OVIPOSITION STRATEGIES OF APHIDOPHAGOUS SYRPHIDAE

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To my parents

ABSTRACT

The principal objective of this study was to examine the oviposition strategies of aphidophagous syrphids.

The phenologies of different syrphid species occurring in annual crop and natural habitats are described and the factors influencing the spatial and temporal distribution patterns of the adults are discussed. These factors include the distribution of adult and larval food resources, shelter and the emergence patterns of the insect.

The effect of different climatic factors on the diel patterns of syrphid flight was investigated. The most important factor influencing flight activity was found to be temperature: different syrphids species have different threshold temperatures above which they become flight-active.

The oviposition patterns of different syrphid species in different brassica crops are described. The relative importance of aphid-associated and aphid host-plant-associated factors in determining oviposition site selection is considered.

The biology and behaviour of *Episyrphus balteatus* Degeer was studied in the laboratory. A technique for rearing this species in captivity is described. The number of eggs laid by gravid *E. balteatus* females is closely related to aphid density. The behavioural mechanism of this density-dependent oviposition response was investigated: gravid females made more landings on higher density plants and laid a fixed number of eggs during each plant visit.

The role of syrphids as biological control agents of aphids is discussed. Manipulation of adult oviposition behaviour may increase the effectiveness of syrphids in controlling aphid populations. The application of nutritional food sprays to brassica crops attracted

adult syrphids into the crop and stimulated oviposition at a time when the level of aphid infestation was low. This technique may be a useful means of improving synchronisation between pest and predator populations.

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CHAPTER 1

AN INTRODUCTION TO THE SYRPHIDAE

1.1 A REVIEW OF THE LITERATURE

The purpose of this chapter is to present a general review of current knowledge regarding the family Syrphidae. The chapter ends with a brief outline of the present study and its relevance to this knowledge.

1.1.1 Classification

Thompson's (1980) survey of regional catalogues indicates that there are some 5326 known species of Syrphidae in the world: 1530 spp in the Palaearctic (Pederson and Thompson, in prep), 857 spp in the Nearctic (Wirth et al, 1965); 1605 spp in the Neotropics (Thompson et al, 1976), 526 spp in the Afrotropics (Smith and Vockeroth, 1980), 716 spp in the Oriental (Knutson et al, 1975) and 366 spp in Australasia (Thompson, in prep). In addition, there may be a further 10,000 undescribed species (Thompson, 1980).

The British syrphid fauna comprises some 250 named species with a further six species and at least nine forms whose name or taxonomic status is currently uncertain (Stubbs and Falk, 1983).

The family can be divided into three main groups: the Milesiinae, Syrphinae and Microdontinae (Goffe, 1952; Hartley, 1961; Thompson, 1972; Boyes et al, 1980). The Milesiinae is by far the largest subfamily; almost two-thirds of the British hoverfly fauna fall into this group. The Syrphinae contain most of the beneficial species: the larvae are all predators, usually of aphids. The Microdontinae are often included in the Milesiinae (eg Kloet and Hincks, 1976), but are more frequently accorded sub-familial status (Coe, 1953; Thompson, 1969). One tribe has proved exceptionally difficult to classify satisfactorily: the Pipizini were originally placed in the Syrphinae because their larvae are aphidophagous, but they are now included in the Milesiinae on the basis of the adult morphology.

1.1.2 Life-histories

There is a considerable body of literature on the life-histories of syrphids (eg Bańkowska, 1964; Bänsch, 1964; Bhatia, 1931, 1939; Claussen, 1980; Chandler, 1968e; Doucette et al, 1942; Dušek and Láska, 1974; Dunn, 1949; Gaumont, 1929; Gilbert, 1981a; Goeldlin, 1974; Grosser and Klapperstück, 1977; Hartley, 1961; Hodson, 1927; Nielsen, 1971; Pollard, 1971; Rotheray, unpubl; Schneider, 1948; Scott, 1939; Speight, 1980; Speight et al, 1975; Stubbs, 1980; Stubbs and Falk, 1983; Sundby, 1966; Zimina, 1957b). Syrphids exhibit a wide range of phenological strategies with uni- and bivoltine species overwintering as diapausing larvae, and polyvoltine species hibernating as adults and/or migrating to warmer parts (Schneider, 1948; Goeldlin, 1974).

1.1.3 Habitat preferences

Several studies have described the habitat preferences of adult syrphids (eg Bánkowska, 1980; Claussen, 1980; Chandler, 1969; Coe, 1953; van der Goot, 1967; Malinowska, 1979; Nielsen, 1971; Nielsen et al, 1954; Scudder, 1956; Speight et al, 1975; Stubbs and Falk, 1983; Yano et al, 1979). Most species are associated with forest or woodland habitats although many occur also in open areas such as meadows, crops, mountain meadows, marshes or moors. Some species have also been found in xerothermal habitats such as sands, coastal dunes and inland dunes.

1.1.4 Larval feeding habits

Syrphid larvae exhibit a wide range of feeding habits. These may be divided into three main groups: phytophages, saprophages and entomophages. Phytophagous larvae feed mainly on living plant tissue.

The larvae of *Cheilosia* species attack leaves, stems and roots of herbaceous plants (Dušek, 1962; Smith, 1979; Bánkowska, 1980). Larvae of *Merodon* (Doucette *et al*, 1942) and *Eumerus* (Hodson, 1927; Craeger and Spruijt, 1935) species feed on bulbs. Some species are thought to feed on sap exudates from tree wounds (eg *Ferdinandea cuprea* Scop., *Brachyopa scutellaris* Robin.-Desv.- Hartley, 1961). Three closely-related *Cheilosia* species feed on fungi: *C. scutellata* Fall. and *C. soror* Zett. have been reared from truffles, and *C. scutellata* and *C. longula* Zett. have been found feeding on *Boletus*, *Leccinum*, *Suillus* and *Gyroporus* fungi (Smith, 1980).

Saprophagous larvae feed on decaying organic material. Some species live in partially decomposed plant material such as decaying bulbs, rhizomes and roots (eg *Rhingia*, *Tropidia*, *Syritta*). Many Milesiinae larvae feed on wood in different stages of decomposition (eg *Sphegina*, *Spilomyia*, *Temnostoma*, *Brachypalpus*, *Criorhina*). The larvae of many terrestrial saprophagous species inhabit tree rot-holes which are rich in detritus (eg *Callicera*, *Myiatropa*, *Mallota*, *Pocota*). Other species are to be found in drains (eg *Helophilus*, *Eristalis*), cesspits (eg *Eristalis*), stagnant ponds (eg *Helophilus*, *Anasimyia*, *Cheilosia*, *Chrysogaster*), compost heaps (eg *Syritta*, *Xylota* and *Eristalis*) and cow dung (eg *Rhingia* and *Syritta*). The larvae of species occupying such habitats are usually well adapted for an aquatic existance. Eristaline larvae have an extensible caudal respiratory tube for obtaining atmospheric oxygen, anal papillae for facilitating ionic exchange and an elaborate filtering apparatus for feeding on detritus (Hartley, 1963; Hase, 1926; Krogh, 1943; Krüger, 1926; Roberts, 1970; Wahl, 1900; Wichard and Komnick, 1974).

