E. balteatus* and *Metasyrphus* species were also relatively more abundant in the second year of the present study. The different census durations may have contributed to this variation although personal observations indicated that there were higher numbers of these species in the headland area in 1990. Owen and Gilbert (1989) showed that population stability was related to the degree of predator specialization; generalists and narrow specialists had less stable populations than moderate specialists. Therefore, fluctuations in abundance between years may be an inherent property of syrphids with larvae which are generalist predators. However, in the present study differences in the availability of adult food sources in the headland between the two years may have also affected the abundance of flies of several species within the area.

Gilbert and Owen (1990) used Malaise trap catches collected over a 15 year period to look for evidence of competition between syrphid species in a garden community. They concluded that there was no evidence for competition between adult feeding guilds or within guilds of highly or moderately specialized predatory larvae or between generalist predators and the rest. The rank abundances of species were preserved from year to year indicating some sort of structure to the community; however, the authors concluded that this had little to do with interspecific competition among larvae or adults and was not affected by morphology. They suggested that species were tracking resources independently; the long term maintenance of rank abundances was resource based and not a result of competitive relationships. Therefore, the higher relative abundance of *E. balteatus, M. corollae* and *Syrphus* species in 1990 may represent parallel fluctuations in density of generalist foragers tracking common resources. *E. balteatus* forages predominantly on pollen while *M. corollae* and *Syrphus* species take a mixture of pollen and nectar, although pollen predominates. The higher densities of individuals of all these species may have been a result of the increased availability of pollen (and nectar) sources in the headland in 1990 compared to 1989. There was also a difference in the relative density of *Melanostoma* individuals between the two years; they were relatively more abundant during 1989. These flies feed primarily on anemophilous pollens, which were relatively less abundant in 1990. The relative abundance of adult *Eristalis* did not differ widely between the two years; these species are also generalists taking a mixture of nectar and entomophilous pollen. This might suggest that the difference in the relative abundance of species between years was not influenced by availability of adult food sources. However, although these species are generalists they take more nectar than pollen (Gilbert and Owen, 1990). The common poppy, *Papaver rhoeas* was the most abundant flower in the headland in 1990, therefore, the relative availability of nectar sources for *Eristalis* may not have differed substantially between the years accounting for the similarity in the relative abundance of these species between years. Studies which identify the "key-factor" in the populations of syrphids, in particular those with generalist predatory larvae, are required to clarify the relationship between the availability of adult food sources and syrphid population levels.

Gilbert and Owen (1990) suggested that competition may occur between generalist predatory larvae; therefore, the availability of larval food supplies may be more important than the availability of adult food sources in determining the population levels of these flies. An understanding of the relative importance of the availability of adult food sources in determining the population levels of the flies is necessary to identify the potential for using field margin manipulation to enhance the bio-control potential of syrphids. The benefits of such techniques may be limited to the redistribution of flies between fields or areas of farmland. In this case it is particularly important to know the scale of movement of the flies and the relationship between adult feeding sites and the location of oviposition sites. Work described in Chapter seven was designed to assess the potential for using marking techniques to examine habitat use and the scale of movement of *E. balteatus* adults on farmland.

DIURNAL ACTIVITY PATTERNS

Introduction

The periodicity of insect activity is influenced by both endogenous and exogenous factors. Exogenous factors include light intensity, temperature, humidity and wind velocity; insects experience the microclimatic variation of these factors which appear to act by imposing thresholds which limit the duration of activity (Corbett, 1966). Taylor (1963) determined the temperature threshold for flight in several species by comparing catches of the insects at different temperatures. The percentage of occasions when flight occurred was calculated for each temperature and the values plotted against temperature. The failure to detect a sharp transition from no flight to 100% flight was attributed to variation amongst the population and limitation in the temperature measurements.

Gilbert (1981) reviewed the diel periodicities reported for syrphids in the literature; peaks were recorded early in the morning (Nielson, 1966; Stelleman and Meeuse, 1976; Grosser, 1979: Morse, 1981), nearer mid-morning (Kormann, 1972; Maier and Waldbauer, 1979; Zimina, 1957), near midday (Lewis and Taylor, 1974) or in late afternoon (Zimina, 1957). He attributed these differences in the reported periodicities to the different activities being observed or to climatic factors. Maier and Waldbauer (1979) recorded syrphids moving into woodland around midday when hygrothermal stress increased in the adjacent open spaces where the flies had previously been feeding. Other authors recorded flies becoming inactive during the hottest part of the day (Nielsen, 1966; Bankowska, 1964; Zimina, 1957; Hurkmans, 1985).

The hygrothermal (water & thermal) balance of an insect is dependent upon its size and its cuticular surfaces (Willmer, 1982). Size and coloration affect heating and cooling rates (Digby, 1955; Willmer and Unwin, 1981) and hence thermal balance whilst size and cuticular permeability affect evaporative losses and hence water balance (Edney, 1977, 1978). These factors (in conjunction with diel rhythmicity) are also important in determining the activity patterns of particular insect species. Willmer (1983) studied the activity patterns in nectar feeding insects, including syrphids. Foraging appeared to be largely determined by the visitors thermal requirements and the restrictions imposed by avoidance of overheating. The size and surface reflectance or colour of an insect affect both the temperature excess of the insect in constant radiation, and its rate of attaining that excess (Willmer and Unwin, 1981). In Willmer's study there was a consistent trend in the mean reflectance and weight of insects visiting flowers through the day; the mean weight of visiting insects was high early and late in the day and low when the flowers were strongly irradiated. Mean reflectance was low at dawn and dusk (blacks, browns and greys) and high through the middle of the day when light coloured and metallic insects were foraging.

Gilbert (1981, 1985) used time budgets, constructed from censuses of woodland and garden habitats, to examine the environmental factors influencing the diurnal activity patterns of syrphids. The results confirmed the importance of thermal balance in structuring diurnal activity patterns of the flies. Larger syrphids were active at lower temperatures than small ones, with the exception of *M. scalare* which was shade tolerant and tolerant of low temperatures. Gilbert suggested that the ability of individuals of this species and others (*Toxomerus marginatus* (Mesler, 1977) and *Platycheirus monticolus* (Nielsen 1972)) to be active at low temperatures may be associated with the observation that the flies specialize in feeding mainly on the pollen of anemophilous flowers which is high in starch and proline. The ability to fly in the shade at low ambient temperatures may be related to proline-fuelled flight.

In the present study observations of syrphid behaviour made during the standard census walks in the headland were used to construct activity profiles for five commonly-occurring species. The observed activity patterns are discussed in relation to environmental factors, in particular whether the observed patterns are consistent with the importance of size and thermal balance in determining activity. In addition, the observed patterns are discussed in relation to those recorded for syrphids in garden habitats by Gilbert (1985).

Results

Time of day and temperature

Fig. 8 shows the percentage of the total number of active flies (all behaviour categories excluding "inactive") observed during each hour for six commonly occurring syrphid species. During 1990 there was a single census on each date which was usually carried out between 08.00 and 11.00 GMT. Therefore, values in Fig. 8 are calculated from observations made during census walks in the headland during 1989. Three species (*E. balteatus, M. corollae* and *M. scalare*) had peaks in activity prior to 10.00h with the percentage of the total number of active individuals observed declining after this time. Fig. 9 shows the distribution of the percentage of the total number of flies of these species with respect to temperature. The values are calculated from observations made during census walks in 1989 and 1990. The lowest temperature at which active flies were observed was 11°C; fewer than 5% of the total number of *M. corollae, E. balteatus* and *M. scalare* adults were observed in each temperature category below 14°C and above 26°C. Between these extremes *M. corollae* and *E. balteatus* showed peaks of activity in the range 13-16°C and 20-24°C. *M. scalare* adults did not show a bimodal activity peak.

Fig. 8 shows a second group of three species (*E. tenax, S. pipiens* and *Syrphus* species) in which a larger percentage of the total number of individuals were recorded after 10.00h. Fig. 9 shows that *E. tenax* and *Syrphus* species had a single peak in activity in the range 20-24°C; less than 5% of the total number of observations were recorded in each temperature category below 19°C.

Fig. 10 shows the √ arc sine proportion of the total number of *E. balteatus* males and females observed in relation to temperature. In both sexes the proportion of flies observed declined above 24°C; when these temperatures were excluded from the analysis there was a significant

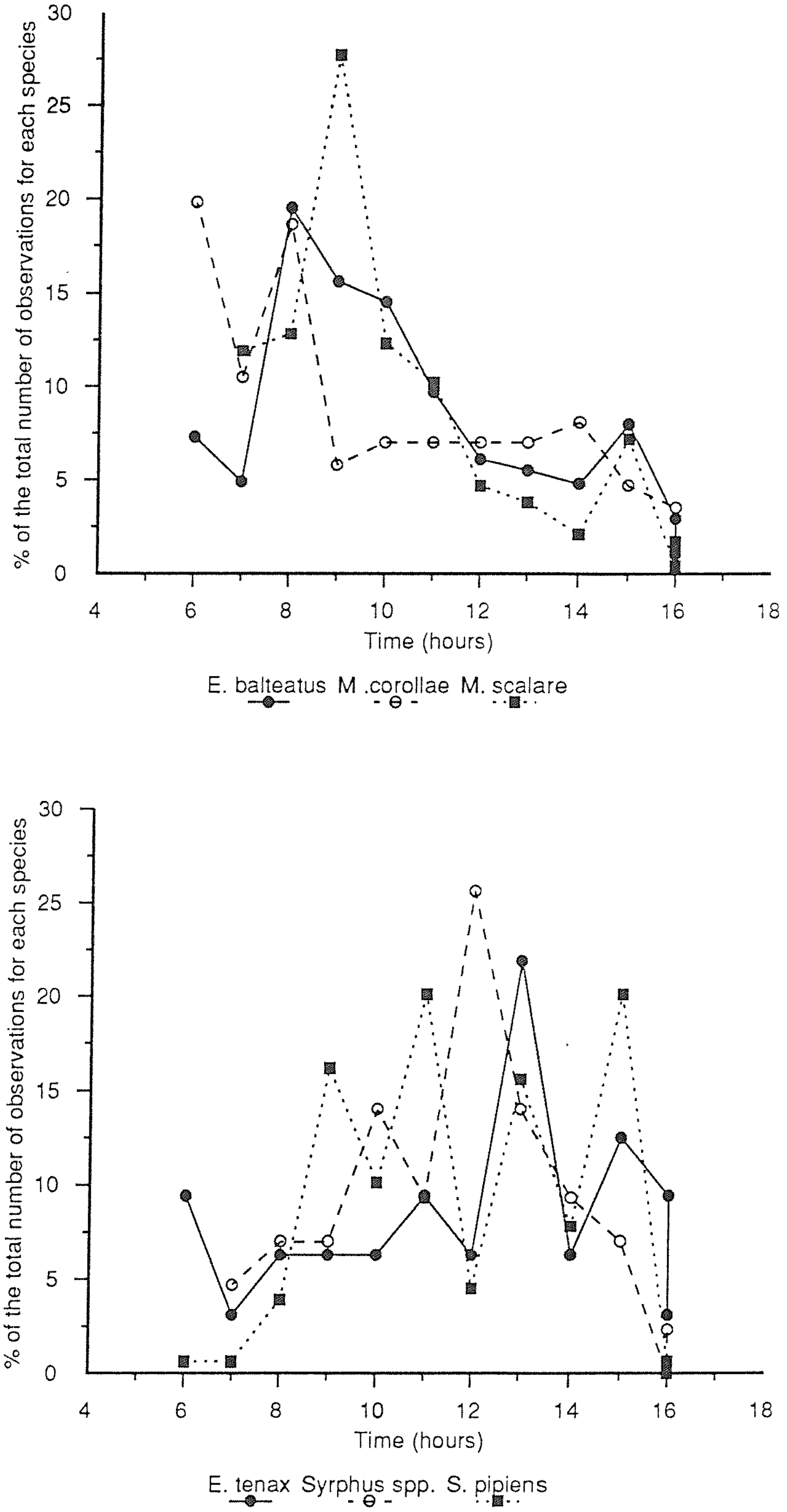


Fig. 8 The percentage of the total number of individuals of six commonly occuring species observed with time.

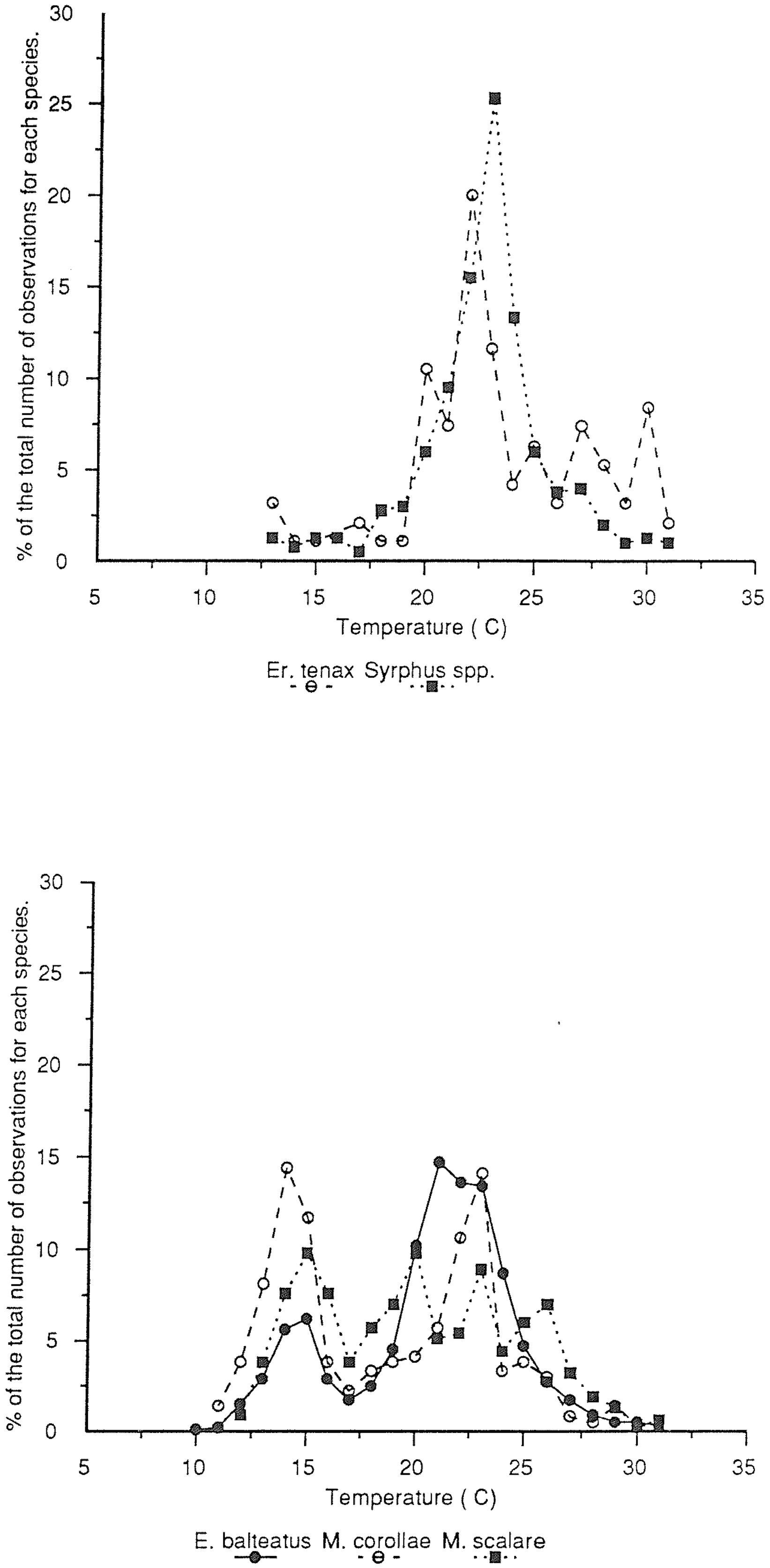
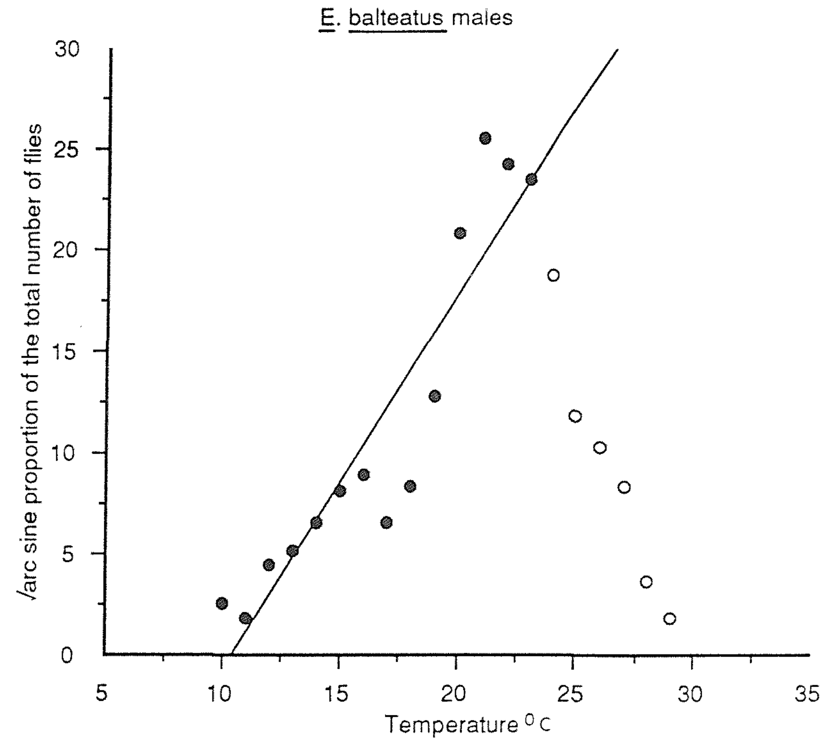


Fig.9. The relative activity of flies with respect to temperature Values represent the percentage of the total number of active flies of each species recorded at each temperature.



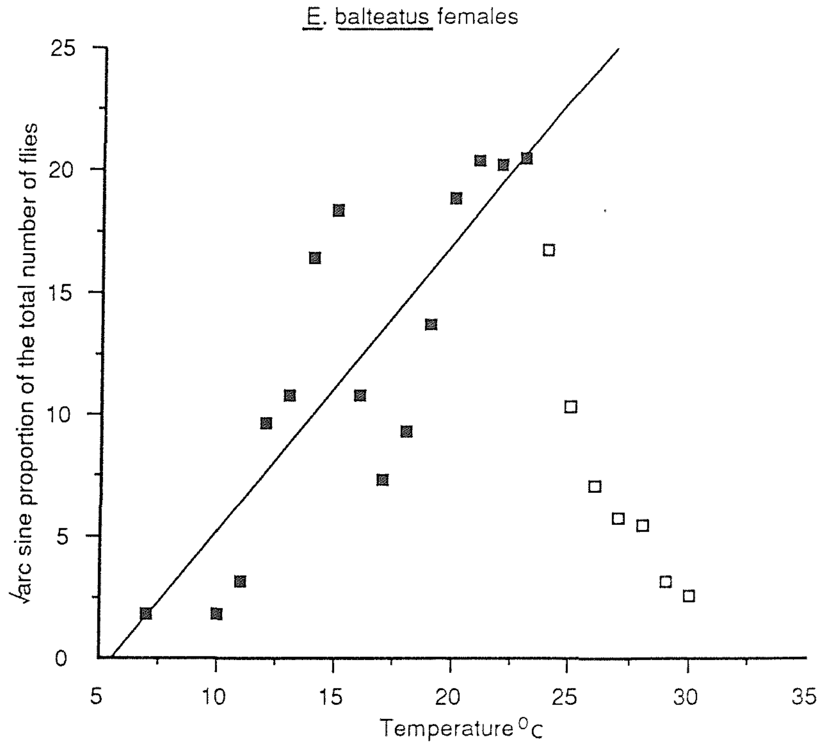


Fig.10. Relationship between the √arc sine proportion of the total number of flies observed during 1989 and 1990 and air temperature.
Values represented by open symbols were not included in analyses of the *relationship*.

positive relationship between the √ arc sine proportion of the total number of flies and temperature (males: t = 8.221, P<.001, r = 0.916; females: t = 5.207, P<.001, r = 0.822, d.f= 13).