The larvae of entomophagous species prey mainly on aphids and other small Homopterans. However, a few species specialize on other insect prey: *Xanthandrus comtus* (Harris) larvae feed on small Lepidopteran caterpillars (Smith, 1936; Lucchese, 1942; Lyon, 1968). *Dasysyrphus tricinctus* (Fall.) attacks Lepidopteran and sawfly larvae (Gäbler, 1938), and *Parasyrphus nigritarsis* (Zett.) larvae feed mainly on eggs and larvae of *Melasoma* chrysomelids (Schneider, 1953).

Larvae of the genus *Volucella* are scavengers in the nests of social wasps (*Vespa* and *Vespula* spp) and bumblebees (*Bombus* spp); they are believed to feed on dead larval hymenopterans and other debris within the nest. An unusual commensal relationship exists between larvae of the genus *Microdon* and ants: the larvae inhabit the nests of *Lasius* and *Formica* ants and feed on buccal pellets produced by the ants. A less certain relationship occurs with *Doros*, *Chysotoxum* and *Xanthogramma* species: larvae belonging to these genera have been found in ant nests and probably feed on root aphids tended by the ants (Dixon, 1960; Bánkowska, 1980).

The larvae of some species may be only facultatively entomophagous. Davidson (1922) reported that *Melanostoma obscurum* developed more rapidly on a diet of decaying chickweed than on aphids. Hamrum (1966) observed *Metasyrphus* and *Allograpta* larvae feeding on cabbage leaves and Rotheray (unpubl) managed to successfully rear *Melanostoma scalare* Fabr. larvae on decaying leaf litter.

1.1.5 Larval anatomy and physiology

The anatomy and physiology of syrphid larvae have been studied in only a few species and these usually belong to the Eristalini (eg Aubertot, 1932; Buckton, 1895; Dolley and Farris, 1929; Dunavan, 1929; Gäbler, 1930; Hartley, 1963; Hase, 1926; Ibrahim and Gad, 1975; Jarczyk, 1957; Krogh, 1943; Krüger, 1926; Roberts, 1970; Wahl, 1900; Wichard and Komnick, 1974). Other species studied include *Meliscaeva auricollis* Meig. (Borelli, 1920), *Metasyrphus luniger* Meig. (Vine, 1895), *Syrphus vitripennis* Meig. (Novák and Bičík, 1965), *Volucella* (Künckel d' Herculais, 1875), and *Mallota posticata* Fabr. (Maier, 1978).

Studies of aphidophagous larvae are usually concerned with larval voracity: the number of aphids required to complete development (eg Barlow, 1979; Benestad, 1970b; Bombosch, 1963; Cornelius and Barlow, 1980; Polak, 1980; Rüžícka, 1975; Tawfik *et al*, 1974a). Prey-seeking behaviour has also been studied in a few aphidophagous species (eg Bänsch, 1964, 1966; Schaller and Bänsch, 1963; Chandler, 1969; Rotheray, unpubl).

Studies on larval development have shown that polyvoltine species normally have very short larval lives (eg less than 10 days in Metasyrphus corollae Fabr., Benestad, 1970b). In contrast, the larval stage of univoltine species such as Merodon equestris Fabr. (Doucette, et al, 1942) and Epistrophe eligans Harris (Schneider, 1948) may last for a year before pupation occurs.

1.1.6 Adult anatomy and physiology

The anatomy of adult syrphids has been studied in only a few species. These include Eristalis tenax L. (Buckton, 1895; Giacomini, 1901; Mercier and Villeneuve, 1927), Helophilus trivittatus Fabr. (Vater, 1962), Syrphus spp (Zimina, 1957a) Volucella elegans (Arnal, 1955) and Volucella spp (Künckel d'Herculais, 1875). A particularly detailed study of the anatomy of Episyrphus balteatus Degeer has been carried out by Nayar (1964a, b, c; 1965a, b, c, d, e; 1966).

Syrphids are excellent fliers: Lyon (1965) reports that Episyrphus balteatus can cover distances of up to 10 km in a day. Magnan (1934) recorded a maximum speed of 3.5 ms^{-1} in flying Volucella.

Many species have been recorded migrating over great distances in coastal and mountain areas (eg Aubert, 1962; 1964; Burton and Owen, 1954; Gray, Locke and Putnam, 1953; Johnson, 1969; Lack and Lack, 1951; Snow and Ross, 1952; Williams et al, 1956). The origin and aim of these large-scale migrations and the effects on population dynamics of the migrating species are still unknown. Migrations in autumn may be related to the search for winter quarters.

The aerodynamics of hovering flight in syrphids have been studied by Magnan (1934), Weis-Fogh (1973), Rees (1975a, b), and Ellington (1981). The visual capabilities of syrphids during flight have been studied in Syritta pipiens L. (Collett, 1980a, b; Collett and Land, 1975b) and in Eristalis species (eg Beersma et al, 1977; Bernard and Stavenga, 1979; Bishop and Chung, 1972; Buddenbrock and Moller-Racke, 1952; Dolley, 1929, 1930, 1932, 1936; Dolley and White, 1951a, b; Dolley and Wierda, 1929; Fransevich and Zolotov, 1973; Ilse, 1949; Kugler, 1950; Mast, 1923; Pichlea, 1977; Stavenga, 1976, 1979; Strausefeld, 1970;

Swartz, 1942; Tsukuhara and Horridge, 1977a, b; Tsukuhara *et al*, 1977; Wagner, 1947; Zolotov, 1978).

1.1.7 Adult feeding

Adult syrphids are flower feeders and pollen has been shown to be essential for ovarial maturation (Schneider, 1948; Doucette and Eide, 1955; Adashkevich and Karelin, 1972). Adult flies have also been reported feeding on aphid honeydew (Zoebelein, 1956) and other substances present on leaf surfaces. Gilbert (1981b) has shown that the diets of adult syrphids are closely related to the morphology of their mouth parts: body size together with the size and shape of the proboscis are the most important factors correlated with the proportions of pollen and nectar in the diet.

1.1.8 Adult oviposition

Studies on syrphid oviposition are confined mainly to entomophagous species. Chandler (1968a, b, c) suggested that aphidophagous syrphids could be divided into two main groups on the basis of the stimuli required to elicit oviposition. 'Aphidozetic' species respond primarily to aphid-associated stimuli and tend to lay eggs singly close to aphid colonies. The larvae of aphidozetic specis are normally obligate entomophages. 'Phytozetic' species respond mainly to plant-associated factors and often oviposit on uninfested plants; those species frequently lay their eggs in small batches and the larval stage is thought to be only facultatively entomophagous. The factors influencing oviposition in *Metasyrphus corollae*, an aphidozetic species have been particularly well studied in the laboratory (Bombosch, 1962; Bombosch and Volk, 1966; Peschken, 1965; Volk, 1964; Sanders, 1979, 1980, 1981, 1982). Oviposition in *Sphaerophoria* (Ivri and Dafni, 1977) and *Eristalis tenax* (Campan, 1973; Campan and Campan, 1979) has also been studied.

1.1.9 Natural enemies of syrphids

Syrphids are parasitized by several different Hymenopteran families (Braconidae, Ichneumonidae, Encyrtidiae, Eupelmidae, Pteromalidae, Chalcididae, Phigitidae, Ceraphronidae and Diaprridae (Schneider, 1948; Weems, 1954; Rotheray, 1981). Many of these parasites are specific to one or a few closely related host species (Schneider, 1969). In Britain, the most common syrphid parasites belong to the Ichneumonidae: the females oviposit in eggs or newly-hatched larvae of the host and the adult parasite emerges from the host puparium. According to Rotheray (1981), female parasites locate aphid colonies by responding to aphid odours and then respond to contact chemicals on the integument of the syrphid larva. Differences in host specificity may be due to haemolymph factors affecting tolerance for or against the parasite egg or larva, habitat preferences of the adult parasite, and behavioural defensive mechanisms used by syrphid larvae to resist attack (Schneider, 1969; Rotheray, 1981). Rates of parasitism in syrphid populations may vary considerably from one year to the next (Dean, 1983). Bombosch (1959) reported that up to 40% of syrphid larvae attacking *Aphis fabae* Scop. on sugar beet were parasitized. A dipteran Tachinid parasite has been reported from *Merodon* larvae (Collin, 1945). Schneider (1969) reports that syrphid larvae are frequently taken by birds.

Nematode parasites have been recovered from adults of *Ferdinandea cuprea*, *Episyrphus balteatus* and *Xylota segnis* L. (Gilbert, 1981a).

Predators of adult syrphids include birds (Kozena, 1979; Parmenter, 1954, 1957, 1959; Reid, 1955; Rettenmeyer, 1970; Schneider, 1947; Siegfried, 1971; Walsh, 1978), Hymenoptera (Boreham, 1952, 1958; Faester, 1944; Hamm and Richards, 1926; Jones, 1928; Pickard, 1975) other Diptera (Hobby and Smith, 1961a, b; Parmenter, 1941, 1959; Poulton, 1906; Smith, 1952; Wootton, 1967), Odonata (Hobby, 1932; Moore, 1953) and spiders (Hobby, 1940; Morse, 1979, 1981; Turner, 1946).

Adult syrphids are frequently reported to be attacked by fungal pathogens, usually *Entomophthora*, *Empusa muscae*, or *Empusa syrphi* (Brongniart and Cornu, 1879; Grensted, 1946; Ingold and Plunkett, 1979;

Leatherdale, 1961; Petch, 1932; Smirnoff and Macleod, 1975; Turian, 1962; Venkatraman et al, 1960; Wallace and Whiteley, 1979). Melanostoma and Platycheirus species seem to be particularly susceptible and their corpses are often to be found on flowering heads of grasses and Plantago (van der Goot and Grabandt, 1970).

Bacterial disease of syrphid larvae has been reported from laboratory cultures (Kamal, 1927; Speyer, 1936; Dušek and Láska, 1962; Steinhaus and Marsh, 1962; Clark, 1963; Tokmakoglu, 1965).

1.1.10 Economic importance

Syrphids may be regarded as insects of economic importance for two reasons. Firstly, the adults pollinate flowers and secondly, the larvae of aphidophagous species have potential as biological control agents of aphids.

There are numerous records of syrphid visits to flowers in the literature and many authors have claimed that syrphids are important in the pollination process (Bohart et al, 1970; Brantjes, 1981; Brightmore, 1979; Clifford, 1964; Dafni and Ivri, 1980; Hagerup, 1951; Haslerud, 1974; Ivri and Dafni, 1977; Kay, 1976; Lyon, 1965; Meeuse and Schneider, 1980; Parmenter, 1961; Pion and de Oliveira, 1980; Schmid, 1970; Stelleman and Meeuse, 1976). However, the efficiency of syrphids as pollinating agents is contraversial. Some authors claim that syrphids do not pollinate (eg Percival, 1965; Eyde and Morgan, 1973). Estes and Thorp (1974) and Miliczky and Osgood (1979) showed that, in some cases, syrphids do not necessarily fertilise the plants they visit. Kevan (1972) believed that Diptera are only important as pollinators in areas where floral diversity is low and bees are scarce (eg the Arctic).

The larvae of aphidophagous species are widely recorded as being important predators of aphids, eg Bakhetia and Sharma, 1979; Barbosa, 1952; Bartoszech, 1976; Dean, 1974; George, 1958; Hughes, 1963; Mackauer and Way, 1976; Pollard 1971; Tamaki, 1973, 1974; Tamaki et al, 1967; Way et al, 1969; Wnuk, 1977; Wnuk and Fuchs, 1977). Their effectiveness in maintaining aphid populations below some economic threshold is often limited by their phenology: poor synchronisation between pest and predator populations often enables aphid populations to evade control (van Emden, 1966; Schneider, 1969). However, syrphids are believed to play a significant role in the control of orchard pests (Tamaki *et al*, 1967).

Attempts have been made to introduce certain *Cheilosia* species as biological control agents of the thistle (*Cirsium palustre*) which is currently a major pest in parts of Canada; *C. grossa* larvae attack the shoots and *C. cynocephala* Loew. and *C. aenea* Roser feed on the roots. However, the programme has been unsuccessful due to problems in the mass-rearing of the flies.

A few hoverflies can be regarded as pests. These include the large bulb fly (*Merodon equestris*) and the lesser bulb fly flies (*Eumerus tuberculatus* and *E. strigatus*) which attack bulbs. *M. equestris* is an important pest of hyacinths and narcissus in Europe and North America (Bânkowska, 1980). The two *Eumerus* species are pests of carrot, onion, turnip and potatoes (Bânkowska, 1980). *Cheilosia antiqua* Meig. has been reported to be a pest of *Primula* (Carpenter, 1913).

1.2 THE PRESENT STUDY

First-instar syrphid larvae have limited locomotory abilities and tend to have poorly developed sensory systems for locating aphid prey. The effectiveness of the larvae as aphid predators is therefore determined largely by the way in which the adult female distributes her eggs. This thesis is a study of oviposition in aphidophagous syrphids. The approach taken aims to bring together ecological and behavioural aspects of syrphid oviposition in both field and laboratory studies with a view to placing such studies in an ecological framework and creating a holistic concept of syrphid oviposition strategy.

The first part of the thesis considers factors influencing the general activity patterns of adult syrphids in the field. Chapter 2 describes the phenologies of different syrphid species occurring in annual crop and natural habitats. The spatial and temporal activity patterns of adult syrphids are examined in relation to factors such as the distribution of adult and larval food resources, shelter and the emergence patterns of the insect. Chapter 3 is a study of the effect of climate on syrphid flies.