Fig. 11 shows the relationship between temperature and the √ arc sine proportion of the total number of *Syrphus* spp. males and females. As with *E. balteatus* there was a cut-off point above which the proportion of flies observed declined with increasing temperature; when values corresponding to temperatures greater than 24°C were excluded from the analysis there was a significant positive relationship between the proportion of flies observed and temperature (males: t = 4.206, P<.005, r = 0.847, d.f=7; females t = 4.133, P<.005, r = 0.794, d.f=10). When values corresponding to temperatures above 24°C were excluded from the analysis of the relationship between the proportion of *M. corollae* males observed and temperature a significant positive relationship was produced (t = 2.907, P<.05, r = 0.659, d.f=11). However, Fig. 12 shows that there was no obvious cut-off point above which the proportion of *M. corollae* females observed declined. Analysis of the relationship using values corresponding to all temperature for which recordings were available indicated a significant negative relationship (t = -2.561, P<.05, r = -0.528, d.f=17). Similarly, it was not possible to identify a cut-off point above which the √ arc sine proportion of the total number of both *M. scalare* males and females declined. In this species there was no significant relationship between temperature and the proportion of flies observed (females: t = -1.590, P = N.S., r = -0.360, d.f.=17; males: t = -1.327, P = N.S., r = -0.334, d.f.=14; Fig. 13) although a negative trend was observed with the proportion of active flies decreasing with increasing temperature.

Fig. 14 shows the relationship between relative humidity and air temperature for 1989 and 1990. When data from 1989 and 1990 was pooled for analysis there was a significant negative relationship between air temperature and relative humidity (t = -4.977, P<.005; Fig 14(c)).

Relative humidity

Fig. 15 shows the relationship between the √ arc sine proportion of the total number of flies observed and relative humidity for *E. balteatus* (males: t = -5.821, P <.005, r = -0.604, d.f.=59; females: t = -4.297, P<.005, r = -0.495, d.f.=57;) and *Syrphus* species (males: t = -2.546, P<.05, r = -0.410, d.f.=32; females: t = -2.265, P<.05, r = -0.358, d.f.=35; Fig.16). There was a significant negative relationship between the √ arc sine proportion of the total number of *M. corollae* males and relative humidity (t = -3.288, P<.005, r = -0.486, d.f.=35; Fig. 17). There was no significant relationship between relative humidity and the proportion of *M. corollae* females observed (t = -0.636, P = N.S., r = -0.100, d.f.=40); or *M. scalare* adults of both sexes (males: t = 0.880, P = N.S., r = 0.217, d.f.=48; females: t = 0.879, P = N.S., r = 0.122, d.f.=51; Fig. 18).

Activity profiles

Observations of the behaviour of adult syrphids with respect to microclimatic factors made

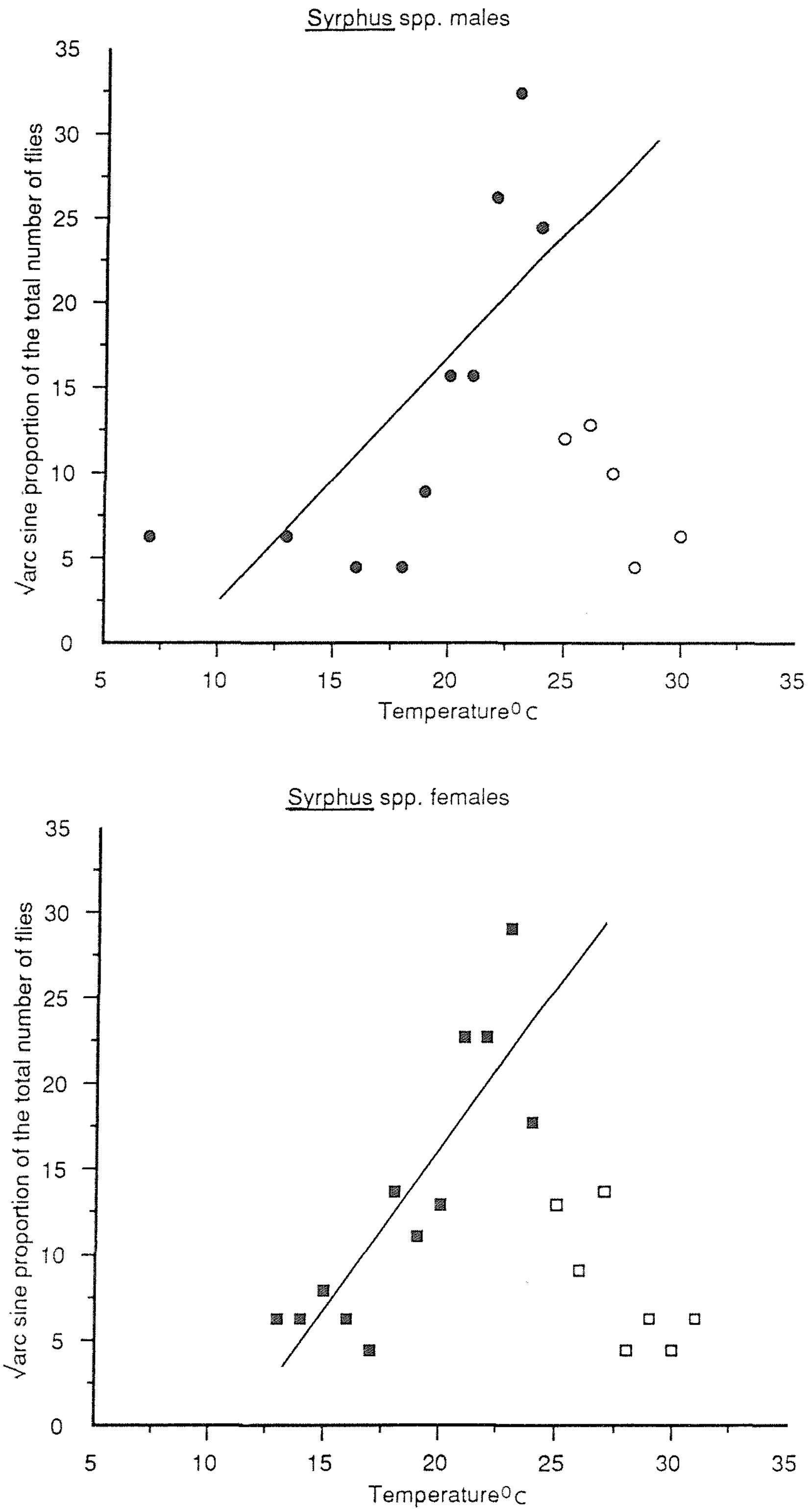
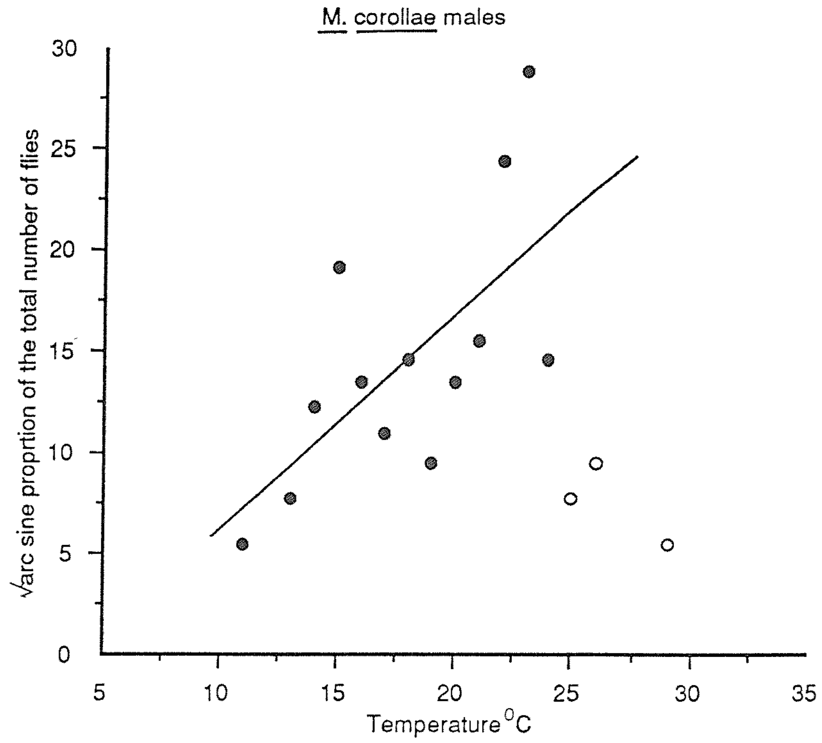


Fig.11. Relationship between the √arc sine proportion of the total number of flies observed during 1989 and 1990 and air temperature.

Values represented by open symbols were not included in analyses of the relationship


M. corollae males

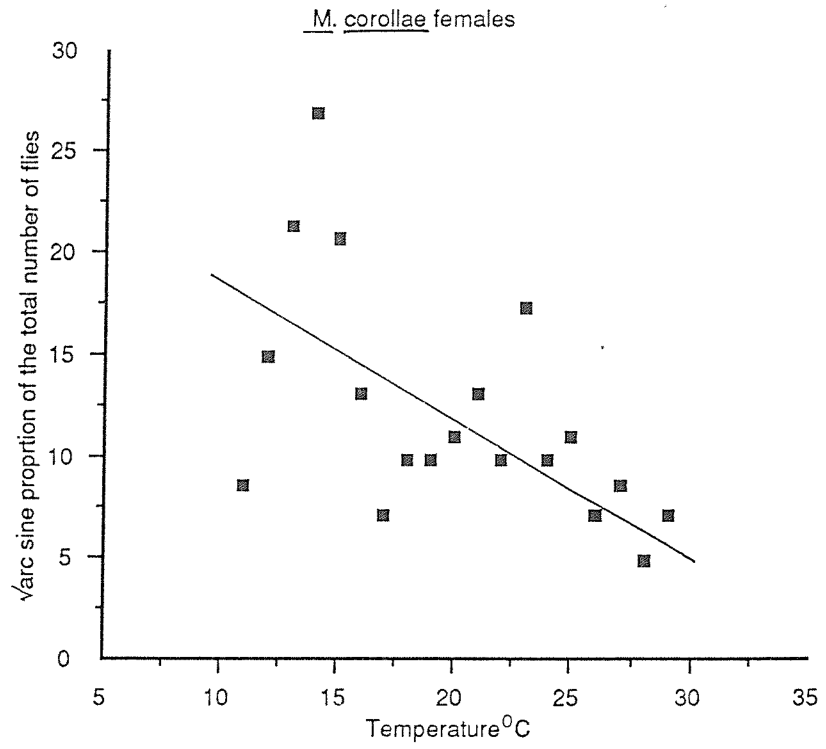
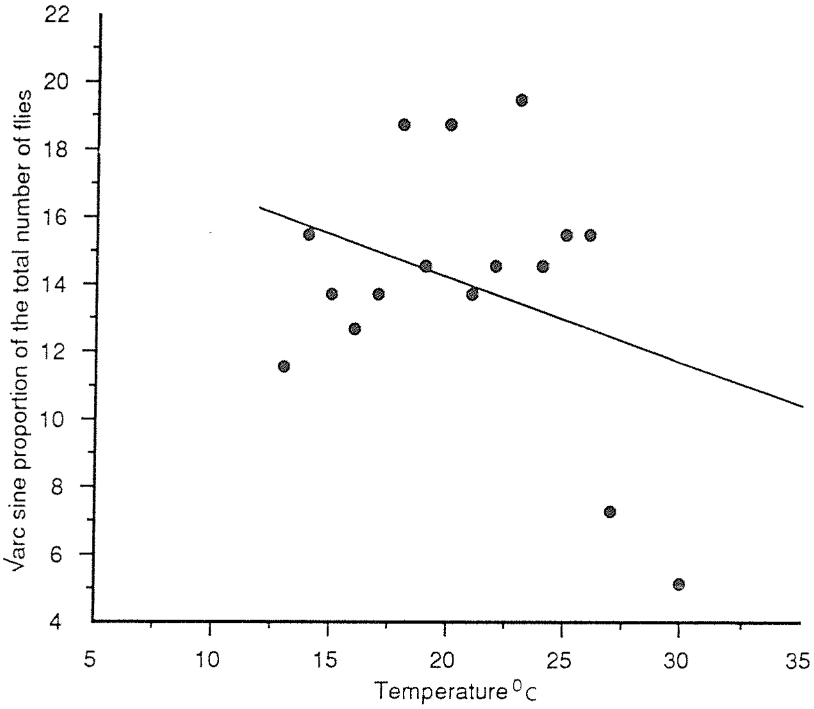

M. corollae females

Fig.12 Relationship between the √arc sine proportion of the total number of flies observed during 1989 and 1990 and air temperature. Values represented by open symbols were not included in analyses of the relationship.

M. scalare males



M. scalare females

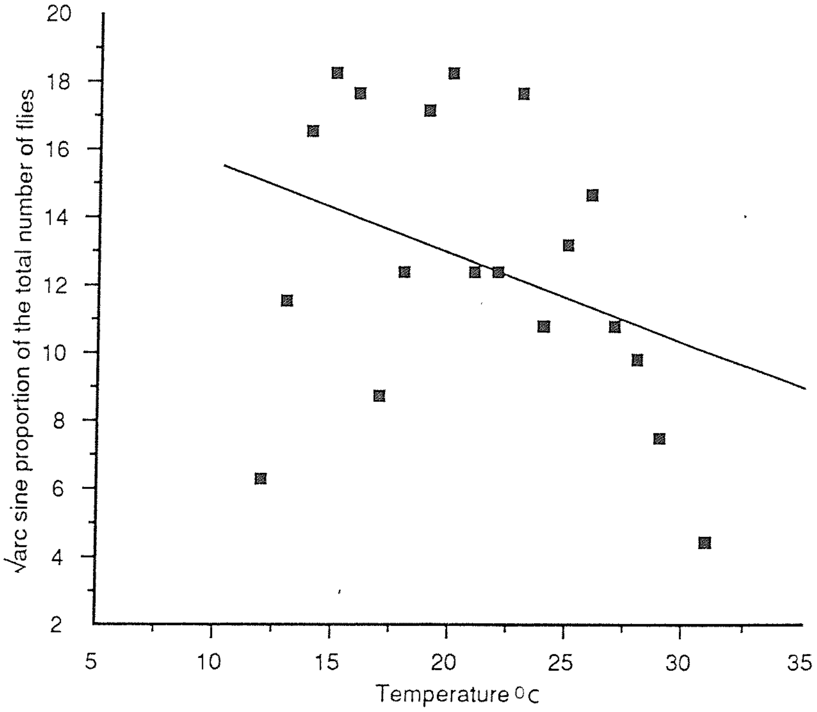


Fig.13. Relationship between the √arc sine proportion of the total number of flies observed during 1989 and 1990 and air temperature.

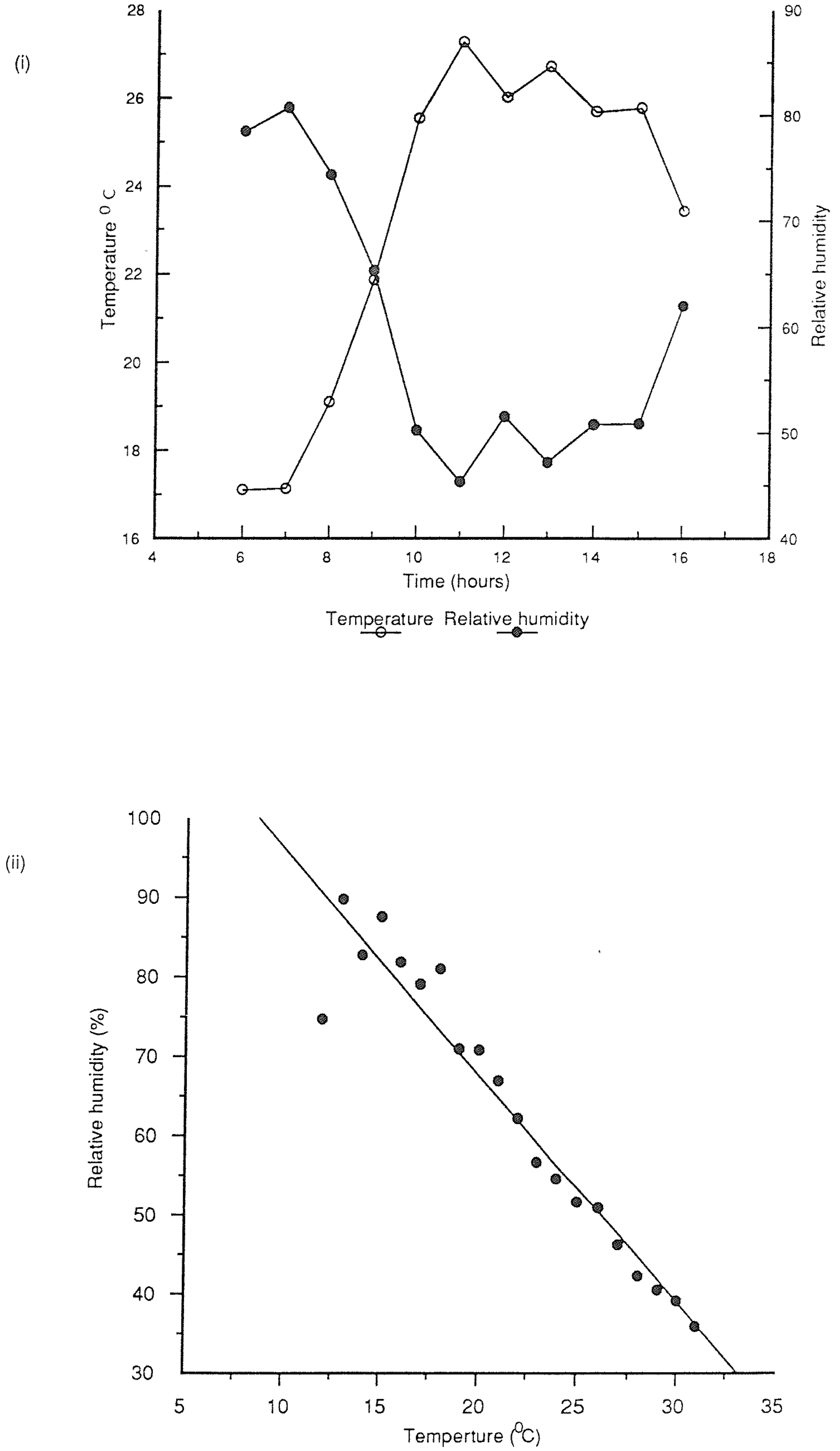


Fig.14a (i) variation in air temperature and relative humidity with time; data from all standard census walks in the headland of Side Scammel during 1989. (ii) Relationship between relative humidity and air temperature, 1989.