The thesis then proceeds to focus specifically on oviposition activity. Chapter 4 examines the oviposition patterns of different syrphid species in brassica crops and investigates the relative importance of aphid-associated and aphid host-plant-associated factors in determining oviposition site selection. Chapter 5 is a laboratory study of aspects of the biology and behaviour of _Episyrphus balteatus_ Degeer. This is one of the most common aphidophagous syrphids occurring in Britain. A technique for rearing large numbers of this species in captivity is described.

A question of current interest in ecology and evolutionary biology is how foraging animals allocate their time in environments of patchily-distributed resources. Chapter 6 considers how a gravid _E. balteatus_ female foraging for oviposition sites distributes her time and eggs between plants infested with different densities of aphids. A simple model is proposed to explain the patterns of egg distribution observed in both field and laboratory studies.

The potential of aphidophagous syrphids as biological control agents of aphids has already been discussed. Chapter 7 describes a technique for manipulating oviposition behaviour in the field so as to increase the effectiveness of syrphids in limiting aphid populations. The final chapter attempts to draw together the findings of all the previous chapters in a holistic concept of syrphid oviposition strategy.

CHAPTER 2

SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF ADULT SYRPHIDS

2.1 INTRODUCTION

Previous work on syrphid ecology has shown that the spatial and temporal distribution patterns of adult flies are influenced by four main factors;

1) Phenology;
2) Distribution of larval food resources;
3) Distribution of adult food resources;
and 4) Shelter.

Phenology is conventionally expressed in terms of the number of generations per year. Syrphids exhibit a wide range of phenological strategies with uni- and bivoltine species normally overwintering as diapausing larvae and polyvoltine species usually hibernating as adults or migrating, or both (Schneider, 1948; Pollard, 1971; Goeldlin, 1974). Diapause may be obligatory (invoked endogenously, irrespective of environmental conditions) or, more frequently, facultative (induced by various environmental parameters eg photoperiod, temperature, humidity and food quality). In univoltine species, obligatory diapause always occurs in the last larval instar and may last several months, Larval diapause in bi- and oligovoltine species tends to be much shorter and may be obligatory or facultative (Schneider, 1969).

The distribution of larval food resources may be the most important factor determining the spatial distribution patterns of adult syrphids. In a comparative study of syrphid community structure in urban and wooded habitats, Gilbert (1981a) found that the proportion of species whose larvae live in rot-holes increased as the study area became more wooded. The proportion of species with a facultatively aphidophagous larval stage showed a similar increase. The number of species whose larvae feed on aquatic debris increased in sites with standing water.

Many aphid species overwinter on perennial trees and shrubs and then migrate to secondary annual hosts during early summer. Many aphidophagous syrphids exploit these seasonal changes in aphid distribution accordingly. Spring-occurring species are usually restricted to woodland habitats where they are most likely to encounter aphid populations on trees and shrubs. In contrast, species that occur in the summer are often found in more open habitats exploiting aphid populations in crops, grassland and herbs. Species that have several generations per year are often found in woodland habitats early on in the spring but occur in more open habitats later in the summer.

Chandler (1968d) showed that the gravid females of some aphidophagous species prefer to oviposit at a particular height above the ground and have well-defined searching zones. These height preferences conform well with their habitat preferences. Univoltine spring species (eg *Epistrophe eligans* Harris and *Syrphus lasiophthalmus* which occur when aphid infestations are present on shrubs and trees but are uncommon on herbaceous plants laid significantly more eggs at 120 and 180 cm than at 30 cm above the ground. In contrast, *Sphaerophoria scripta* (L.), a summer species, laid more eggs at 30 cm than at 120 or 180 cm above ground. According to Dušek and Láska (1966), *Sphaerophoria* spp prefer to oviposit amongst aphid colonies present on ground flora. The syrphid species that are common throughout the year (eg *Episyrphus balteatus* Degeer, *Syrphus ribesii* (L.) and *Metasyrphus luniger* Meigen do not seem to have a preferred height for oviposition. Such flexible behaviour is no doubt advantageous for locating aphids on a range of different host-plants at varying heights.

Several studies have noted the importance of adult feeding in the Syrphidae (Schneider, 1948; Doucette and Eide, 1955; Adashkevich and Karelin, 1972). Adult flies have been reported feeding on nectar, pollen and aphid honeydew. Pollen appears to be essential for ovarial maturation.

During most of the year, the only flowers available in arable areas are in the field edges, particularly hedgerows. Van Emden (1965) recorded increased syrphid oviposition on sprout plants close to a flowery field edge. In contrast, Chandler (1968c) found that flowers had no effect on oviposition and he suggested that Van Emden's results may have been due to a shelter effect. Pollard (1971) captured more adult syrphids in a flowery hedgerow than in arable crops but could find no evidence of increased oviposition close to flowers.

Gilbert (1981b) showed that the patterns of feeding on pollen and nectar can differ widely between species. Some syrphids feed almost exclusively on pollen (eg *Melanostoma*, *Episyrphus* and *Syrphus* species). Others feed mainly on nectar (eg *Syritta* and *Eristalis* species) and a third group appear to feed on a more or less equal mixture of nectar and pollen (eg *Metasyrphus* and *Platycheirus* species). These patterns are determined largely by body size and the length and shape of the proboscis: increasing proboscis length results in a decrease in the proportion of pollen in the diet. Flies with larger probosces tend to visit flowers with longer corollae which contain more nectar sugar.

There is some evidence that some hoverflies are selective in the flowers they visit (eg Pollard, 1971; Gilbert, 1981a; Haslett, 1981). Gilbert (1981a) has made an exhaustive survey of the literature for records of flowers visited by syrphids and has classified species into three groups: specialists, moderate specialists and generalists. The more common species (eg *E. balteatus*, *S. ribesii*, *Eristalis* species) appear to be relatively general in their feeding and probably take pollen and/or nectar in the proportion that each food occurs in the habitat. Finch and Coaker (1969) examined the effect of different flowers on the fecundity and longevity of the cabbage root fly

(Delia radicum L.) and found that the nutritive value of different flowers varied considerably. It is possible that flower selectivity in hoverflies is related to differences in the nutritional value of different flowers although evidence to support this is scarce. Thus, a possible explanation for the contradictory findings of Pollard (1971), Chandler (1968c) and Van Emden (1965) in relation to the effect of flowers on syrphid oviposition may well involve the actual flower species present. Most aphidophagous syrphids feed mainly on pollen and therefore the availability of a suitable pollen source may be a critical factor in the attraction of gravid and immature females.

The final factor that may influence the spatial distribution patterns of adult syrphids is shelter. Van Emden's (1965) observations of increased syrphid oviposition on sprout plants close to a flowery hedgerow have already been discussed and it seems likely that these results are due to a shelter effect (Chandler, 1968c). Lewis (1965) found concentrations of syrphids close to artificial barriers. Pollard (1971) concluded that shelter has a greater effect on oviposition by woodland species than those associated with more open habitats.

The following chapter is a study of the adult syrphid communities associated with agricultural and natural habitats. The structure of the syrphid community in each habitat is described, together with the phenologies of the constituent species. The spatial and temporal distribution patterns of adult syrphids are discussed in relation to the distribution of adult and larval food resources.