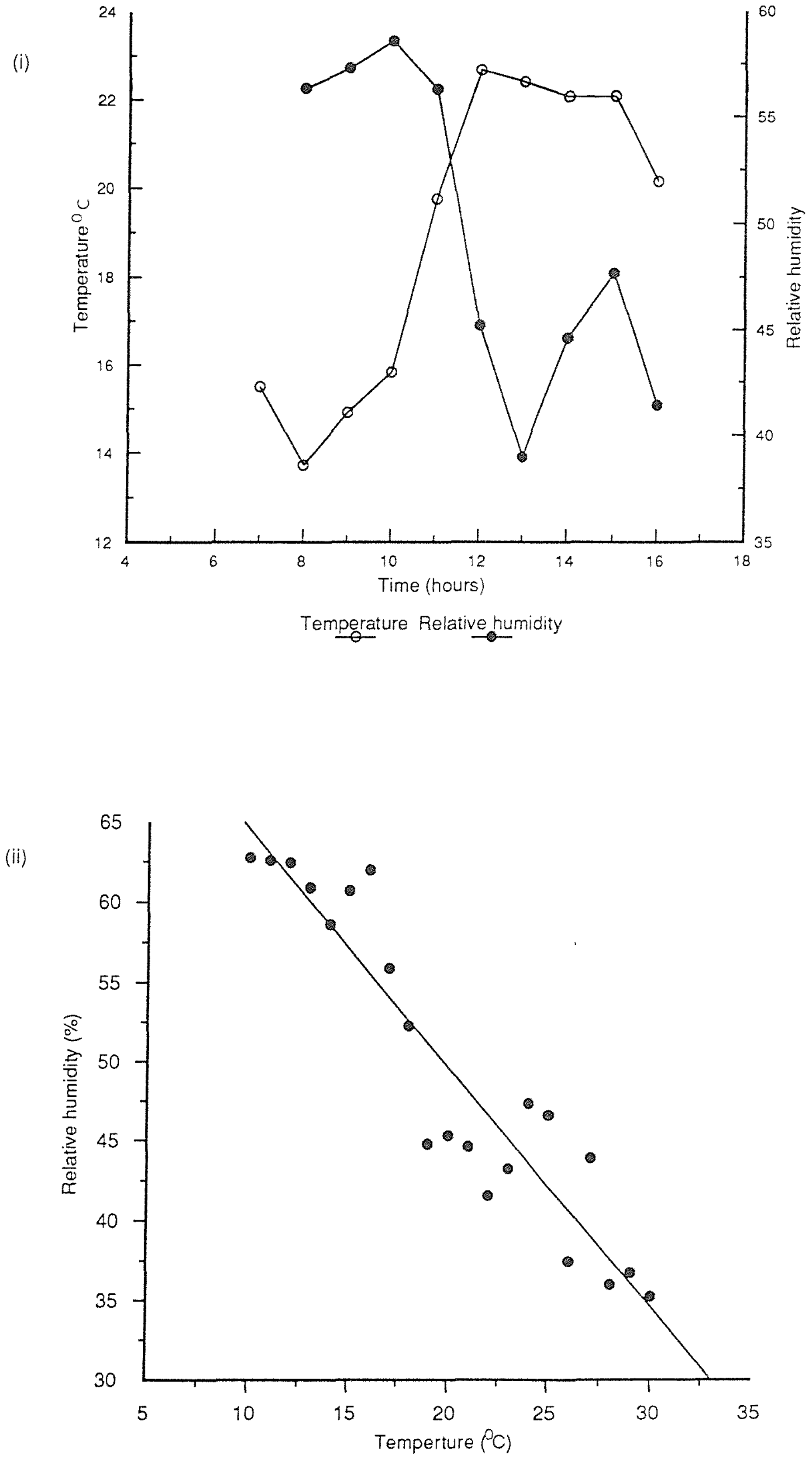


Fig. 14b(i) variation in air temperature and relative humidity with time; data from all standard census walks in the headland of Side Scammel during 1990. (ii) Relationship between relative humidity and air temperature, 1990.

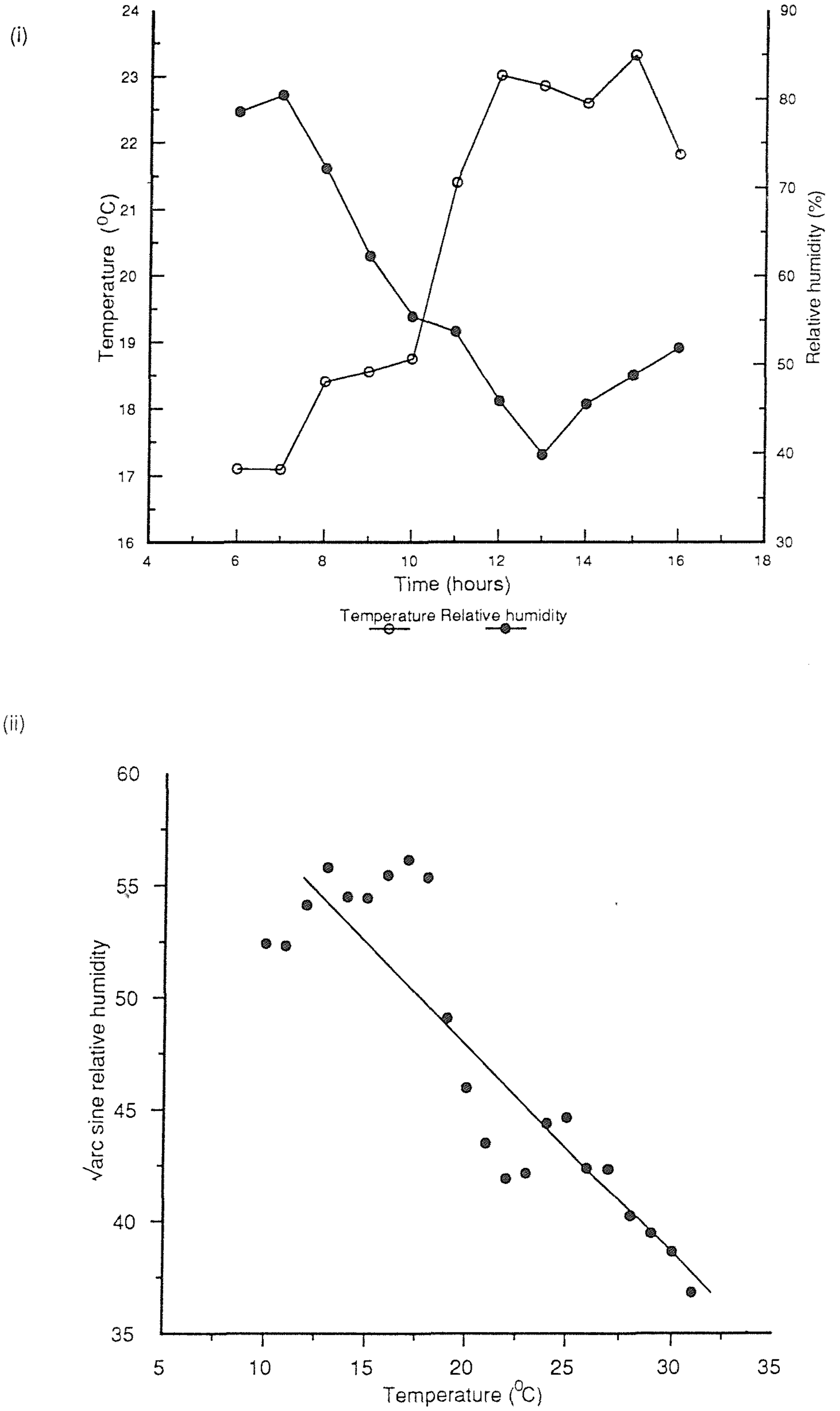
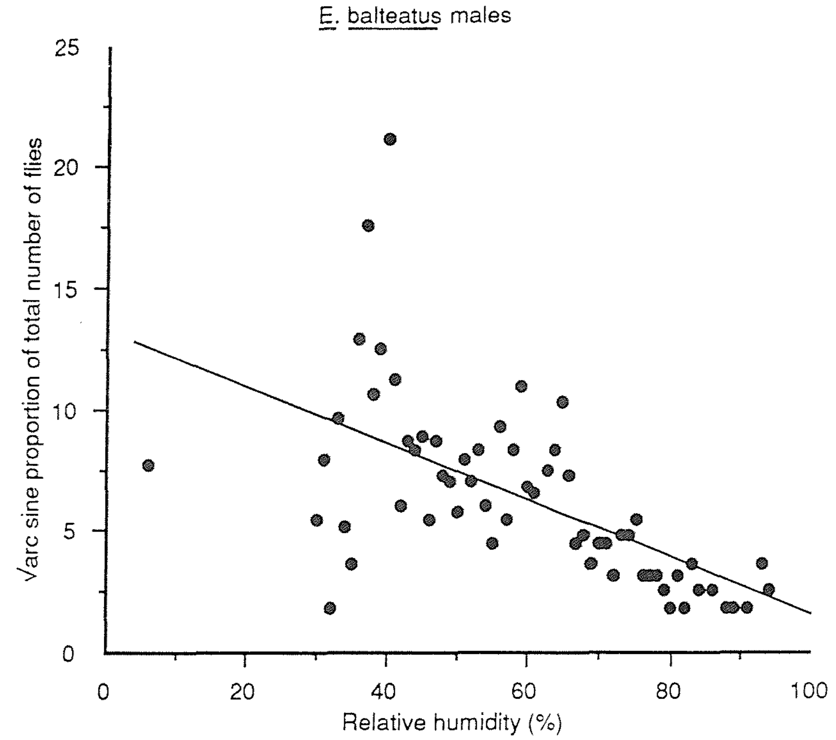


Fig. 14c(i) Variation in air temperature and relative humidity with time.
(ii) relationship between relative humidity and air temperature, 1989 and 1990
(Data from 1989 and 1990 combined)



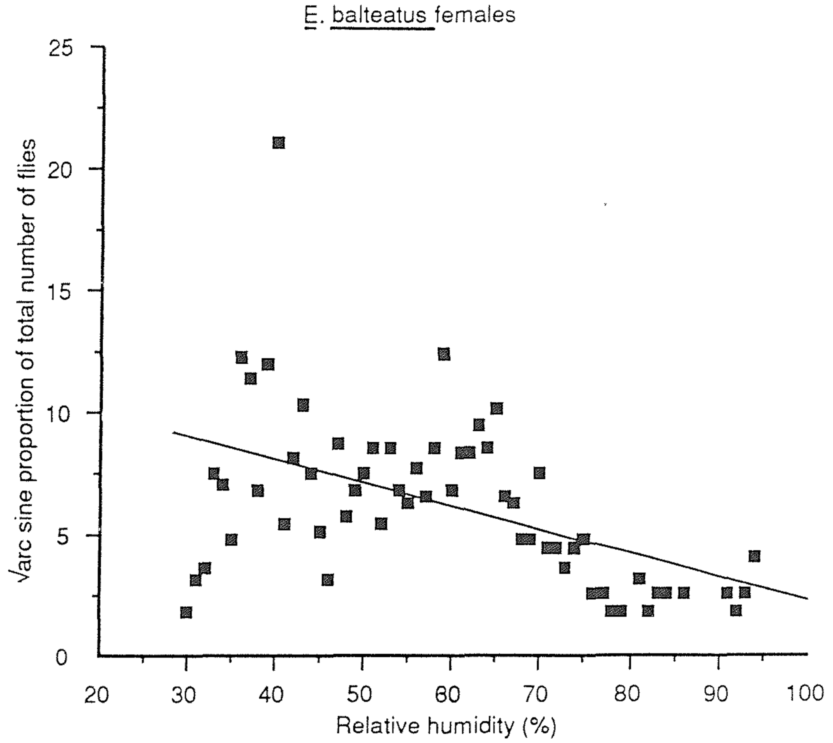
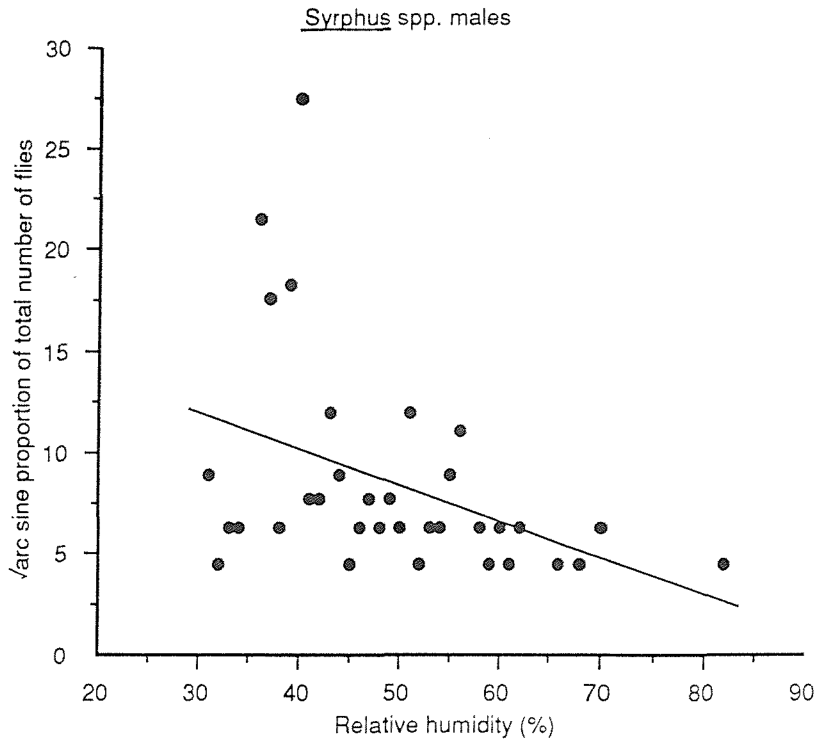


Fig.15. Relationship between the√arcsin proportion of the total number of flies observed during 1989 and 1990 and relative humidity.



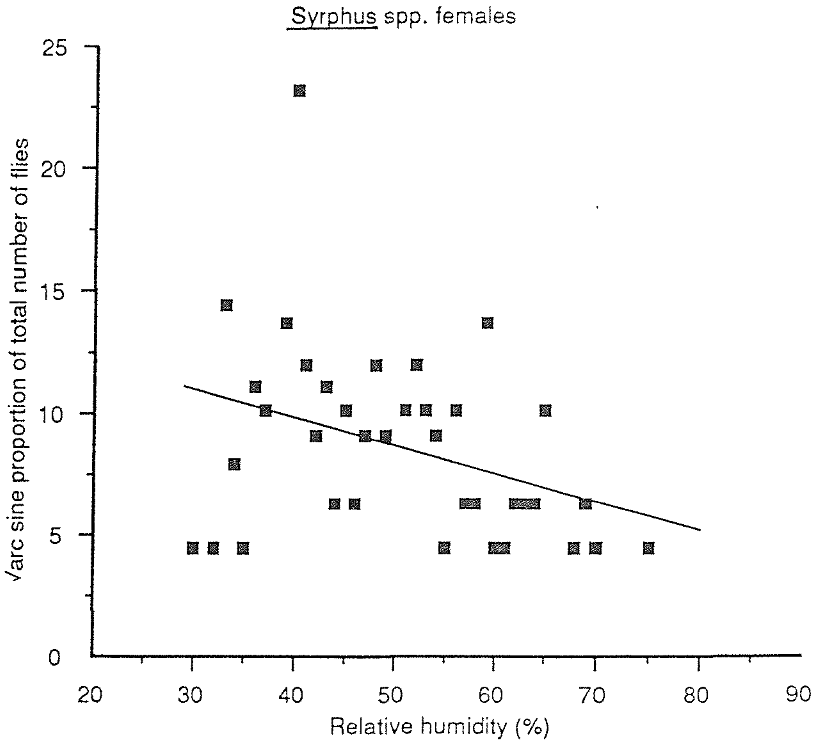
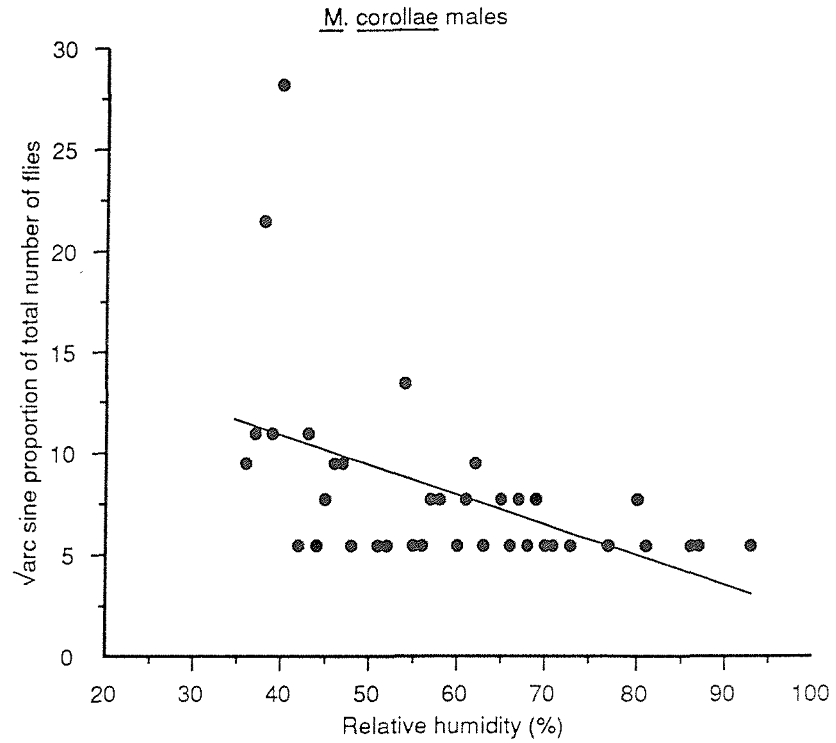


Fig. 16. Relationship between the√arc sine proportion of the total number of flies observed in 1989 and 1990 and relative humidity.



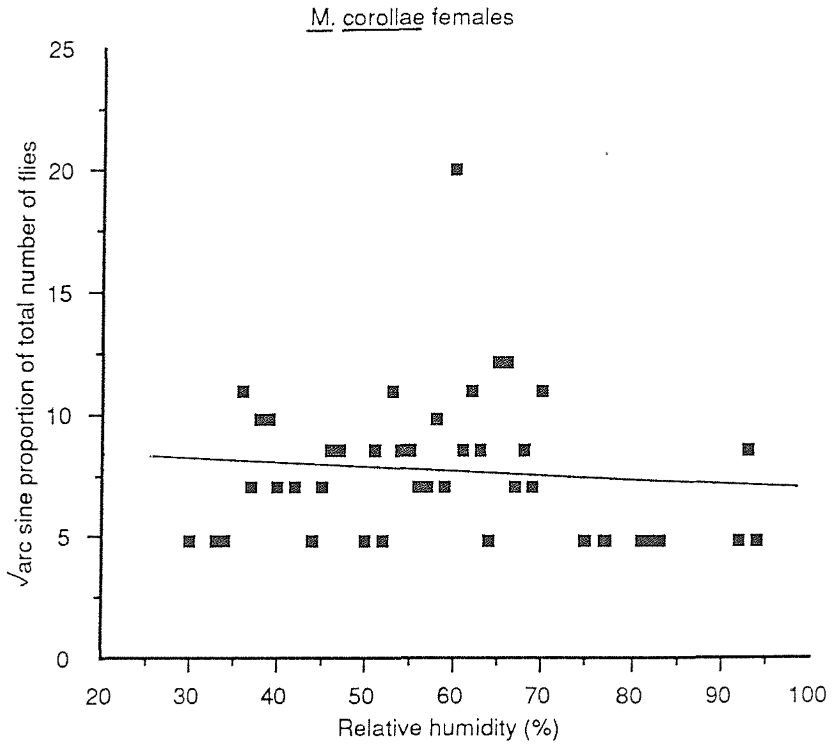
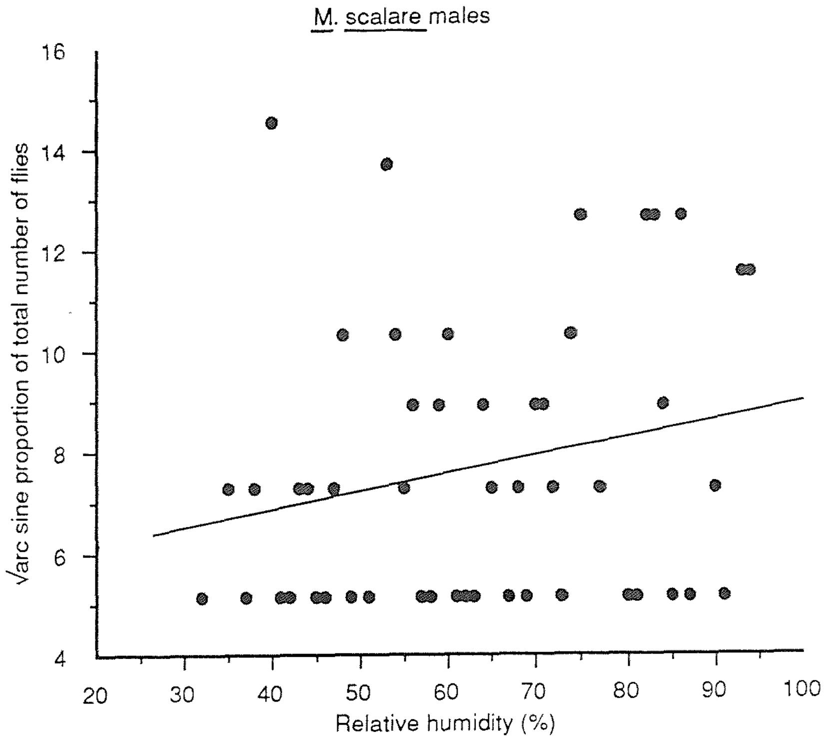


Fig.17. Relationship between the √arc sine proportion of the total number of flies observed in 1989 and 1990 and relative humidity.