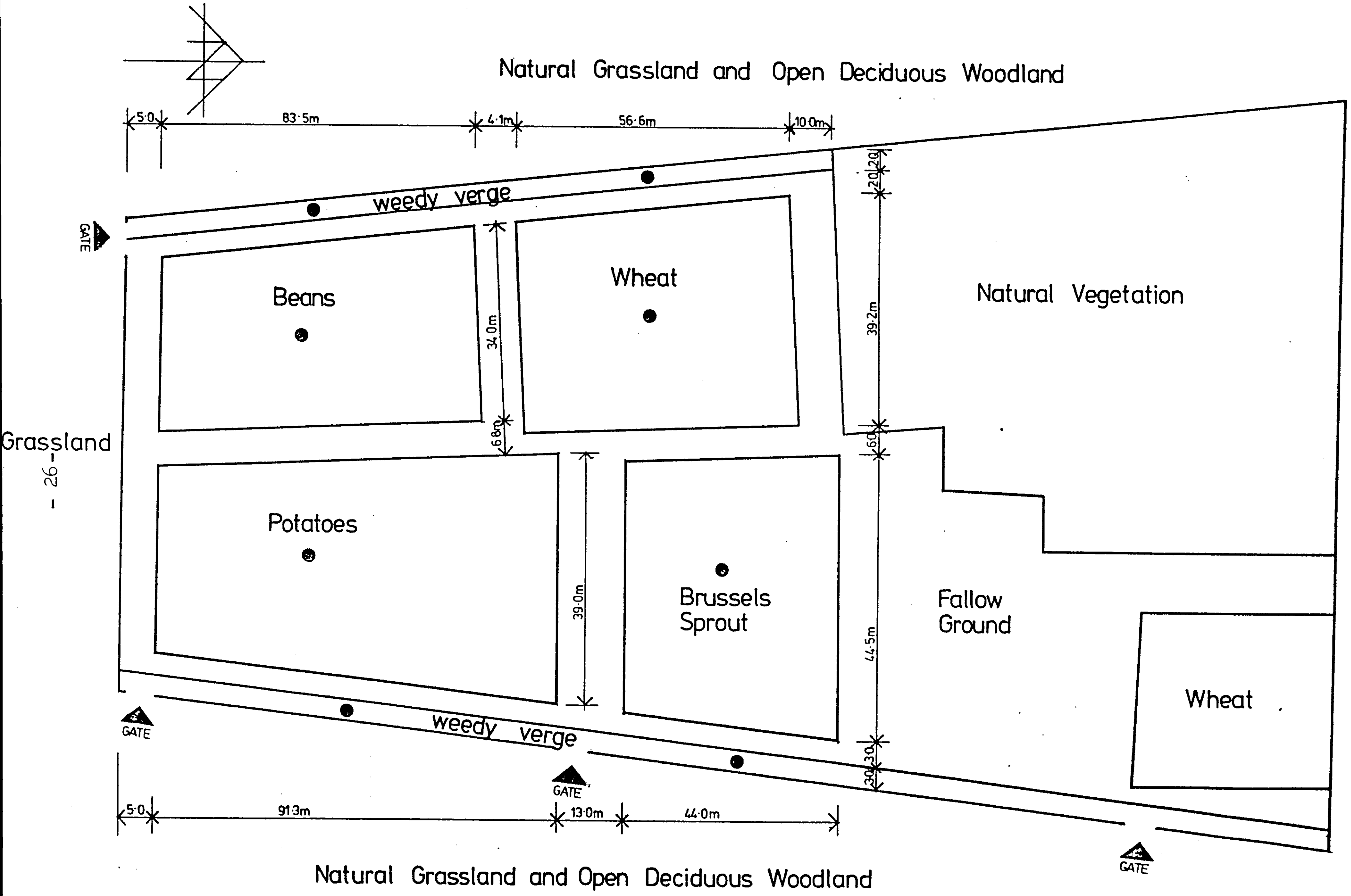
2.2 Description of the study site

The work was carried out at the Imperial College Field Station, Silwood Park, Ascot, Berkshire (OS Map Reference SU 946686)

The study site consisted of four annual crops bordered by a variety of edge growth. The four crops were winter wheat (cv Mardler), field beans (cv Ticmner), potatoes (cv Pentland Crown) and Brussels sprouts

Figure 2.1: Sketch map of the study site (not to scale)

● Malaise trap positions


Natural Grassland and Open Deciduous Woodland
5·0
83·5m
4·1m
56·6m
10·0m
weedy verge
GATE
Beans
Wheat
34·0m
39·2m
2·0
2·0
Natural Vegetation
Grassland
6·8m
6·0
Potatoes
39·0m
Brussels Sprout
Fallow Ground
44·5m
Wheat
GATE
weedy verge
GATE
3·0
3·0
5·0
91·3m
13·0m
44·0m
GATE
Natural Grassland and Open Deciduous Woodland

(cv Winter Harvest). A sketch map of the study site giving the dimensions of individual crops is given in Figure 2.1.

To the south, the crops were bordered by an area of grassland that was regularly mown; the dominant grass species present was Holcus lanatus L.. To the north-east, lay an area of fallow land that was regularly harrowed. On the remaining sides, the crops were bordered by rough grassland (mainly Holcus spp) and open deciduous woodland.

2.3 MATERIALS AND METHODS

The wheat crop was sown during October 1979 and the remaining crops in May 1980. The wheat, beans and potatoes were all sown as seed; the Brussels sprouts were initially grown in cold frames and transplanted to the field as 12-week old seedlings. Records were kept of the times of flowering, fruiting, (ie pod/ear formation), and harvesting of individual crops (Table 2.1).

Table 2.1: Field calendar

Crop details	Wheat	Beans	Potato	Brussels sprout
Variety	Mardler	Ticminer	Pentland Crown	Winter Harvest
Crop sown	20.10.79	22. 4.80	29. 4.80	1. 5.80 (as seedlings)
Crop flowered	Early June	Mid June	Late June	-
Crop fruited (ie pod/ear formation)	Mid June onwards	Mid June onwards	-	-
Crop harvested	8. 9.80	28. 7.80	6.10.80	19. 1.81
Malaise trap operated in crop	14. 5.80- 5. 9.80	14. 5.80- 25. 7.80	2. 6.80- 3.10.80	2. 6.80- 17.10.80

Weekly records were kept of the level of aphid infestation within each crop.

Monthly records were made of the floral resources in the natural habitats immediately adjacent to the crops.

Monitoring of adult syrphid populations at the centre and at the edge of each crop was commenced as soon as individual crops had emerged and the seedlings had become established.

2.3.1 Sampling of aphid populations in crops

Aphid populations within individual crops were monitored from the time of crop emergence to the time of harvest. Fifty randomly-selected plants in each crop were examined at weekly intervals and the number of aphids per plant recorded. The same plants were examined on each occasion. The dominant aphid species associated with each crop were identified using Blackman's (1974) key.