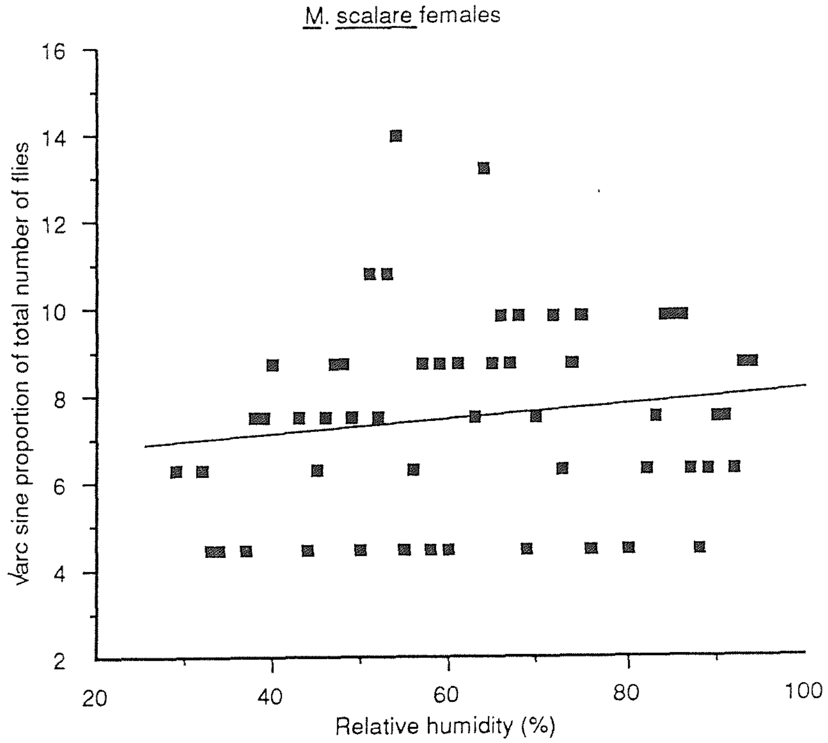


Fig.18. Relationship between the √arc sine proportion of the total number of flies observed in 1989 and 1990 and relative humidity.

during 1989 and 1990 were used to construct activity profiles for flies in each hour and each temperature (and relative humidity) category. The accuracy with which the observed patterns of behaviour represent the actual pattern is influenced by the differential ease of observation of flies engaged in each behaviour and the sample size. In addition, flies of different ages will allocate their time differently; therefore, the profiles can only indicate general trends in the relative occurrence of each behaviour with respect to microclimate or time of day.

Fig. 19 shows diel activity profiles for male and female of *E.balteatus* and *M. scalare*. Individuals of other syrphids were recorded in insufficient numbers to allow the construction of diel activity profiles.

Comparison of the behaviour of *E. balteatus* and *M. scalare* adults (Fig. 19) shows that a higher proportion of both *M. scalare* males and females were foraging during the period 06.00-07.00h than *E. balteatus* individuals of the same sex. *M. scalare* females spent a greater proportion of their time foraging than did males of the same species; *M. scalare* males spent a greater proportion of time inactive or in flight. In both species the number of observations of foraging behaviour peaked between 08.00-09.00h. Fig. 20 shows the composition of flower visits with respect to time for *E. balteatus* and *M. scalare* (both sexes combined) during 1989. In both species the majority of flower visits prior to 12.00h were to the common poppy, *P. rhoeas*.

A comparison of the allocation of time to the four behaviour categories between sexes within a single year using a G-test showed that there was no significant difference in the allocation of time between *E. balteatus* males and females in both 1989 and 1990 (1989: G = 0.167, N.S. df=3; 1990: G = 4.481, N.S., df=3; Table 3). There was a significant difference in the allocation of time to the four behaviour categories for *M. scalare* adults in 1990 but not 1989 (1990: G = 9.412, P<.001, d.f.=2; 1989: G = 6.171, N.S., d.f.=3). *Syrphus* species adults showed the reverse trend. Significant differences in the allocation of time to the behaviour categories between the sexes was recorded in 1989 while calculated G-test values were non significant for 1990 (1989: G = 29.029, P<.001, d.f.=3; 1990: G = 1.568, N.S., d.f.=3). The time budgets for male and female *M. corollae* were significantly different in both years (1989: G = 9.563, P<.01, d.f.=2; 1990: G = 26.708, P<.001, d.f.=3).

Comparisons of the allocation of time among the four behaviour categories between years showed that there were significant differences for females of all species (*E. balteatus* females: G = 33.320, P<.001, d.f.=3; *M. corollae* females: G = 46.725, P<.001, d.f.=2; *M. scalare* females G = 11.171, P<0.1, d.f.=2; *Syrphus* spp. females: G = 73.604, P<.001, d.f.=3). With the exception of *M. scalare* males there was a significant difference in time-budgets between years for the males of all species (*E. balteatus* males: G = 33.32, P<.001, d.f.=3; *M. corollae* males: G = 71.204, P<.001, d.f.=2; *Syrphus* spp. males: G = 73.604, P<.001, d.f.=3: *M. scalare* males: G = 2.401, P = N.S., d.f.=4). Because of the significant differences in the allocation of time among the four

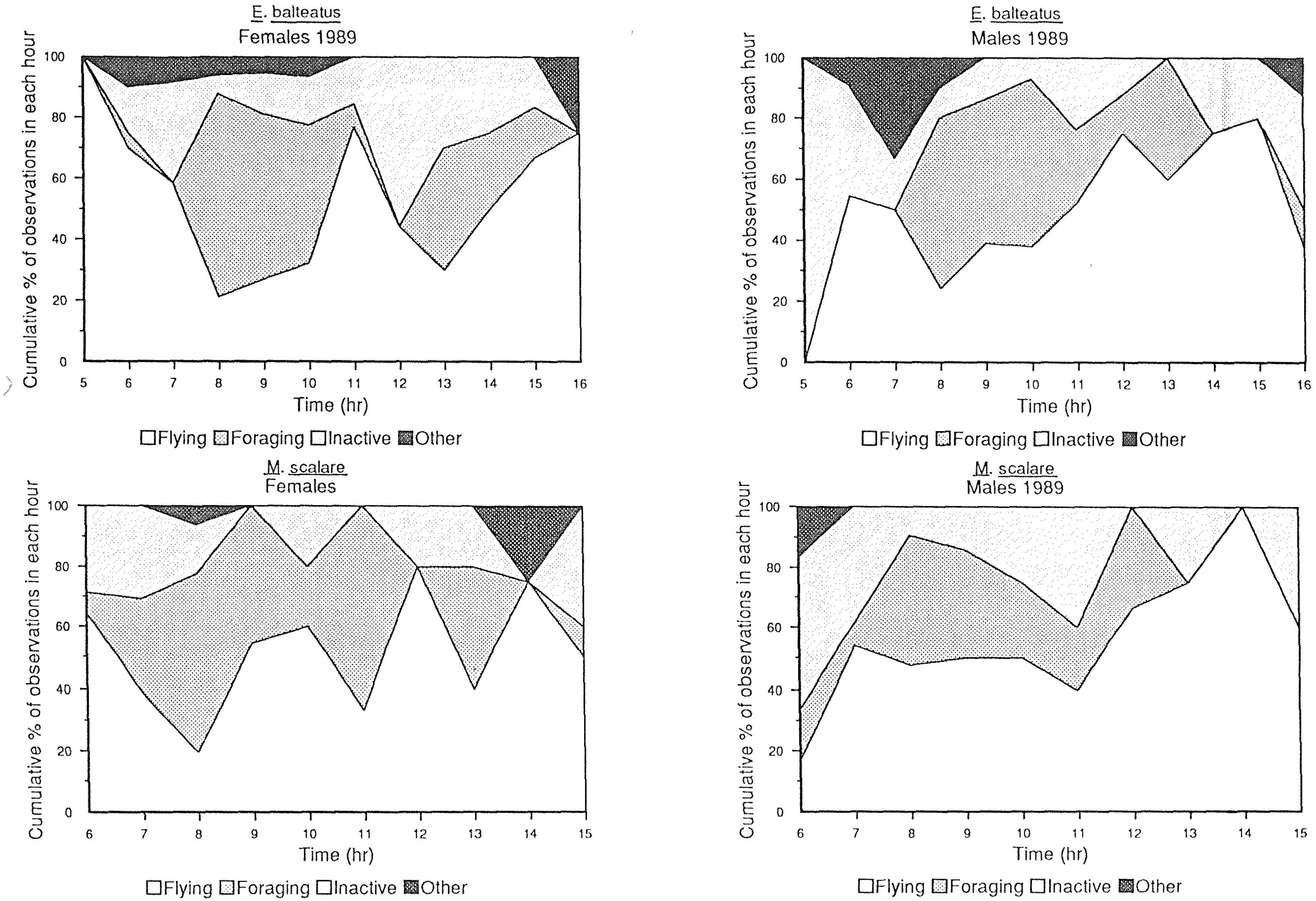


Fig.19 The cumulative percentage of observations in each hour during 1989(1) E. balteatus males and females; (2) M. scalare males and females.

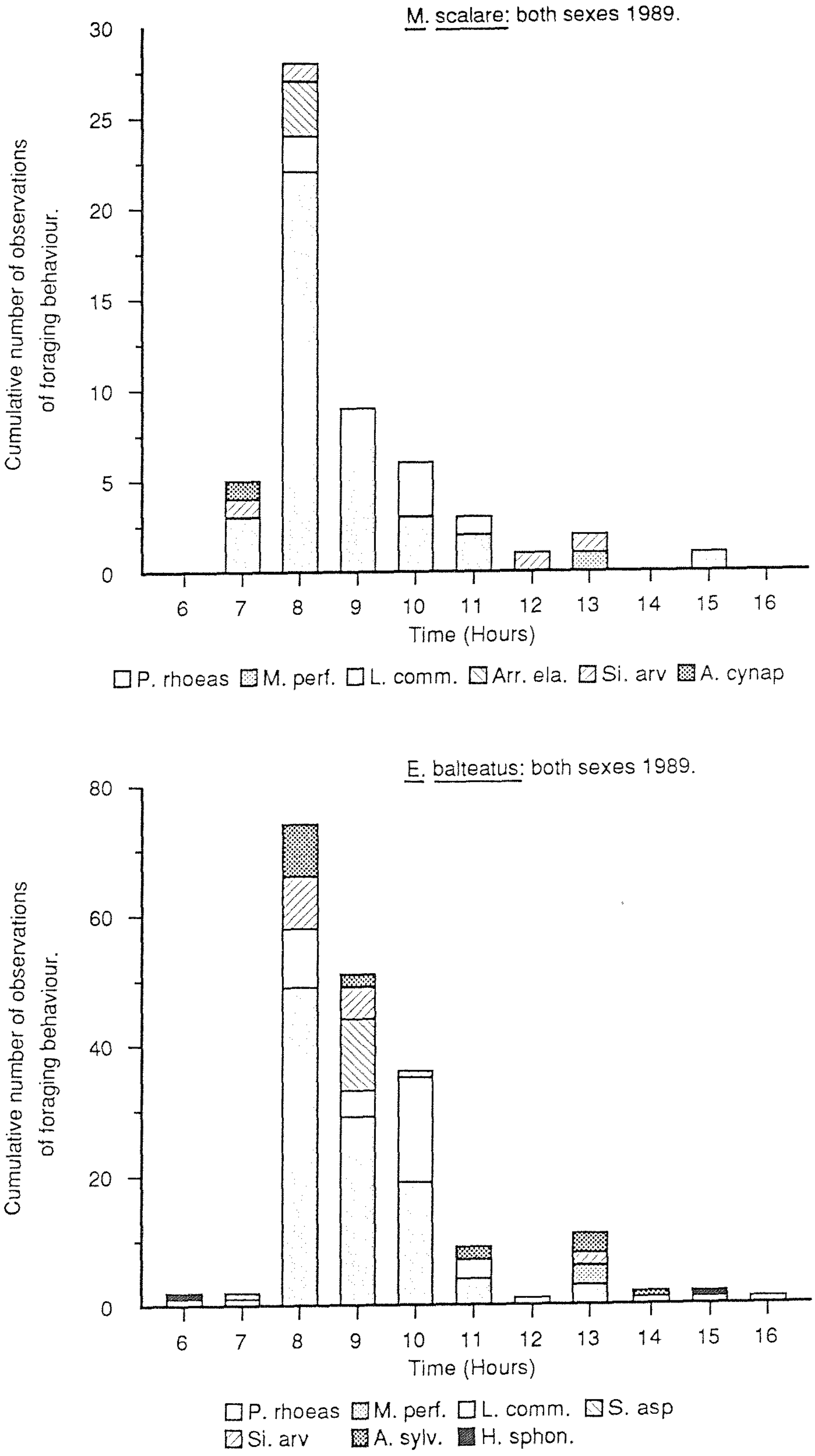


Fig.20. The distribution of observed flower visits for E. balteatus and M. scalare adults according to time.

Table 3. Time budgets estimated from the numbers of observations in each category during the census walks in (a) 1989 (b) 1990.

1989

Species	N	Sex	Percentage of time spent:			
			Flying	Inactive	Feeding	Else
E. balteatus	197	M	43.1	16.2	36.0	4.6
	185	F	42.4	17.3	35.1	5.4
M. corollae	16	M	56.3	25.0	18.8	0.0
	32	F	40.6	34.4	12.5	12.5
Mel. scalare	103	M	50.5	24.3	23.3	1.9
	129	F	42.6	20.9	33.3	3.1
Syrphus spp.	8	M	12.5	12.5	62.5	12.5
	11	F	18.2	27.3	36.4	18.2

1990

Species	N	Sex	Percentage of time spent			
			Flying	Inactive	Feeding	Else
E. balteatus	1070	M	22.7	10.4	66.7	0.2
	882	F	27.1	15.6	56.7	0.6
M. corollae	105	M	40.0	5.7	49.5	6.3
	116	F	21.6	19.8	50.9	7.8
Mel. scalare	23	M	43.5	26.1	30.4	0.0
	44	F	29.5	34.1	36.4	0.0
Syrphus spp.	156	M	14.7	6.5	72.5	6.3
	150	F	20	6.7	68.0	5.3

behaviour categories between years the two data sets are discussed separately.

Fig. 21 shows the behaviour of *E. balteatus* males and females in each temperature category, during 1989 and 1990. The temperature range for which observations were available differed between the two years. However, in both years the majority of male *E. balteatus* were recorded as inactive or in flight at temperatures below 14°C whereas more than 50% of the females observed at these temperatures during 1990 were foraging. During 1990 the majority of flies of both sexes were observed foraging at temperatures above 20°C; the proportion of flies foraging generally increased with increasing temperature and it was the predominant activity at 27°C. However, during 1989 flight and inactivity were predominant above 20°C. Individuals of the remaining species occurred in insufficient numbers in one of the two years to allow between year comparisons.

Fig. 22 shows the behaviour of *M. scalare* males and females in each temperature and relative humidity category in 1989. In this species females spent a greater proportion of their time foraging than did males; foraging was the predominant activity in the range 17-21°C and 70-75% relative humidity.

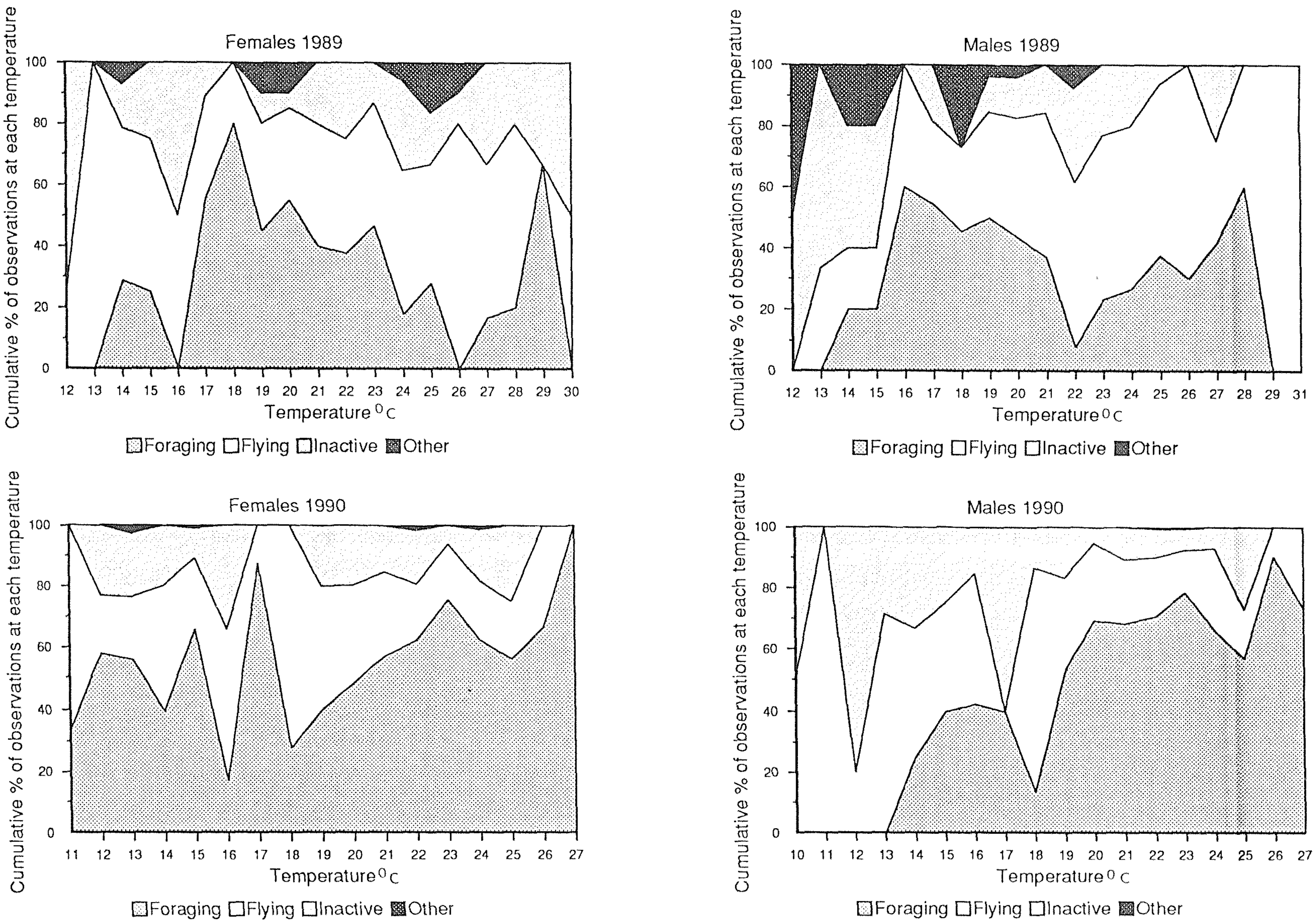
In *M. corollae* females foraging was the predominant behaviour at all temperatures with the exception of temperatures in the range 16-19°C and at temperatures above 24°C. Males showed a similar pattern although the first decline in the proportion of individuals observed foraging occurred in the range 14-17°C with a further decline in foraging behaviour at temperatures above 24°C (Fig. 23).

Fig. 24 shows the behaviour *Syrphus* spp. males and females in each temperature and relative humidity category. In both sexes foraging was the predominant behaviour above 19°C although the proportion of the total number of individuals of both sexes which were observed foraging declined above 22°C.

Fig. 25 shows the distribution of flower visits by individuals of four species which were commonly recorded during 1990. In both *M. corollae* and *E. balteatus*; there was a change from foraging predominantly on *P. rhoeas* during mid morning to *M. perforata* in early afternoon. *Syrphus* spp. showed a similar trend although the flies were not observed foraging in the headland until later in the day and at higher temperatures than *M. corollae* and *E. balteatus* therefore, the period during which the flies were observed foraging on *P. rhoeas* was compressed into a shorter time period between 11.00-13.00h.

Table 4(a) categorises the percentage of the total number of observations of each behaviour (foraging, flying, inactive, other) according to whether the observation was in shade or direct sunlight. In three species, *E. balteatus, M. corollae* and *M. scalare*, a higher percentage of observations in each of the four behaviour categories occurred in the shade. In the remaining species a higher percentage of observations of behaviour, except inactivity, occurred in direct sunlight.

Table 4(b) shows the percentage of the total number of observations of each species which



21a. The cumulative percentage of observations in each temperature category for *E. balteatus* females and males during 1989 and 1990.

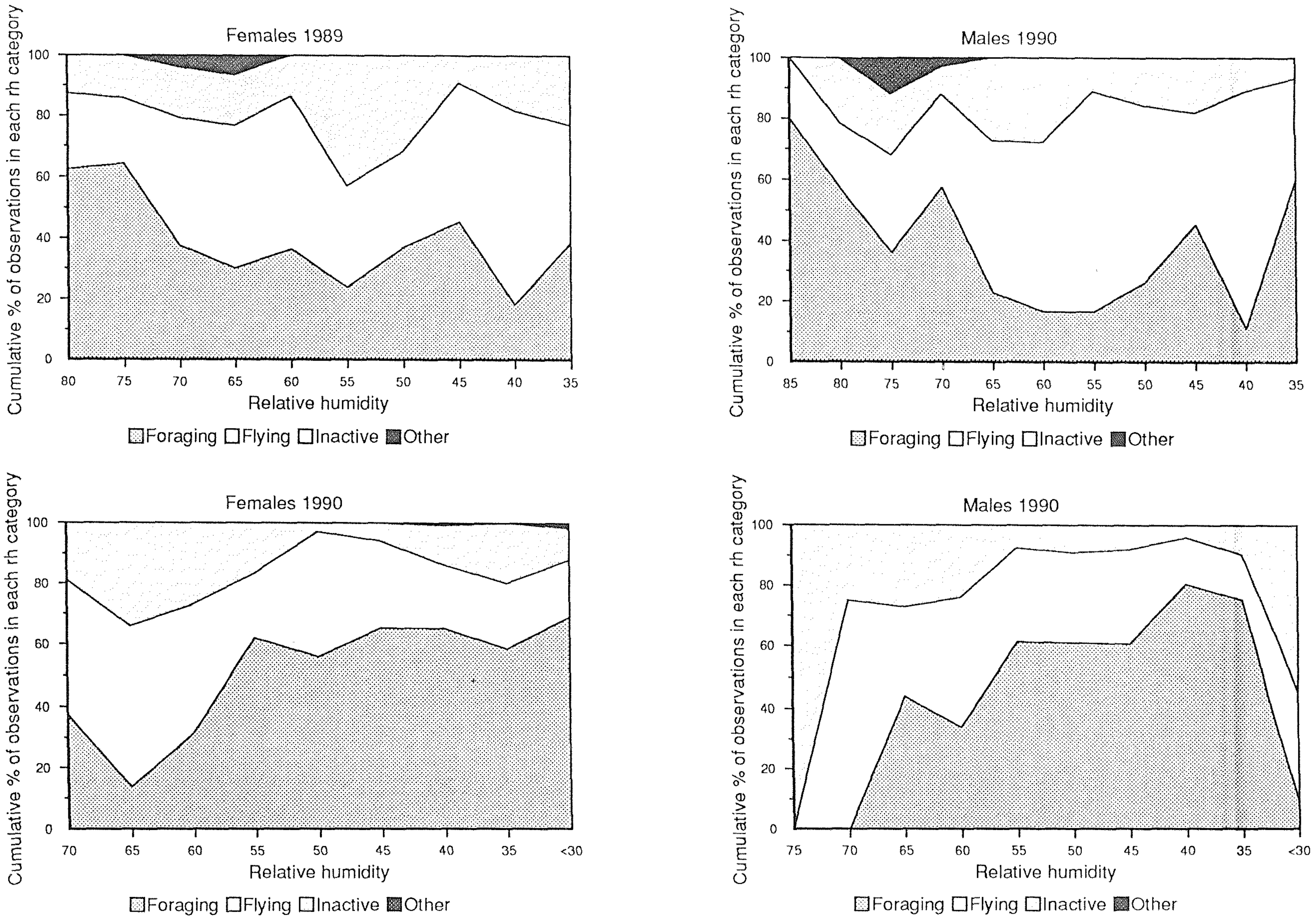


Fig.21b The cumulative percent of observations in each relative humidity category for E. balteatus females and males during 1989 and 1990

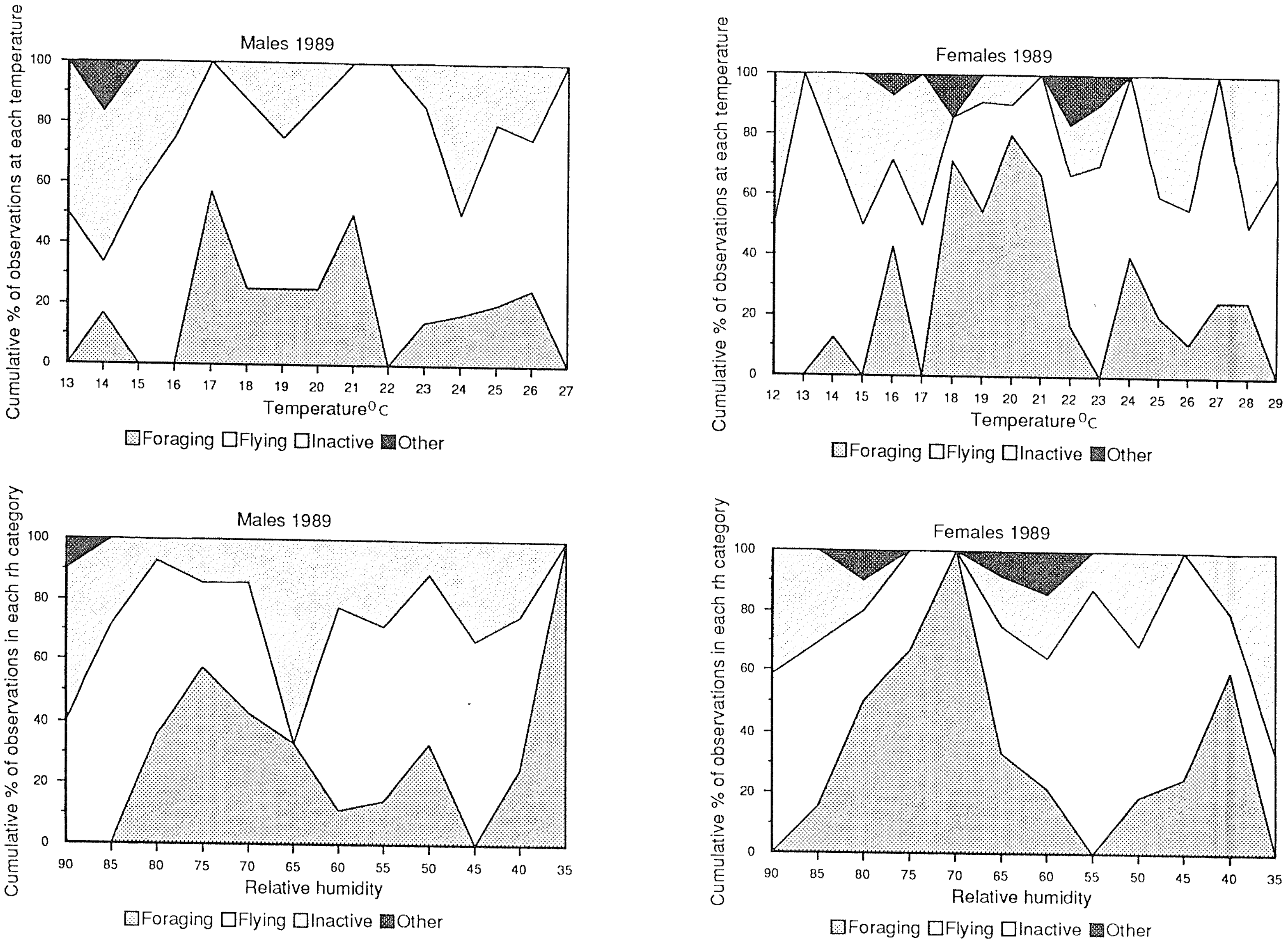


Fig.22 The cumualtive percentage of observations in each (1) temperature(2) relative humidity category for M. scalare males and females in 1989.

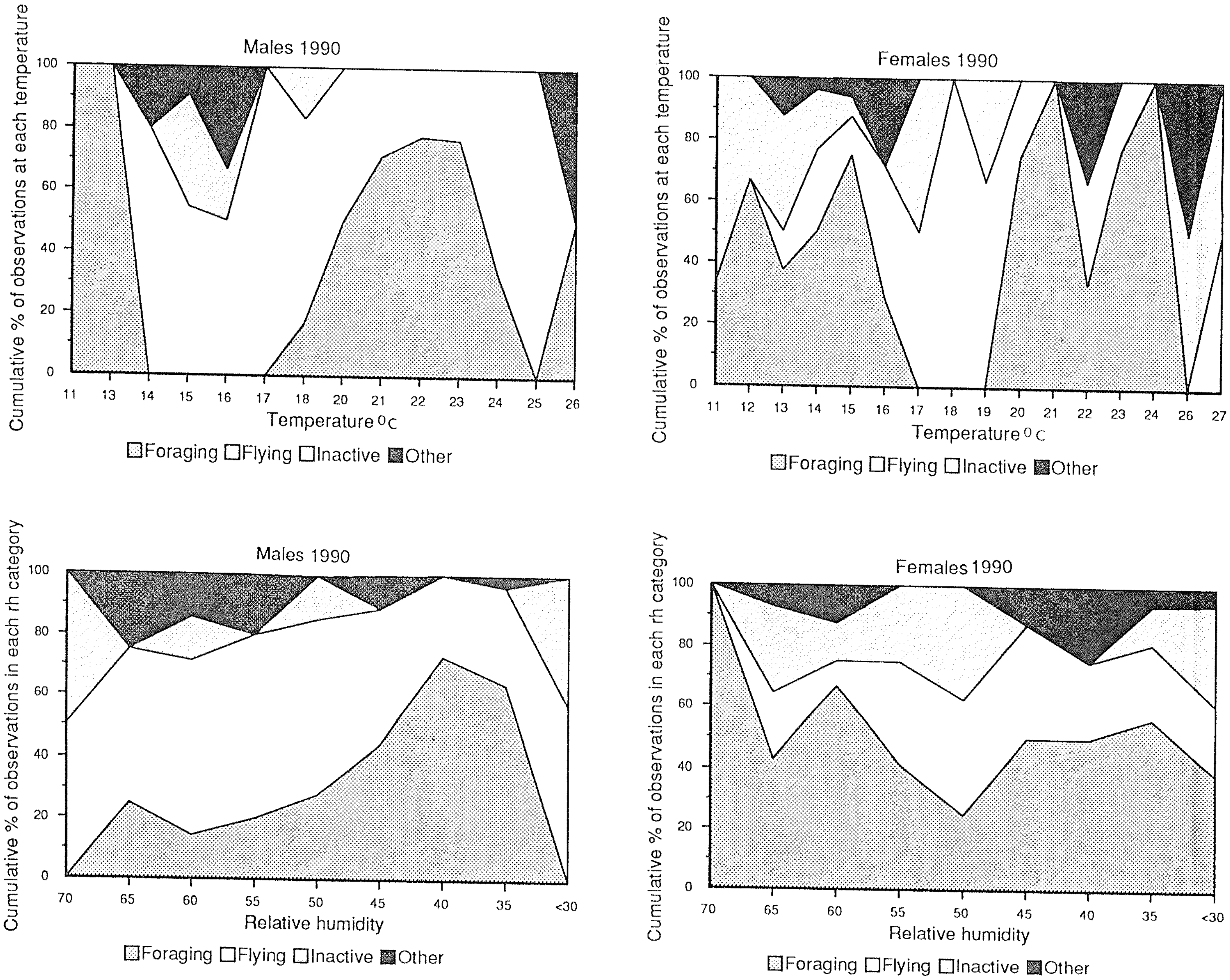


Fig.23 The cumulative percentage of observations in each (1) temperature (2) relative humidity category for *M. corollae* males and females in 1990.

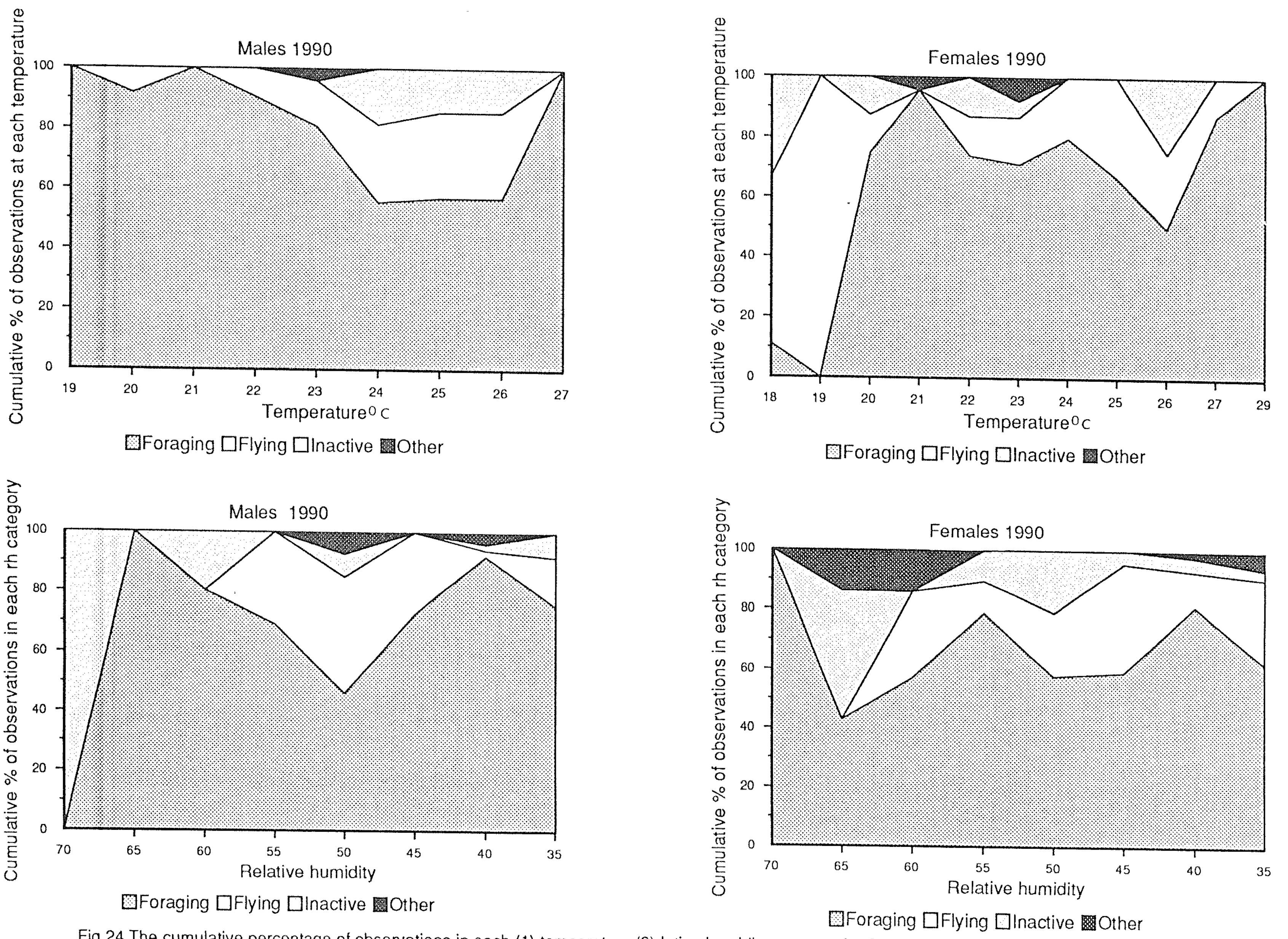


Fig 24 The cumulative percentage of observations in each (1) temperature (2)relative humidity category for Syrphus spp. males and females in 1990.