2.3.2 Sampling of edgegrowth floral resources

Monthly records were kept of the main floral resources in the edgegrowth immediately adjacent to the four crops. Plant species were identified principally using the keys of Fitter et al (1980); Clapham et al (1962), and Hubbard (1978). A crude estimate of the relative abundance of the main flowering species was made by eye.

2.3.3 Sampling of adult syrphid populations

Malaise traps (Southwood, 1978) were used to sample adult syrphid populations within the four crops and in the edgegrowth immediately adjacent to the crops. The type of trap used was a modified brown netting form of the Townes Malaise trap (British Natural History Museum model) and is illustrated in Figure 2.2. Insects entering the trap were collected in a bottle containing 70% alcohol attached at the apex. The Malaise trap has been shown to be particularly effective tool for sampling flying insects such as syrphids (Owen, 1981). It can operate continuously both night and day and in all weather conditions. In addition, it is thought to be a passive, non-attractant technique that captures only those insects that have independently entered its air space. It is thus unlikely to exert any serious depletory effect on the insect population it samples. One disadvantage of the technique is that it does not produce an unbiassed estimate of the abundance of individual species. Due to its mode of operation, not all species have an equal chance of entering the trap: those that normally fly low down in the vegetation (eg *Platycheirus* and *Melanostoma* spp) are more easily captured than those species that tend to fly some distance above the ground (eg *Eristalis* spp). Considerable care must therefore be taken when comparing the relative abundances of individual species. In this study it has been assumed that the sampling 'bias' for any one syrphid species remains constant and that 'long-term' changes in the numbers of an individual species reflect actual changes in species phenology and population size.

A grid of eight traps was set up with one trap sited at the centre of each crop and another placed in the edgegrowth immediately adjacent to the crop. The precise position of each trap is shown in Figure 2.1. Care was taken to ensure that the traps were positioned across a likely line of flight. The traps were erected as soon as each crop had emerged and become established and were thereafter operated continuously for five days each week from 14 May onwards. Traps at the crop centres were operated until the crop was harvested; dates of operation of each trap are given in Table 2.1. The traps were sampled four times daily (at 1000, 1400, 1800 and 2100 hours BST) from 14 May to 4 July, and once daily (at 1000 hours) for the remainder of the study period.

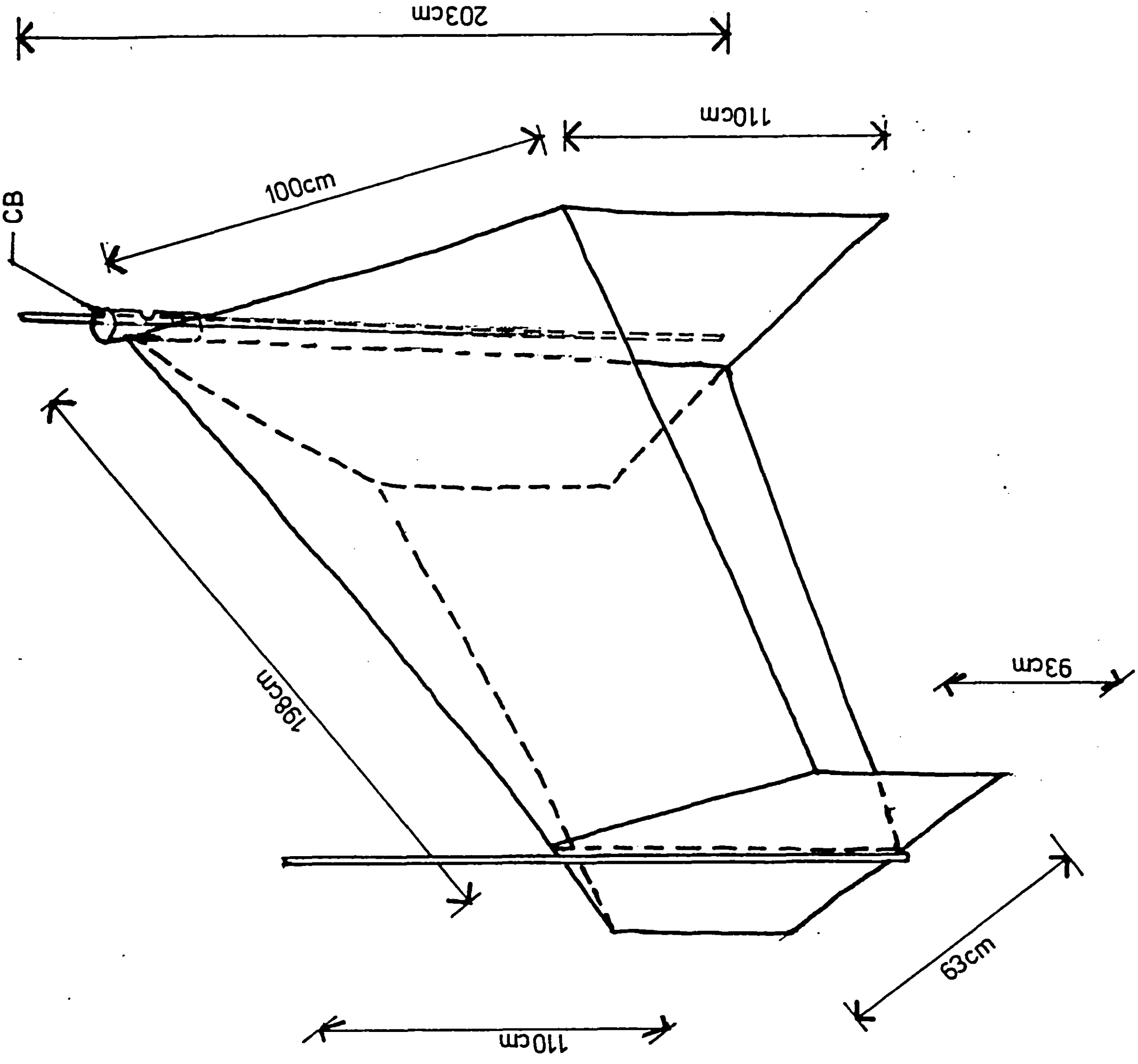
Flies were identified principally using the keys of Stubbs and Falk (1983) and Coe (1953). Reference was also made to the works of Speight (1978), Speight *et al* (1975), Vockeroth (1969) and Verrall (1901). Nomenclature throughout follows Kloet and Hincks (1969). It is believed that the majority of specimens were identified accurately. The only dubious individuals belonged to the genus *Sphaerophoria*; females of this genus cannot be reliably identified using existing keys. Only three *menthastri* males were recorded, the remainder were *scripta*; it was therefore assumed that all females captured were *scripta*.

Females were classified as gravid or immature depending on the presence or absence of mature eggs in the ovaries.

Figure 2.2: Diagram of the Townes Malaise Trap

Key

CB - Collecting bottle


203cm
110cm
100cm
CB
198cm
93cm
63cm
110cm

2.4 RESULTS AND DISCUSSION

2.4.1 Plant species present in the edgegrowth

A full list of all plant species recorded in the four edgegrowth sites is given in Table A1 (Appendix A). The life-form (ie annual, biennial, perennial or shrub) and the flowering period of each species is shown.