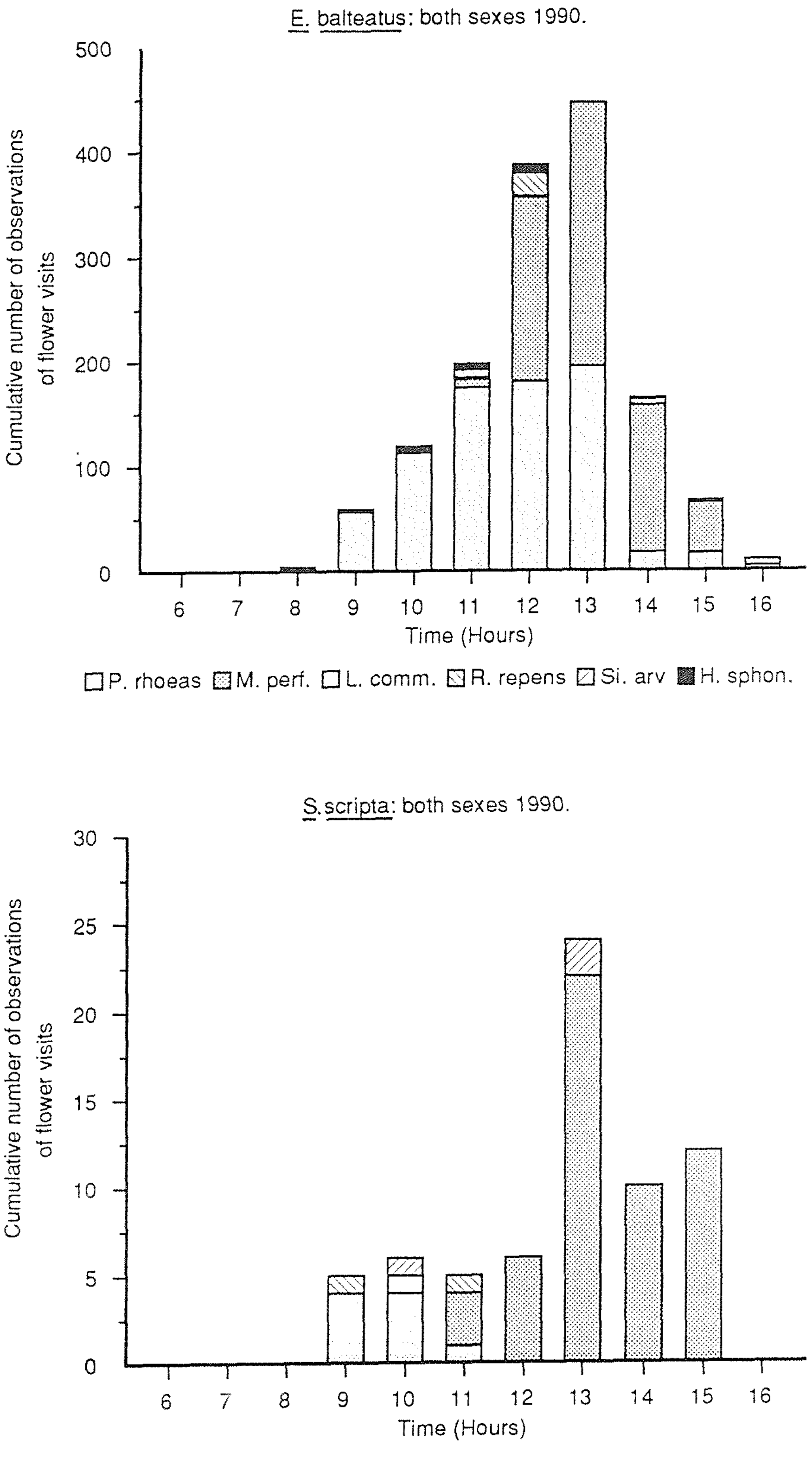
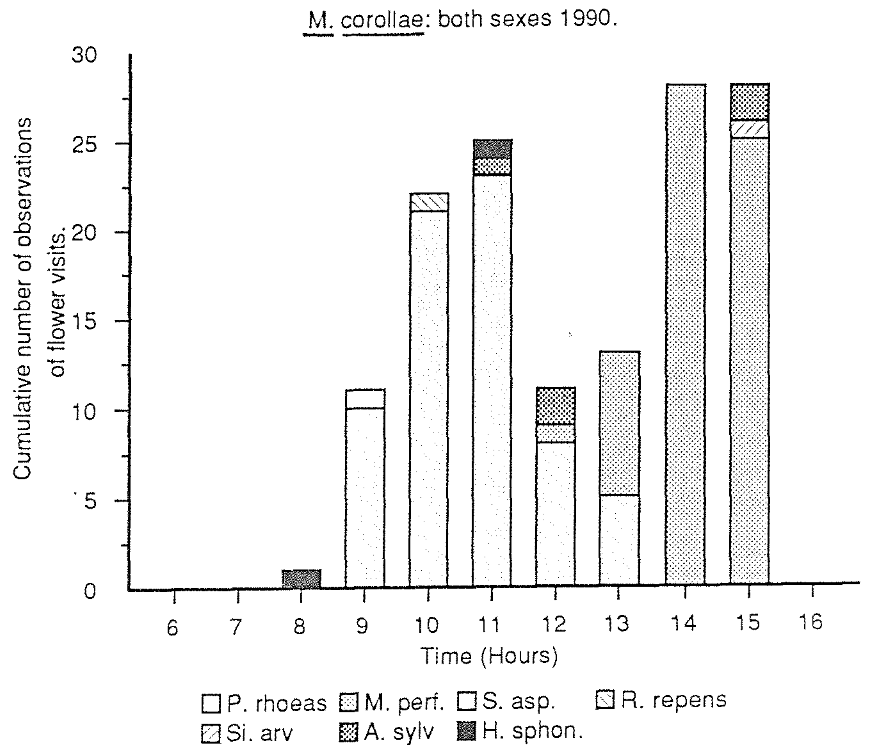


Fig. 25. Distribution of observed flower visits for E. balteatus and S. scripta adults; data from all standard census walks during 1990.


M. corollae: both sexes 1990.

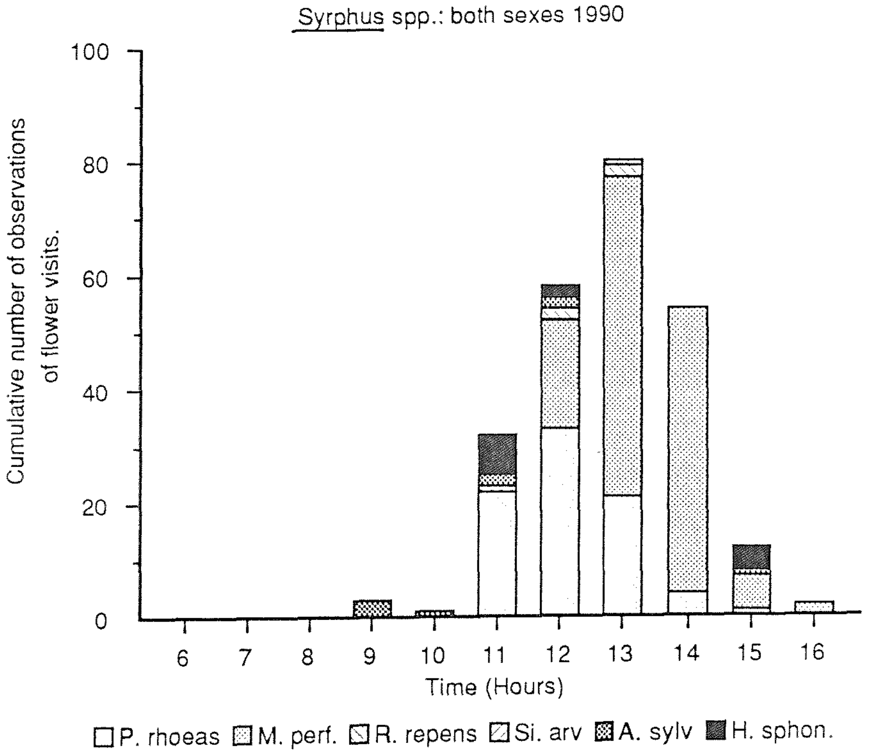

Syrphus spp.: both sexes 1990

Fig. 25(contd.). Distribution of observed flower visits for M. corollae and Syrphus spp. adults according to time.

Table 4a. Percentage of the total number of observations in each behaviour category which occured in the sun or shade.

Species	Behaviour									
	Foraging		Flying		Inactive		Other		N	
	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
E. balteatus	42.3	57.7	38.6	61.3	35.6	64.4	26.7	73.3	1248	1860
M. corollae	38.0	62.0	36.8	63.2	31.7	68.3	42.1	57.9	135	233
M. scalare	19.8	80.2	25.9	74.1	24.7	75.3	40	60	76	240
Syrphus spp.	59.8	40.2	52.6	47.4	56.8	43.2	45.5	54.5	229	170
P. albimanus	52.4	47.6	61.8	38.2	50	50	37.5	62.5	43	36
P.manicatus	54.2	45.8	52.6	47.4	63.6	36.4	100	0	31	24
S. scripta	54.3	45.7	43.8	56.2	11.1	88.9	100	0	88	107
Er. tenax	69.6	30.4	66.7	33.3	50	50	100	0	64	31

Table 4b. Percenatge of the total number of individuals of each species observed in each cloud cover category; 1989 and 1990 data combined.

Species	Cloud cover category									
	0	1	2	3	4	5	6	7	8	Total number of observations
E. balteatus	4.9	4.2	2.4	1.4	4.1	1.0	46.0	25.4	10.5	1248
M. corollae	5.9	6.7	5.9	4.4	4.4	5.2	43.7	9.6	14.1	135
M. scalare	30.3	15.8	6.6	1.3	5.3	1.3	9.2	9.2	21.1	76
Syrphus spp.	11.8	7.0	1.3		1.3	2.2	52.8	21.8	1.7	229
P. albimanus	25.6	20.9	11.6	2.3	4.7	9.3	7.0	4.7	14.0	43
P. manicatus	16.1	35.5	6.5		29.0		3.2		9.7	31
S. scripta	12.5	12.5	3.4	1.1	2.3	4.5	42.0	15.9	5.7	88
Er. tenax	18.8	4.7	12.5	7.8	7.8	1.6	29.7	14.1	3.1	64
All syrphid species combined	9.3	6.8	3.3	1.7	4.6	2.7	41.0	20.9	9.8	2219

Scale: 0 = no cloud ; 8 = complete cloud cover.

occurred in eight cloud cover categories. Individuals of all species were recorded at the two extremes of the nine point scale, that is, no cloud and complete cloud cover.

Discussion

The present study has identified species-specific differences in the temperature at which activity commences and in the patterns of behaviour of the flies with respect to microclimatic factors. The observed patterns of behaviour are broadly similar to those previously described for syrphids in garden habitats (Gilbert, 1981, 1985). However, the order in which species were recorded through the day differed from previously observed patterns. In addition there were differences in the percentage of observations in each behaviour category which occurred in direct sunlight and in shade.

Significant relationships were recorded between the proportion of insects which were active and air temperature and relative humidity for several species indicating that local climate was an important determinant of activity in these flies. However, temperature and relative humidity were highly negatively correlated and therefore it is doubtful whether the calculated values give any indication of which conditions the insects detected or responded to. *M. scalare* was a typical in that no significant positive relationship was detected between temperature and the proportion of active flies. This agrees with Gilbert (1985) who recorded that individuals of this species are capable of activity at low temperatures (Gilbert, 1985).

Gilbert (1985) recorded the temperature at which more than 50% of individuals of several syrphid species were observed as active; the order in which species appeared reflected size differences between the flies, with the largest flies (*E. tenax* and *S. ribesii*) appearing first. In the present study a small percentage of the total number of observations of both *Syrphus* species and *E. tenax* occurred below 20°C; medium sized syrphids such as *E. balteatus* and *M. corollae* were active at lower temperatures than the larger flies and a larger proportion of the total number of observations of these species occurred at temperatures below 15°C. In the case of female *M. corollae* there was a tendency for the proportion of the total number of observations to decrease as temperature increased. Individuals of both sexes of *M. corollae* and *E. balteatus* were predominantly observed in shade. This is in direct contrast to observations of Gilbert(1981) who recorded that *M. corollae* was "a creature of the sun" which appeared only when cloud cover was low and that individuals were significantly more likely to be seen in the sun than in the shade when compared with the overall pattern for all syrphid species.

The higher proportions of individuals of *E. balteatus* and *M. corollae* which were recorded in the shade in the present study is partly a result of weeds and wheat shoots producing small patches of shade in the crop even when the headland was in direct sunshine. Flies which were active in the crop passed through these patches as a result of their movement between plants and areas of crop. The practice of recording the behaviour and location of flies at first siting tended to over-represent the number of flies which occurred in the shade and therefore the values do not accurately document the selection of shaded habitats by the flies.

During the study individuals of several species including *E. tenax* and members of the genus *Syrphus* were recorded in direct sunlight more frequently than in shade. Large dark insects such as *E. tenax* will be more at risk from overheating during prolonged exposure to direct insolation than smaller species with higher reflectance values, such as *E. balteatus* and *M. corollae* (Willmer and Unwin, 1981). This suggests that air temperature and the levels of radiation were not restricting the distribution of these flies to shaded patches of the headland and further supports the conclusion that the recorded values over estimate the proportion of *E. balteatus* and *M. corollae* individuals which occurred in shaded locations. The introduction of inaccuracy tended to occur during early morning because before 09.30h there were relatively large patches of shade in the headland caused by the position of the sun in relation to the shelterbelt at that time. *E. balteatus* and *M. corollae* adults were recorded in the headland throughout the period 08.00-10.00h whereas *Syrphus* adults were not recorded in large numbers before 11.00h. These differences account for the smaller proportion of *Syrphus* species which were recorded in the shade compared with *E. balteatus* and *M. corollae.*

Willmer (1983) showed that the diel patterns of activity of flies visiting *Tilia* and *Heracleum* could be explained in terms of the thermal balance of the flies. In the present study a significant relationship between air temperature (relative humidity) and activity was recorded for several species, indicating that microclimate was an important determinant of activity in the flies. However, the observed order of appearance of flies in the headland with respect to time and temperature does not agree with the order predicted on the basis of the relations between size, colour and activity. That is, medium sized syrphids such as *E. balteatus* and *M. corollae* were active at lower temperatures than larger flies.

The observed order of appearance of flies may have been affected by the larger relative abundance of *Syrphus* species during 1990. During 1990 the standard census walks began at 08.00h, therefore, it is possible that the flies were active before the census began and that the low numbers of flies recorded before 11.00h (and below 19oC) was a result of the flies moving out of the headland.

In both 1989 and 1990, the common poppy, *P. rhoeas* was the predominant non-crop plant (in terms of both rooted plant density and floral area/0.5m^2) although mayweed, *M. perforata* was also relatively abundant in 1990. The limited number of observations of *Syrphus* species before 11.00h were of flies foraging on the umbellifer, *A. sylvestris.* The maximum number of observations of foraging behaviour in *Syrphus* species was recorded during early afternoon when the flies were taking nectar from *M. perforata.* Therefore, the low numbers of active flies observed earlier in the day may have been a result of the flies selectively foraging on flowers outside the headland.

E. tenax is regarded as a generalist forager which predominantly takes nectar (Gilbert, 1981). Willmer (1983) recorded that members of the genus *Eristalis* foraged towards dawn and dusk on *Tilia* and between 08.00-11.00h on *Heracleum* and that the flies avoided the hottest part of the day. The paucity of nectar supplies in the headland in addition to the low numbers of flies recorded during the study may have resulted in observed patterns of behaviour which are unrepresentative of the actual patterns shown by this fly.

Adult *M. corollae* are also generalists which take pollen and nectar; Gilbert (1981) recorded two peaks of pollen collection by individuals of this species; they were between 09.00-11.00h and between 13.00-14.00h, depending on the site. Nectar was taken between these peaks and after 14.00h. In the present study individuals of this species were most abundant during 1990. The foraging behaviour of individual flies (taking nectar, taking pollen, taking pollen and nectar) was not recorded during the standard census walks so it is not possible to make a direct comparison with the patterns of foraging behaviour observed by Gilbert. However, the changing distribution of flower visits throughout the day suggests that the proportions of pollen and nectar in diet did vary with the time of day. The flies predominantly foraged on *P. rhoeas* (which provides only pollen) before 13.00h whereas after 13.00h higher numbers of flies were recorded on *M.perforata* which provides both pollen and nectar.

The observed pattern of foraging behaviour for *E. balteatus* differed between the two years of the present study. During 1989 the standard census walks began earlier, accounting for the larger number of observations of foraging behaviour before 09.00h. In 1990 the largest proportion of observations of foraging behaviour occurred after 10.00h whereas during 1989 the majority of observations were recorded between 08.00-11.00h with a small peak in activity at 13.00h. Comparison of environmental conditions for a given time, between the two years shows that conditions were similar in both years. Although these values do not reflect the actual microclimatic variation in air temperature and relative humidity experienced by the flies they do suggest that climatic factors were not responsible for the observed differences in the diel periodicity between the years. However, there were significant differences in the floral composition of the headland between the two years. Gilbert (1985) recorded that *E. balteatus* fed on pollen above 12°C and began taking nectar above 20°C. Therefore the low number of observations of foraging behaviour after 10.00h in 1989 may have been a result of flies leaving the headland after an initial period of pollen feeding during early morning, because of the limited availability of plants other than *P. rhoeas* in the headland.

The differences in the observed patterns of behaviour for *E. balteatus* adults between years and the low number of observations of *Syrphus* adults before 11.00h highlight the importance of scale in determing the accuracy with which the standard census walk technique documents diel changes in activity. The technique cannot separate the effects of patchiness of habitat from real diel changes in abundance or activity; diel changes are accurately documented in a small area but the results are affected by the movement of the flies into and out of the site. In a larger area the observations are less affected by the movement of flies into and out of the area but the resolution of diel changes is poor. In the present study the shelterbelt was homogeneous along its length and patchiness within the study area was restricted to the differing abundance of non-crop plants between the conservation headland and fully sprayed headland plots, however, the area censused was small and therefore the results were influenced by the movement of flies out of the headland into the adjacent green lane and margins of nearby fields. These movements presumably account for the anomalies between the present study and previous studies of syrphid behaviour which have been carried out on different spatial scales.

CHAPTER SEVEN
SPATIAL DYNAMICS OF SYRPHIDS

Introduction

Migration of several members of the subfamily Syrphini, including *S. vitripennis, M. corollae, M. luniger, Sc. pyrastri* and *E. balteatus,* has been observed at coastal locations in Sweden, Denmark and England (Svensson and Janzon, 1984; Overgarrd Nielsen, 1968; Owen, 1956; Johnson, 1960; Parmenter, 1960; Spreadbury, 1960; Sutton, 1969) in addition to mountainous areas in Europe (Lack and Lack, 1951; Aubert and Goeldlin de Tiefenau, 1981). The records of migrating syrphids in coastal areas in northern Europe describe large numbers of flies coming in off the sea during 1 or 2 days; the majority of the observations occurred in August. Svensson and Janzon (1984) studied the sex ratio, size variation, pollen content and reproductive state of migrating *M. corollae* recorded on the south-east coast of Sweden. More females than males were recorded in their catch of migrating flies; the females did not contain mature eggs in their ovarioles. The authors suggested that low aphid density was the trigger for migration.

The ability of syrphids such as *M. corollae* and *E. balteatus* to migrate over large distances has led some authors to suggest that spring migration of the flies, particularly *E. balteatus*, may affect the differences in the timing of appearance and relative abundance of the flies between regions. For example, Van der Goot (1979) considered that the increase in the abundance of *E. balteatus* in June was only partly due to the emergence of native flies and was influenced by the immigration of flies from the south. Poehling, Tenhumberg and Groeger (1991) compared the timing of appearance of *E. balteatus* adults in winter wheat fields in northern and southern Germany. In both years of the study there was a time lag of several weeks between the appearance of the flies in the south and the north. The authors concluded that further research was required to examine whether migration of flies from the southern to northern regions was responsible for the observed time lag.

On a smaller spatial scale a quantitative description of habitat use and dispersion of syrphids on farmland is necessary to gain an understanding of the relationship between adult feeding sites and oviposition sites and to asses the potential for using the provision of adult food sources to enhance syrphid oviposition within crops.

The dispersion of a population is the pattern of spacing which characterises individuals at a given time. Much of the pattern of dispersion is a consequence of organisms' moving out (or not as the case may be) from one place to others. Loosely speaking these movements are dispersal and their general consequence is to increase inter-individual distances (Macdonald and Smith, 1990). The pressure for dispersal is a current or anticipated deterioration in the fitness of individuals, compared to probable opportunities elsewhere, as a result of a depletion of resources, an increase in competition or the degree of inbreeding. The optimum dispersal strategy will depend on a combination of both the spatial variability of suitable habitats and their temporal predictability (Roff, 1975; Lande, 1987).

Mark-release recapture methods have been used to study dispersal in Diptera; however, the studies have concentrated on crop pests or vectors of disease. For example, Baker, Chan and Zavala (1986) studied dispersal and orientation of tephritid fruit flies in coffee and mango plantations using flies which had marked themselves with fluorescent dust as they emerged from the pupal stage. Lillie, Kline and Hall (1985) also used fluorescent dusts to study the mean distance travelled by mosquitoes, *Culicoides* spp. Radioisotopes (Davies, 1965) paints (Gillies, 1961) and dyes (Brenner, 1984) have also been used in studies of dispersal.

In the case of syrphids, mark-recapture techniques were initially used to study population size and adult longevity. For example, Nielsen (1969) used paints to estimate the average daily survival rate and population size in *Heliophilus hybridus* and *Sericomyia silentis* in a 1200m^2 forest clearing. Conn (1976) used similar techniques to study the population dynamics of *Merodon equestris* infesting a 450m^2 plot of daffodil bulbs.

More recently mark-recapture techniques have been used to study habitat utilisation and dispersal in syrphids. Haslett (1981) studied the movement of paint marked flies of several species along a woodland ride. Flies were anaesthetized, marked and placed on the ground at one end of the ride while still unconscious. On recovering, individuals of *Rhingia campestris* and *Cheilosia albitarsis* climbed to the top of nearby grass stalks where they remained inactive for several minutes before taking off on a short flight (<1m) to a nearby leaf or flower head. 43% of marked *R. campestris* and 71% of marked *C. albitarsis* were resighted after six hours. The movements of individuals of both species were fairly localised; the maximum distance that *R. campestris* was recorded from the release point was 72m. Individuals of the remaining four species which were studied (*E. balteatus, Volucella pellucens, Eristalis tenax* and *Eristalis pertinax*) were not relocated successfully; on becoming active the flies soared 20-30m into the air and were lost from the site for good. Haslett recorded that no modification of the technique could solve the problem. However, Holloway and McCaffery (1990) have subsequently described the successful use of marking techniques to study habitat use and dispersion in *E. pertinax*. Flies were marked *in situ* while foraging on *Cirsium arvense*; this removed the disturbance associated with netting flies and presumably accounted for the flies remaining in the site after marking. The flies were marked in a woodland clearing; the authors recorded that the rate at which the flies spread out across the clearing from the point of marking was slow and the insects never attained a random distribution across the site.

In the present study techniques modified from those described by Holloway and McCaffery were used to study habitat use in *E. balteatus* adults.

Materials and Methods

Marking: Laboratory studies.

Preliminary studies were carried out to determine whether the enamel paints (Humbrol enamel) chosen for the marking experiment had any detrimental effects on the longevity of the flies.

E. balteatus eggs were obtained from a culture of adults maintained at Southampton; eggs were collected from the culture over a two hour period on a single date. On hatching larvae were transferred to individual transparent plastic boxes (8cm x4.5cm x2cm) and provided with an excess of second and third instar pea aphids, *Acrythosiphon pisum*. The upper surface of the boxes was perforated with terylene covered holes; the boxes were kept under constant conditions: 20°c, LD 18:6 and 75% rh. Under these conditions larvae pupated within 11. 5 ± 0.98 (range = 10-14) days of being laid.

Pupae were transferred to a single, large (55x60x90cm) Perspex box. The boxes were illuminated from above and maintained at 20°C, LD 18:6. Adult emergence extended over a 48 hour period; random numbers were used to determine which flies were marked and which remained unmarked. Before the study began a small group of adults in the main culture had either been marked with spots of paint on the wing tip (as described by Holloway and McCaffrey) or on the thorax. Observation of the marked flies indicated that marking the thorax was less likely to result in damage to the flies than marks on the wing. Comparison of the behaviour of unmarked and undamaged marked flies did not reveal any pronounced differences in behaviour between individuals of the two groups. Therefore, in subsequent experiments flies were marked on the thorax.

Two replicates of the experiment to compare longevity in marked and unmarked flies ran simultaneously in separate Perspex boxes. The first box contained ten unmarked and nine marked males and nine marked and unmarked females on day one of the experiment. The second box contained three unmarked males, seven marked males, six unmarked females and three marked females on day one. Flies in both boxes were provided with an excess of *Poa trivialis* pollen, a 25% sucrose solution and broad bean (*Vicia faba*) seedling (Sutton Dwarf) infested with *A. pisum*. It was not possible to run more than two replicates simultaneously because of a lack of space.

The number of dead or moribund flies was recorded at the same time each day. The broad bean plant was removed and replaced with a fresh plant infested with aphids. The number of eggs (if any) laid on the old plant was recorded.

Field studies

The marking site for the study was an area of crop ($25m^2$) in a conservation headland plot midway along the headland. The site contained a high density of poppy (*P. rhoeas*) flowers in several discrete patches. Flies foraging on the flowers were marked *in situ* with a date- specific mark.

Marking took place between 23 June and 15 July and was usually restricted to a two hour period on each date. The most effective marking period was between 07.00h and 08.30h GMT; after this time flies were easily disturbed while foraging and the rate of successful marking declined. On several dates weather conditions prevented marking taking place; it was cold, wet and windy and there were low numbers of active flies.

The headland and adjacent "green lane" were searched for marked insects on each marking date. A set route through the middle of the headland (6 m from the shelterbelt edge) and along the "green lane" was walked at a constant speed. The paint colours used meant that it was easy to spot marked flies over a distance of several metres. There was a considerable amount of variation between dates in the time at which searching commenced; the minimum duration between marking and searching was one hour.

Results

Tables 1 and 2 summarise the longevity of flies, and the number of eggs recorded from the bean plants, in the two boxes. In box one there was a significant difference in the proportion of marked and unmarked male flies alive when the two values for each date were compared using Wilcoxon's signed ranks test: Z = 3.4816, P< .005); a higher proportion of marked males were dead, at a given time compared with unmarked males. However, in the case of female flies this trend was reversed, a larger proportion of unmarked rather than marked females were dead at a given time (Wilcoxon's signed ranks test: Z = 2.242, P<.05). In box two only data for the first fourteen days of the study was compared, to allow for the differences in the total number of flies in each group. There was no significant difference in the proportion of males alive in the two treatments (Wilcoxon's signed ranks test: Z = 0.603, P= N.S.). However, the differences were significant for female flies (Z= 1.809, P<0.05).

Table 3 shows the number of flies marked on each date, and the number of flies resighted, during the field study. There were three periods (30 June-1 July; 4-5 July; 7-9 July) during which no marking or searching for marked flies was carried out due to bad weather. A total of 2910 flies were marked during the study. There was no significant difference in the number of males and females marked (Mann-Whitney U; U = 1.333, N.S., n = 28). However, on individual dates its was often the case that higher numbers of females were marked during the first half of the marking period; as temperature and level of insolation in the headland increased the number of males marked increased. 24 marked flies were resighted during the study, including 3 flies which were resighted on the same day they had been marked. With the possible exception of one fly on 3 July all the flies resighted were different individuals. The marking technique used often produced marks with characteristic shapes, therefore it was possible to differentiate between the limited number of resighted flies. All the resighted flies were recorded in the headland and with the exception of two of the flies resighted on the same day of marking, the flies were resighted in the vicinity of the marking site. This may have been a result of the longer amount of time spent in this area compared with the rest of the headland and the green lane and may also have been affected by the high density of flowering plants in the area.

Table 1. Comparison of the longevity of marked and unmarked syrphids provided with 25% sucrose solution and an excess of *Poa trivialis* pollen: experiment 1.

Day	Number of unmarked ♂	Number of unmarked ♀	Number of marked ♂	Number of marked ♀	Number of aphids/plant	Number of eggs
1	10	9	9	8	n/a	
2	10	9	9	8	n/a	
3	9	7	8	7	n/a	
4	9	7	6	5	79	
5	8	6	6	5	55	
6	8	6	6	5	58	62
7	8	6	6	5	24	59
8	8	6	6	5	38	166
9	8	6	6	5	34	87
10	8	6	6	5	23	291
11	7	6	4	5	31	261
12	7	6	4	5	59	215
13	7	6	4	5	78	222
14	7	6	4	5	99	303
15	7	6	4	5	52	152
16	6	5	4	5	44	145
17	6	5	4	5	88	151
18	6	5	4	5	96	74
19	5	5	1	5	115	110
20	4	4	1	5	105	70
21	4	3	1	5	120	18
22	3	2	1	5	99	28
23	2	2	1	4	123	11
24	2	2	1	4	83	29
25	2	1	1	4	120	36
26	1	1	1	4	20	32
27	1	1	1	4	100	26
28	1	1	1	4	23	14
29	1	1	1	4	58	25
30	1	1	1	4	224	66
31	1	1	0	3	75	20

Table 1 (contd.).

Days	unmarked ♂	unmarked ♀	marked ♂	marked ♀	aphids/plant	eggs
32	1	0	0	3	60	8
33	1	0	0	3	163	8
34	1	0	0	3	99	44
35	1	0	0	3	171	22
36	0	0	0	2	36	0
37	0	0	0	2	62	20
38	0	0	0	2	91	56
39	0	0	0	2	153	26
40	0	0	0	1	103	5
41	0	0	0	1	56	0
42	0	0	0	0		

Table 2. Comparison of the longevity of marked and unmarked syrphids provided with 25% sucrose solution and an excess of *Poa trivialis* pollen: eperiment 2.

Days	unmarked ♂	unmarked ♀	marked ♂	marked ♀	aphids/plant	number of eggs
1	3	6	7	3	n/a	
2	3	5	7	3	23	
3	3	5	7	3	36	
4	3	4	6	2	62	
5	3	4	6	2	59	
6	3	4	6	1	44	
7	3	4	4	1	41	
8	3	4	4	1	21	
9	3	4	4	1	58	
10	2	4	4	1	58	
11	1	4	4	1	73	
12	0	4	4	1	58	
13	0	3	4	0	105	
14	0	3	3	0	89	
15	0	3	3	0	245	47
16	0	3	2	0	187	107
17	0	3	2	0	164	145
18	0	3	2	0	240	144
19	0	2	1	0	158	144
20	0	2	1	0	103	151
21	0	1	0	0	121	140
22	0	0	0	0	121	

Table 3. The numbers of male and female *E. balteatus* marked on each date during the field study, 1990. The numbers of flies which were resighted on each date and their date of marking are also recorded.

Date	Number of females marked	Number of males marked	Marking period (B.S.T.)	Number of flies resighted	Date of mark on resighted flies
23 June	31	24	9.30-12.00am		
25 June	20	10	6.30-7.30pm		
26 June	80	83	9.00-10.30		
27 June	102	111	9.30-11.30am	3♂; 1♀	26 June
28 June	99	124	10.00-12.00am	4♂; 4♀ 27 June;	1♀ 25 June; 1♂ 25 June
29 June	146	170	9.50-11.45am		
2 July	128	145	10.30-12.00am		
2 July	23	27	2-2.30pm		
3 July	160	240	9.00-11.00am	2(3)♂; 1♀	2 July
6 July	82	130	10-11.00am		
10 July	101	121	10.30-12.00am		
11 July	97	105	9.00-10.30am	1♂	10 July
12 July	120	151	8.00-9.30am		
14 July	120	160	8.30-9.30am		
15 July				2♂; 1 sex not recorded	14 July; 11 July
Total	1309	1601			

Discussion

There was considerable variation in the longevity of both marked and unmarked flies in the laboratory experiments; this may have reflected the marking technique used rather than toxicity of the enamel paints. During the initial marking period most flies had to be caught to be marked because it was difficult to mark active flies in the confined space of the Perspex boxes. Unmarked control flies were not handled and this may have accounted for the differences in longevity between the two groups. This was presumably not a problem in the field since all flies were marked *in situ* without being handled. The difference in mean longevity between the two experiments may have been a result of differences in pollen quality between the two boxes; flies in the two experiments were provided with *P. trivialis* pollen from two separate batches. Pollen quality may have also affected the length of the pre-oviposition period in the two experiments. Ankersmit *et al.* (1986) recorded the mean pre-oviposition period for *E. balteatus* females at 20°C as 8.1 days (range 6-10 days). In the present study the first eggs were recorded after 6 and 15 days respectively in the two boxes.

The percentage of the total number of marked flies resighted was very low (0.72%) (6.38% when sum of the proportion resighted per date is calculated). A larger proportion of male flies was resighted (4.29%) than female flies (2.09%). The majority of flies were resighted the day after marking, although two females and a single fly (sex not recorded) were recorded three days and four days after marking respectively.

The low rate of resighting may have been a result of the majority of marked flies leaving the headland and adjacent green lane. If correct, this was not a response to marking; before 09.30h flies were sluggish and not readily disturbed: they continued foraging during and after marking. After 10.00h when the marking site was in direct sunlight flies still did not leave the site immediately after marking; at the end of a marking period approximately 60% of the flies foraging on *P. rhoeas* in the site were marked. However, when the area was searched one or more hours after the end of the marking period, no marked flies were recorded although the density of flies per unit area/ unit time was similar (approximately 254 flies 150m^2/ 5 minutes).

During the majority of the study the flies which were marked were recently emerged, immature individuals, distinguished by their pale coloration and lack of wing abrasion and absence of eggs in the females. Therefore, the low rate of resighting may be a result of newly emerged flies feeding on flowers in the immediate vicinity of the site of emergence before dispersing. This would explain the constant turnover of new individuals observed at the site through the day. The higher rate of resighting at the beginning of the study (5.70% during the period 27-28 June compared to 0.20% during the period 10-15 July) may have resulted from the marking of older flies which remained in the area. Gilbert (1981) suggested that the distribution of mature females was affected by the availability of oviposition sites; immature flies remain in the vicinity of pollen and nectar sources while distribution of males was determined by availability of mates. Holloway and McCaffrey (1990) suggested that the differences in the distribution pattern of male and female *E. pertinax* were associated with the movement of flies between feeding and oviposition sites. Chambers (1991) observed that gravid syrphid females occurring in cereals were sufficiently mobile when searching for oviposition sites for a reproductive numerical response to aphid density to be recorded between fields. This suggests that the probability of resighting even mature marked females in the headland would be low, unless the flies exhibit a diurnal pattern of movement.

Maier and Waldbauer (1979) recorded the diurnal activity patterns of six syrphid species in an area of abandoned fields and sand prairie; flies foraged during the morning while in the afternoon females of two species *Mallota postica* and *Somula decora* moved into adjacent forest where they oviposited in rot cavities in trees. Schneider (1958) recorded a long-distance (up to 5 km) daily circulation between feeding and resting places in *Sc. pyrastri* while Rotheray (unpublished) observed syrphids moving from woodland to meadows during early morning and returning in the evening. In the present study syrphids, particularly *E. balteatus*, were recorded hovering in the vicinity of the shelterbelt during the evening (>21.00h GMT); as it became cooler the flies landed on the shelterbelt vegetation, walked to the underside of the leaf and became inactive. No marked flies were observed during this period; therefore, it was not possible to determine whether the individuals which were observed regularly returned to the shelterbelt or whether there was a constant turnover of new individuals which showed no site specificity.

The limited number of flies marked during the study also reduced the probability of resighting marked flies. During the searches of the headland more than 133 *E. balteatus*/ 110m^2/ 5 minutes (± 115.1) were recorded in the conservation headland plots and 4.2 flies 110m^2/ 5 minutes (± 3.42) in fully sprayed plots. As a result on any one date the number of flies marked represented a small proportion of the total number of flies in both time and space. Therefore, although it is possible to successfully mark flies in the field using enamel paints, it is not feasible to mark sufficient flies to provide the necessary information on habitat use and movement of the flies.

An alternative approach to the study of movement in syrphids could involve the use of a biological marker to study the movement of the flies; *Phacelia tanacetifolia* (Hydrophyllaceae) is currently being used in this context (Hickman pers. comm.). *P. tanacetifolia* is a north American annual species which has characteristic pollen grains which are readily distinguishable from those of any native species. Flies are self-marked while foraging on the pollen resulting in a much higher rate of marking than can be achieved using paints. However, the technique as used does not produce a date-specific mark, therefore it is not possible to determine whether the same group of individuals are returning to *P. tanacetifolia* each day or whether there is a constant turn over of new flies, as suggested in the present study. In addition, the mark is not permanent therefore the technique can only assess short term movements of the flies. Nevertheless with knowledge of gut throughput times under different environmental conditions, the location of pollen in the gut of dissected flies could be used to provide a crude estimation of the distance travelled in a given time. If female flies are estimated to stay in the vicinity of the marker only for short periods it would suggest that the benefits, if any, of the provision of adult food source will not be restricted to the field adjacent to the food source.

Dyes have been successfully used to mark the reproductive tissues of invertebrates for example, Parker and Pinnell (1972) marked the eggs of *Pieris rapae* as a result of feeding the larvae with a diet containing red dye. Brenner (1984) used acridine orange as an *in vivo* fluorescent marker for spermatozoa of the Dipteran *Cochliomyia hominivorax* ; the spermatozoa were detectable in the spermathecae of females inseminated by marked males. Syrphid females fed a sucrose solution containing acridine orange produced fluorescent eggs (Hickman pers. comm.). It may be possible to use this technique in the field to mark syrphid eggs. Pleasants, Horner and Ng (1990) have described a technique for radioactively labelling the pollen packages and nectar of milkweeds (*Asclepias* spp.); if this technique can be successfully applied to other plant species it may also be possible to use the technique to mark syrphid eggs via the plants on which females feed and therefore examine the relationship between feeding and oviposition sites. However, the provision of patches of pollen will in itself alter the patterns of dispersion and dispersal which are being studied since the patterns are affected by the carrying capacity of the environment

During the present study no attempt was made to assess the mean distance travelled or the rate of movement of the flies, however, a single marked fly was recovered in a field of italian rye grass approximately 2.5km from the marking site 2 days after marking. Observations of the movement of adult coccinellids have shown that there is an almost continuous flux of the beetles between plots of similar and different crops (Ives, 1981) while Chambers' observations suggest that at least in the case of gravid female syrphids there is movement of flies between fields. The present study indicates that despite the presence of a high density of flowers immature flies were not retained within the vicinity of the headland. The rapid replacement of marked flies with similar numbers of unmarked flies an hour after marking finished suggests that the high density of flies recorded in the weedy conservation headland plots was the result of a constant turnover of new individuals rather than a permanent redistribution of flies from surrounding areas. Flies were never resighted more than once and no flies were resighted more than four days after marking, suggesting that even flies marked at the beginning of the study (which may have been older/mature flies) did not remain in the immediate vicinity of the headland for more than several days. Although the present study did not provide a qualitative description of habitat use by *E. balteatus* or a quantification of the movement of individuals of this species, it has confirmed the importance of differentiating between mature and immature flies when studying dispersal. In addition, it supports the conclusions of Chapter three that future studies of the effects of cultural practices on syrphids should be conducted on a much larger scale than currently employed, possibly using separate farms, or at least fields, as replicates.

CHAPTER EIGHT

GENERAL DISCUSSION

During the first year of the study (1988) fewer individuals of *E. balteatus* and *M. corollae* were observed in the margin of Field 14 than in the margin of Aero 4 (Leckford Estate); however, *Melanostoma* species were relatively more abundant at Field 14. These observations indicate that the availability of adult food sources is an important factor affecting the abundance and species composition of syrphids at a particular site since grasses predominated at Field 14 whereas composites and umbellifers were the predominant plant species at Aero 4 during the study. *Melanostoma* species forage primarily on anemophilous pollens of grasses and plantains while the majority the remaining genera (with the exception of some *Platycheirus* species and members of the genus *Xylota*) take entomophilous pollen.

During 1989 and 1990 several syrphid species which normally occur in woodland or woodland edges (*Baccha obscuripennis, Leucozona lucorum* ; Pollard, 1971) were observed in the vicinity of the shelterbelt bordering Side Scammel (South Allenford Farm); these species were not recorded at the hedgerow site in 1988 (Field 14) suggesting that either the hedgerow was not a suitable habitat for the woodland species or possibly because it was sufficiently isolated from true woodland habitats for it not to be colonised by these species.