The floristic composition of the four edgegrowth sites was essentially similar, consisting mainly of grasses and herbaceous plants. The most abundant species present were Rumex acetosa L., Taraxacum officinale Weber, Cirsium vulgare (Savi) Ten., Ranunculus repens L., Trifolium repens L., Anthriscus sylvestris (L.) Bernh., Senecio jacobaea L., and Holcus lanatus L.. Two of the sites contained additional vegetational features which proved particularly attractive to adult syrphids. Several broom bushes (Cytisus scoparius (L.) Link) were present in the edgegrowth adjoining the bean crop and these flowered during May and June. Heracleum sphondylium L. was particularly abundant in the edgegrowth adjoining the Brussels sprouts; this species flowered mainly during August and early September.

The floral resources of the edgegrowth were most diverse in the spring and early summer with flowering grasses abundant at this time. Later on in the season, few flowers were available as food resources for adult syrphids.

2.4.2 Syrphid communities in crop and edgegrowth sites

Fifty-nine syrphid species were recorded from the Malaise traps during the study period; a full classification of the genera encountered is presented in Table A2 (Appendix A). The range of larval feeding habits for these species is shown in Table A3 (Appendix A). Four main trophic groups may be distinguished: predators (mainly aphidophages; 43 species), phytophages (5 species), terrestrial saprophages (6 species) and aquatic saprophages (5 species). The overwhelming abundance of a species with a predatory larval stage is striking.

A list of the syrphid species associated with each trap site, together with the number of individuals recorded, is shown in Table A4 (Appendix A). Forty one species occurred in both crop and edgegrowth sites. A further eight species were taken only in the crops, and another ten only in the edgegrowth; these last eighteen species were all comparatively rare with less than ten individuals per species recorded overall. Of the syrphids captured in the crops, 49% were taken in the wheat, 26% in the Brussels sprouts, 21% in the potatoes and 4% in the beans. In the edgegrowth, 35% of all individuals were captured at the edge of the Brussels sprout crop, 33% at the edge of the beans, 15% at the edge of the potato and 13% at the edge of the wheat.

The structure of the syrphid communities associated with the different sites was compared both qualitatively and quantitatively. The species diversity of syrphid communities in different crop and edgegrowth sites was compared using Sorenson's Coefficient of Similarity:-

$$C_s = \frac{2C}{A + B}$$

where A = total number of species in community A
B = total number of species in community B
C = number of species common to both communities

For further information on Sorenson's Coefficient of Similarity, see Mueller-Dumbois and Ellenberg (1974).

Dominance was calculated using the Berger-Parker Dominance Index:-

$$D = \frac{n_i}{N}$$

where n_i = number of individuals in the i^{th} species
N = total number of individuals in the sample

Apart from giving a quantitative measure of importance for the most dominant species, this index can also be used to quantitatively assess the importance of any other species of interest.

Equitability refers to the apportionment of individuals to species within a community, and thus can be considered as a measure of the evenness of a community. The equitability of different communities may be compared using the following index:

$$E = \frac{\sum(P_{iA}^2 - P_{iB}^2)}{n}$$

where P_{iA} = the proportion of individuals of the i^{th} species in community A

P_{iB} = the proportion of individuals of the i^{th} species in community B

n = the total number of species in both communities

As the value of E decreases, so the equitability of the two communities becomes increasingly similar.

These analyses pertain to the syrphid community associated with each site over the entire study period. The syrphid community in the beans cannot be directly compared with the communities associated with the other sites as the beans were harvested in the middle of July. The Malaise trap at this site was necessarily dismantled at the time of harvest and no further records of syrphid activity were made at this location. In the following analyses, the results for the four edgegrowth sites have been combined.

Table 2.2 presents Sorenson's Coefficients of Similarity for species diversity in different sites. The species diversity of the syrphid communities inhabiting the four crops was similar with values of C_s ranging from 0.59 to 0.71. The highest similarity occurred between the wheat and the Brussels sprout crops and the lowest similarity between the wheat and the beans. The diversity of the syrphid community in the edgegrowth showed a high similarity to the syrphid

Table 2.2: Sorenson's Coefficients of Similarity of species diversity

	Edge	Wheat	Brassica	Potato	Bean
Edge		☒	☒	☒	☰
Wheat	0.70		⊞	☒	☒
Brassica	0.67	0.71		☒	☒
Potato	0.70	0.63	0.68		☒
Bean	0.49	0.59	0.61	0.63	

$$C_s = \frac{2j}{a + b}$$

j = number of species common to both samples
a + b = number of species in samples a and b

☰ 0.40-0.55 ☒ 0.56-0.70 ⊞ 0.71-0.85

communities in the wheat, potatoes and Brussels sprouts (C_s = 0.67-0.70), but a much lower similarity to that in the beans.

Dominance indices for different crop and edgegrowth sites are presented in Table 2.3. The highest level of dominance occurred in the wheat crop and the lowest in the beans.

Table 2.3: Dominance indices for crop and edgegrowth sites

Site	Dominance Index D
Wheat	0.45
Potato	0.25
Brussels sprout	0.25
Beans	0.16
Edgegrowth	0.19

Table 2.4: Coefficients of similarity of equitability

	Wheat	Brassica	Edge	Potato	Bean
Wheat		▤	▤	☒	▥
Brassica	1.94×10^{-3}		▤	▤	☒
Edge	2.38×10^{-3}	0.85×10^{-3}		▤	▤
Potato	3.18×10^{-3}	1.24×10^{-3}	1.09×10^{-3}		☒
Bean	7.22×10^{-3}	3.88×10^{-3}	1.09×10^{-3}	3.77×10^{-3}	

▤ $0-3 \times 10^{-3}$

☒ $3.1 \times 10^{-3} - 6 \times 10^{-3}$

▥ $6.1 \times 10^{-3} - 9 \times 10^{-3}$

Table 2.4 presents the results comparing the equitability of distribution of particular species in different communities. The highest similarity in equitability was between the syrphid communities in the Brussels sprouts and edgegrowth (E = 0.001) and the lowest between the wheat and the beans (E = 0.007).

The dominance structure of the syrphid communities in the four crops and in the edgegrowth is illustrated in Figure 2.3. The figure shows the percentage of the community occupied by each of the constituent species. The syrphid community in the wheat consisted of 32 species, 24 of which were aphidophagous. The dominant species was Sphaerophoria scripta L.; this species accounted for 45% of all individuals collected in the wheat. In the potatoes, 32 species were recorded, including 26 aphidophagous. The dominant species Platycheirus albimanus Fabr. and the two subdominant Melanostoma mellinum (L.) and Sph. scripta accounted for 57% of the community. The syrphid community in the Brussels sprouts consisted of 31 species and 24 of these were aphidophagous. The dominant species (Sph. scripta) and subdominants (M. mellinum, P. albimanus and P. peltatus Meig.)

accounted for 66% of the community. Only 19 species were recorded in the beans, these included 16 aphidophagous. The dominant species was Platycheirus angustatus Zett. and the subdominants were M. mellinum, Meligramma cincta and Dasysyrphus venustus Meig.; these accounted for 44% of the community. In the edgegrowth, the syrphid community consisted of 51 species including 35 aphidophagous. The dominant species were Melanostoma mellinum, Sph. scripta and P. angustatus with M. scalare Fabr., P. peltatus and P. albimanus as subdominants.