These observations agree with studies of species composition of syrphids in differing field margin types in Germany, which have shown that habitat quality is important in determining the diversity and abundance of syrphids in the vicinity of a particular field margin. Molthan and Ruppert (1989) studied the species composition of syrphids in three naturally occurring field margins; the number of species and abundance of flies in narrow margins consisting of grasses was lower than in wider (1.5-2m) margins consisting of a range of dicotyledonous plants. The greatest diversity and largest number of individuals were recorded from an 8m wide margin with an adjacent embankment and a high diversity of flowering plants. Kühner (1988) compared the relative abundance of syrphids in three locations in Hesse, Germany; syrphids were more abundant at the two locations with a diverse range of dicotyledonous plants than at the third location at which grasses predominated.

Observations of the foraging behaviour of the commonly occurring syrphids, *E. balteatus* and *M. corollae*, indicated that although these species are generalists they do use plant species selectively; the relative importance of individual plant species varied with time. These observations facilitated the identification of the components of field margin vegetation which are worth encouraging through selective herbicide use.

The growth of several of the selected plant species is encouraged through the adoption of the Game Conservancy Trust's conservation headland guidelines. The effect of the adoption of the technique on the relative abundance of syrphids in a headland was examined by comparing the numbers of adult syrphids in conservation and adjacent fully sprayed headland plots. In 1989 few flowers were recorded in the conservation headland plots and the proportion of flies observed in the two treatments was not significantly different. However, during 1990 when there was a significant difference in mean floral area (i.e. the number of flowers) between the two treatments, significantly higher proportions of *E. balteatus* were recorded in conservation headland plots than in fully sprayed plots.

Although flies were retained in the conservation plots as a result of their foraging on the flowering non-crop plants it was not possible to determine the scale on which the redistribution of flies was occurring. Different syrphid species exhibit a range of mobilities. For example, Haslett (1981) recorded that the maximum distance that marked individuals of *Rhingia campestris* were recorded from a release point was 72m. Holloway and McCaffrey (1990) recorded that the rate at which marked *E. pertinax* spread out across a woodland clearing was slow and the flies never obtained a random distribution across the site. Observations of marked immature male and female *E. balteatus* (Chapter seven) showed that the flies were not retained within the headland despite the high densities of adult food sources; the observations suggested that there was a constant turnover of new individuals in the headland, with probable long-distance movement.

Mature females of several syrphid species were observed foraging on pollen in the headland. In addition, greater than 90 per cent of dissected gravid females collected in another study contained pollen in their guts (Hickman pers. comm.). However, the spatial relationship between feeding and oviposition sites has not been studied and no information is available in the literature which quantifies the area or distance to which syrphids such as *E. balteatus* and *M. corollae* respond in carrying out their functions, such as feeding and reproduction. Gravid females are sufficiently mobile to show a numerical response to aphid density between plots within a single field (Chapter four) and between fields (Chambers, 1991), the largest of which was 32ha. These observations presumably account for the failure to detect an edge effect (the absence of higher numbers of eggs per aphid in the vicinity of the margin than at the centre of the field) in Chapter five. Because of the short window of time in which the study described in Chapter five was carried out, it was only possible to examine the distribution of *E. balteatus* and *M. corollae* eggs within the field. Further studies are required to examine the spatial distribution of *Syrphus, Melanostoma* and *Platycheirus* eggs within and between cereal fields.

The margins of the study field described in Chapter five were poor "quality" and comprised naturally occurring vegetation with a low number of flowers per unit area. High density, single species stands of flowering plants have been sown in field margins in an attempt to enhance the level of syrphid oviposition in the adjacent fields (Klinger, 1987; Sengonca and Frings, 1988). These high density patches may influence the patterns of movement of flies such as *E. balteatus* by increasing the carrying capacity of the habitat; limited availability of resources is one of the factors promoting dispersal. Sengonca and Frings (1988) compared the numbers of syrphid adults and eggs in plots of sugar beet with and without margin strips of *Phacelia tanacetifolia*. Although higher numbers of adults were recorded in the vicinity of the *P. tanacetifolia*, higher numbers of syrphid eggs and larvae were recorded in the control, where aphid density was by chance the highest. Therefore, on the limited spatial scale studied, aphid density was the important factor in determining the distribution of syrphid eggs. Studies being carried out at Southampton are intended to compare the number of eggs per aphid in fields with margins drilled with *P. tanacetifolia* with the numbers recorded in fields with naturally occurring, unmanipulated boundary vegetation. It is possible the use of separated fields on a single farm may still be insufficient to detect an effect of habitat/ field margin manipulation on the level of oviposition by syrphids such as *E. balteatus* and it may be necessary to study the relationship using widely separated farms as replicates.

Observations of the distribution of syrphid eggs between fully sprayed and conservation headland plots (Chapter three) have shown that in the genus *Melanostoma* oviposition sites are not determined by aphid density. Eggs belonging to this genus were predominately recorded from non-crop plants, often in the absence of aphids. These observations indicate that the presence of non-crop plants within the crop stimulates females of these species to oviposit within the crop. Currently it is not known whether there is a threshold weed density below which oviposition does not occur; however if the presence of weeds at low densities is sufficient to stimulate oviposition it is possible that the larvae of these species will become more common in cereals if the current trend towards lower herbicide inputs continues. The foraging behaviour of the larvae of *Melanostoma* (and *Platycheirus*) species requires further study, in particular to examine whether they move from weeds at the base of the crop onto the crop itself and predate cereal aphids. Even if the larvae are shown to remain on low growing plants in the base of the crop they may have a role in limiting the development of pest aphid populations on these plants. In the present study *Melanostoma* species adults and eggs were recorded early in the season (early May; G.S.49). At this time *S. avenae* was recorded from non-crop plants, particularly *Poa* spp., at the base of the crop; predation by syrphid larvae may limit the spread of aphids from these plants onto the crop. In addition, to providing oviposition sites for *Melanostoma*, and possibly *Platycheirus* spp., imperfect weed control has also been shown to have positive benefits in terms of the numbers of polyphagous predators (for example, Powell, Dean and Dewar, 1985; Speight and Lawton, 1976).

During the present study no attempt was made to examine the effect of the pollens of differing flowering plants on the fecundity of, or the timing of the onset of oviposition by, individuals of a particular syrphid species. Saidov (in Way, 1966) is reported to have found that fecundity in *M. corollae* varies according to the type of pollen offered. During the present study variation in quality between different batches of the *Poa trivialis* pollen were presumably the cause of the observed differences in the timing of the onset of oviposition by *E. balteatus* females (Chapter seven). It is possible that the limited availability of "good quality" pollen sources in field margins may affect the timing of the onset of oviposition and/or the numbers of eggs laid by individual females.

In the agroecosystem, adult syrphids are dependent on patches of natural vegetation which occur as small fragments more or less isolated in a matrix of intensively managed fields. The theory of metapopulation dynamics provides a framework for considering the survival of a species in a network of habitat patches. Levin (1970) introduced the term metapopulation to describe an overall population which is made up of many and changing sub-populations linked by dispersing individuals. At any one time the species will be present in some patches and not in others; over time extinction resulting from predation, disease or unpredictable environmental events will result in the loss of some sub-populations while immigration will re-establish others. Even though the populations in these individual patches may fluctuate widely from abundance to extinction the metapopulation can be roughly constant, although it too can cycle or fluctuate erratically or even expand or decline with time (Southwood and May, 1990). The provision of a network of field margins containing appropriate weed species might be expected to result in an expansion of the overall metapopulation; evidence from some insect populations points to a close tracking of the carrying capacity of the environment, i.e a constant number of individuals per unit of resource (e.g., Dempster 1983; Oghushi and Sawada, 1985). Gilbert and Owen (1990) suggested that syrphid species respond largely independently to fluctuations in essential resources; the similarity in density fluctuations between various groupings of syrphid species was a result of species "tracking" covarying or common resources. For example, parallel fluctuations of the group of anemophilous-pollen specialists, the *Melanostoma* and *Platycheirus* group have been recorded (van der Goot and Grabandt, 1970; Stelleman, 1978). However, the effect of the provision of such patches on the long term population levels of syrphids on farmland will depend on the "key factor" (*sensu* Varley and Gradwell, 1960) in syrphid populations.

Gilbert and Owen (1990) concluded that there was evidence of competitive interactions between species with generalist predatory larvae. Hagvar (1972) examined the effect of intra and interspecific competition on the development of *M. corollae* and *Syrphus ribesii* larvae. The survival of *M. corollae* larvae decreased from 73.1 to 25.0% when the larvae were in competition with *S. ribesii*. If larval mortality is the "key factor" in populations of economically important syrphids on farmland the provision of patches of pollen and nectar sources will not result in a long term enhancement of population levels; aphid density will be more important in determining these levels. However, the applied aim of the provision of extra floral resources in or around fields is not necessarily that of long term enhancement; rather it may be sufficient, on a local scale, to shift sub-populations within the metapopulation to effect a higher level of pest control in one field or farm to the detriment of another. The present study has identified the non-crop flowering plants which are important to syrphids and has examined the potential for using management techniques which encourage the growth of these plant species to enhance bio-control by this important group of aphid predators in arable land.

Future Work

In the present study the provision of adult food sources has been shown to cause a local redistribution of flies; further studies are required to examine the effect of this redistribution on levels of oviposition between fields or farms and to quantify the scale on which an effect, if any, can be detected. Studies currently being carried out at Southampton are examining the levels of oviposition between separate fields with or without margin strips of flowering plants. An alternative approach which may have potential for the study of the spatial relationship between adult feeding sites and oviposition sites is the use of techniques which mark syrphid eggs via the plant on which the female flies forage. Syrphid females fed a sucrose solution containing the fluorescent dye acridine orange have produced fluorescent eggs (Hickman, pers. comm.). Further studies are required to determine the feasibility of using this technique to mark syrphid eggs in the field.

Although mature females of several syrphid species have been recorded foraging it is not known how frequently they take pollen (and nectar). It may be possible to use video techniques or direct observation to record the frequency of flower visits by individual females in laboratory conditions and to identify species-specific differences in behaviour. However, the results may not be directly applicable to the situation in the field where flight is not restricted and therefore the energetic requirements of the flies may be different

Laboratory cultures of syrphids could be used to study the effect, if any, of different pollens on the timing of the onset of oviposition and or fecundity of flies. These factors may have implications for the choice of non native plants to incorporate into field margin management scheme. In addition differences in the nutritive value of pollens may account for the selective use of particular plant species by the flies described in the present study.

In the present study higher numbers of eggs per aphid were recorded in the headland plots containing flowering non-crop plants. This was in part a result of oviposition by phytozetic females, particularly *Melanostoma* species. Little is known about the predatory potential of *Melanostoma* and *Platycheirus* larvae in cereals. Chambers *et al.*(1986) and Dean (1982) recorded *Platycheirus* larvae from cereals; Dean observed the larvae foraging predominately on non-pest species on low growing plants in the base of the crop. Gilbert and Rotheray (1989) suggested that *Melanostoma* larvae may be generalised predators in leaf litter while several of the *Platycheirus* species larvae which occur in cereals may be facultatively aphidophagous. Therefore, field studies of the foraging behaviour of *Melanostoma* and *Platycheirus* larvae are required to clarify the predatory potential of these species in cereals. Examination of the surface patterning of eggs collected from different positions within weedy fields would clarify whether adults of these genera oviposit in the centre of large fields or whether oviposition is restricted to the edges of fields. In the present study eggs collected only from the headland (Chapter three) were identified using the characteristic surface patterning.

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APPENDIX I

Table 1. The proportion of the total number of flower forms at Aero 4 during 1989. (n= total number of flower forms).

	Date								
	21688	29688	7788	13788	20788	27788	6888	13888	22888
Anagellis arv	0.0057	0	0.0009	0.0024	0.0031	0.0029	0.0016	0.0016	0
Achillea mil	0.0055	0.011	0.028	0.0108	0.0249	0.0245	0.0227	0.0211	0.0392
Aethusa cyn	0.0004	0	0.0018	0.0094	0.0121	0.0261	0.0411	0.0389	0.0226
Aegopodium pod	0.0092	0.0009	0	0	0	0	0	0	0
Brassica rap	0.0051	0	0	0	0	0	0	0	0
Artemisia vul	0	0	0	0	0.0133	0.0073	0	0.0097	0
Cirsium arv	0	0.003	0.0108	0.0155	0.0238	0.0206	0.0093	0.0031	0.0043
Convolvulus arv	0.0048	0	0.0038	0.0026	0.0013	0	0.0009	0.0024	0.0072
Crepis cap	0	0.014	0.027	0.0344	0.0372	0.0322	0.0251	0.0165	0.0214
Daucus car	0	0	0	0.0006	0.0009	0.0014	0	0.003	0.0065
Heracleum sph	0.0167	0.0093	0.0092	0.0016	0.001	0.0007	0.0004	0	0
knotgrass	0.082	0	0.018	0.0004	0	0	0.0109	0.0262	0.0187
Leontodon aut	0	0	0.0012	0.0005	0.0009	0.0027	0.0047	0.0139	0.0146
Lamium alb	0.0887	0.0463	0.034	0.017	0.0315	0.0694	0.1173	0.1386	0.1358
Lamium pur	0.0388	0.0073	0.0043	0.0111	0.0235	0.0161	0.0066	0.0021	0.0017
Medicago lup	0	0.0064	0.0221	0.0411	0.0375	0.0178	0.0481	0.0592	0.0559
Matricaria per	0	0.0138	0.0854	0.2717	0.4503	0.6033	0.6455	0.6113	0.5844
rayless may	0.034	0.0469	0	0	0	0	0	0	0
Lapsana comm	0.284	0.619	0.6891	0.5103	0.2997	0.148	0.0375	0.0269	0.0324
Plantago lan	0	0	0	0	0.0006	0	0.0015	0	0.0006
Plantago maj	0	0	0	0	0	0	0	0.0009	0
redshank	0	0	0	0	0	0	0.001	0.0025	0.0028
Sonchus asp	0.001	0.0028	0.0411	0.0493	0.0201	0.014	0.0096	0.0086	0.0187
Sonchus arv	0.006	0	0	0.0006	0.0004	0	0.0035	0.0035	0.0031
Sinapsis arv	0.185	0.0073	0.0017	0.0052	0	0.0042	0.0018	0	0.0008
Silene alb	0.0478	0.0185	0.0146	0.0035	0.0068	0.0017	0.0048	0.0021	0.0091
Silene vul	0.167	0.176	0.0028	0	0	0	0	0	0
Taraxacum off	0.0022	0	0.0001	0.0003	0	0.0001	0.0003	0.0001	0.0007
Senecio vul	0.0152	0.0078	0.0048	0	0	0	0	0	0.0139
Wild parsnip	0	0	0	0.0001	0.0001	0.0012	0.0036	0.0031	0
Veronica per	0.00423	0	0	0.0116	0.0109	0.0061	0.0031	0.0031	0.0018
Ranunuculus rep	0.00102	0.0003	0.0001	0.0002	0	0	0	0	0
Fumitory	0	0.0093	0	0	0	0	0	0	0
Viola arv	0	0	0.0001	0.0005	0	0	0	0	0
Cirsium vul	0	0	0	0	0.0001	0	0.0008	0.0011	0.0013
Black bw	0	0	0	0	0	0	0	0.0031	0.0028

Table 2.The number of observations of foraging behaviour of 15 syrphid species at Site 1 during 1988.

Site 1

Syrphid species		Date: June 1988		
	13.6.88	15.6.88	23.6.88	30.6.88
Episyrphus balteatus	1	1	25	10
Eristalis tenax	8	6	9	3
Eristalis spp.	12	19	22	
Heliophilus spp.	1			5
Melanostoma spp.	3	1	2	
Metasyrphus corollae	3			
Platycheirus albimanus				
Platycheirus clypeatus				
Platycheirus manicatus				
Platycheirus peltatus			1	3
Rhingia campestris				
Sphaerophoria scripta	2		13	
Scaeva pyrastri				
Syrphus spp.	2			
Syritta pipiens	2	10	4	

Site 1

Syrphid species		Date: July 1988	
	8.7.88	14.7.88	29.7.88
Episyrphus balteatus	4	3	1
Eristalis tenax	2		
Eristalis spp.		2	
Heliophilus spp.			
Melanostoma spp.	17	20	9
Metasyrphus corollae	16	6	
Platycheirus albimanus		2	
Platycheirus clypeatus			
Platycheirus manicatus			
Platycheirus peltatus			
Rhingia campestris			
Sphaerophoria scripta	3		
Scaeva pyrastri			
Syrphus spp.			
Syritta pipiens	1	2	

Site 1

Syrphid species	Date: August 1988		Date: May 1988	
	7.8.88	14.8.88	12.5.88	26.5.88
Episyrphus balteatus	10	1	1	
Eristalis tenax	1	1		
Eristalis spp.	4	5		
Heliophilus spp.				
Melanostoma spp.	12	11		2
Metasyrphus corollae				
Platycheirus albimanus	1	1	2	4
Platycheirus clypeatus	2		1	
Platycheirus manicatus	1	1		1
Platycheirus peltatus	10	5	2	11
Rhingia campestris		1		
Sphaerophoria scripta		5		
Scaeva pyrastri				
Syrphus spp.				
Syritta pipiens	9	7		

Table 2 (contd.) The number of observations of foraging behaviour for 15 syrphid species at Site 2 during 1988.

	Date: June 1988			
	7.6.88	14.6.88	21.6.88	22.6.88
Episyrphus balteatus			16	5
Eristalis tenax	5	9	24	10
Eristalis spp.		6	4	
Heliophilus spp.				
Melanostoma spp.		1		
Metasyrphus corollae			7	1
Platycheirus albimanus				
Platycheirus clypeatus				
Platycheirus manicatus				
Platycheirus peltatus	10	2	1	
Rhingia campestris				
Sphaerophoria scripta				1
Scaeva pyrastri				
Syrphus spp.				
Syritta pipiens	1	1	4	4

Site 2 Syrphid species	Date: June 1988	July 1988		
	28.6.88	29.8.88	7.7.88	13.7.88
Episyrphus balteatus	7	26	49	52
Eristalis tenax	2	28	8	5
Eristalis spp.		10	9	3
Heliophilus spp.				
Melanostoma spp.		1	2	6
Metasyrphus corollae		3	19	18
Platycheirus albimanus				
Platycheirus clypeatus				
Platycheirus manicatus				
Platycheirus peltatus		1		
Rhingia campestris				
Sphaerophoria scripta	1	2	1	4
Scaeva pyrastri			2	
Syrphus spp.			2	
Syritta pipiens	1	2	7	5

Site 2 Syrphid species	Date: July 1988	August 1988		
	20.7.88	27.8.88	6.8.88	13.8.88
Episyrphus balteatus	97	125	6	29
Eristalis tenax	6	3	13	5
Eristalis spp.	6	3	7	
Heliophilus spp.				
Melanostoma spp.	15	13	4	15
Metasyrphus corollae	4	9	9	4
Platycheirus albimanus	4	4	4	3
Platycheirus clypeatus		1	1	
Platycheirus manicatus			6	6
Platycheirus peltatus			35	56
Rhingia campestris			1	1
Sphaerophoria scripta	1		4	2
Scaeva pyrastri				
Syrphus spp.				
Syritta pipiens	3	3	30	9

Site 2

Syrphid species	Date: August 1988	
		20.8.88
Episyrphus balteatus		7
Eristalis tenax	2	
Eristalis spp.		1
Heliophilus spp.		
Melanostoma spp.	4	
Metasyrphus corollae		3
Platycheirus albimanus	1	
Platycheirus clypeatus		
Platycheirus manicatus		2
Platycheirus peltatus		34
Rhingia campestris	8	
Sphaerophoria scripta		4
Scaeva pyrastri		
Syrphus spp.		1
Syritta pipiens		18