The results presented so far show that the composition of the syrphid communities associated with the four crops and with the adjacent natural habitat was very similar and this suggested that one main syrphid community operated within the study area. This community was dominated by species with an aphidophagous larval stage. The same few species were dominant in all sites. Thus, Sph. scripta dominated in the wheat and Brussels sprouts and was a subdominant in the potatoes and edgegrowth. P. albimanus was dominant in the potatoes and subdominant in the Brussels sprouts and edgegrowth. M. mellinum was dominant in all four crops, and P. angustatus dominated in the beans and the edgegrowth. These four species are widely recorded as being common in a range of agricultural crops (eg Malinowska, 1979).

Most species were ubiquitous in their distribution but some species were considerably more active in certain sites than in others and this may indicate specific 'preferences' for particular crop or edgegrowth habitats. Such preferences will be discussed more fully in Sections 2.4.5, 2.4.6 and 2.5.

The comparatively low numbers of both species and individuals recorded in the bean crop together with the different dominance structure of the syrphid community here may be explained at least in part, by the comparatively early harvest date of this crop. The following section examines in more detail the changes in community structure that occurred during the study period and it will be seen that up until the date of harvest, the community structure in the bean crop closely resembled that of the other crops.

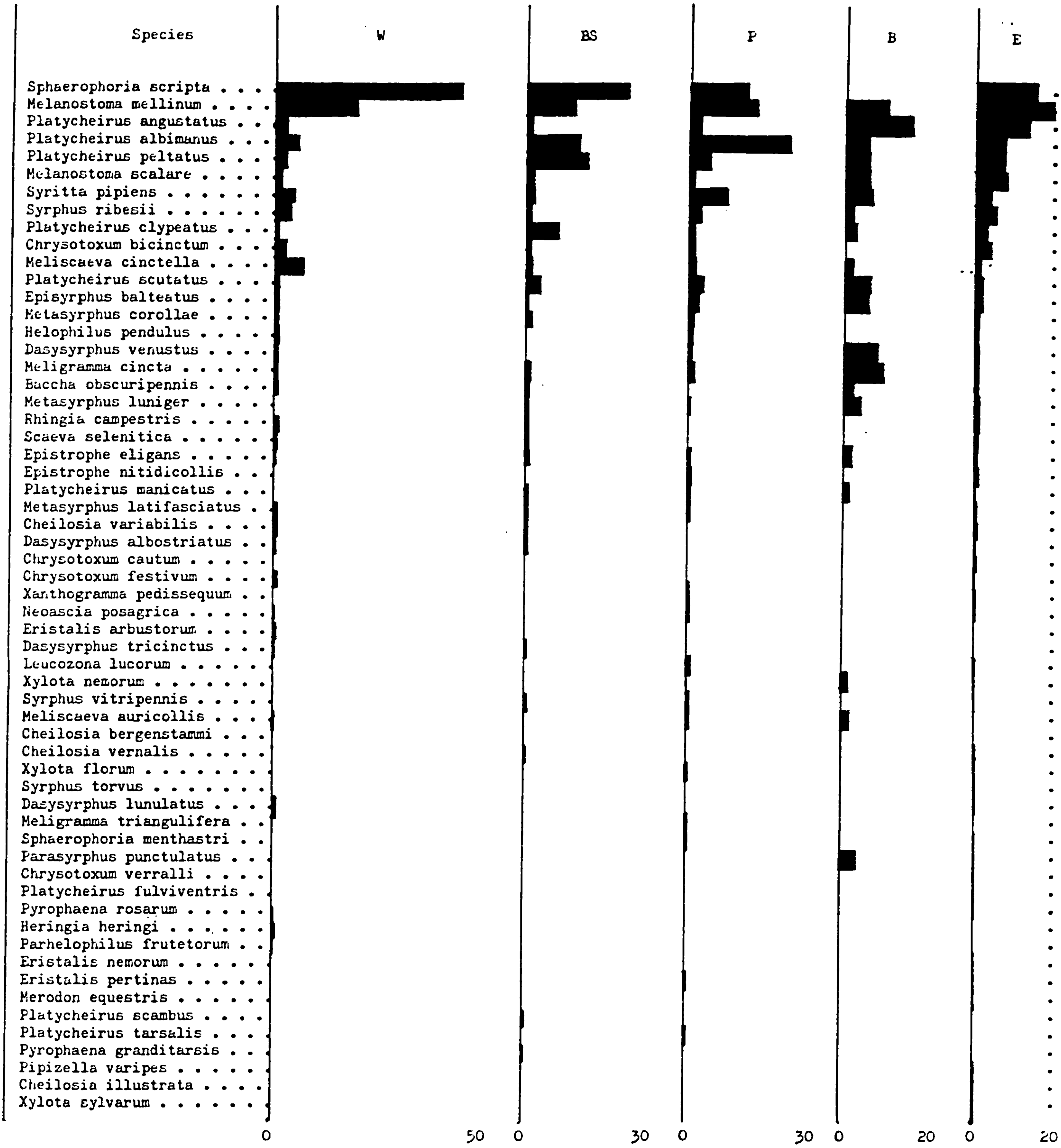
Figure 2.3: Dominance structure of syprhid communities in crop and edgegrowth sites

The figure shows the percentage of the community occupied by each syrphid species in different sites

Key

W - Wheat
BS - Brussels sprout
P - Potato
B - Beans
E - Edgegrowth

Figure 2.3: Percentage of community occupied by each species in different crops



Key W = Wheat BS = Brussels sprout P = Potato B = Beans E = Edgegrowth

Changes in syrphid community structure during the study period

The species composition of the syrphid community associated with the study site changed continuously during the five-month study period, as did the abundance of individual syrphid species. Table A5 (Appendix A) summaries the 'local' changes in community structure that occurred within each crop and in the edgegrowth. To facilitate analysis the study period has been divided up into five four-week periods and one three-week period. For each period, the number of species and the number of individuals recorded, together with the dominance index and the dominant species are given.

The table shows that the overall abundance of syrphid adults in each site fluctuated considerably during the study period, as did the number of species recorded. These fluctuations were due mainly to changes in the phenology of individual syrphid species together with changes in the relative attractiveness of the different sites as syrphid adult feeding and oviposition sites. These factors are discussed more fully in Sections 2.3.6 and 2.3.7. In general, more syrphids were captured in the edgegrowth than in the crops during both May ($\chi^2 = 17.02$, 1 df, $P < 0.001$) and June ($\chi^2 = 38.08$, 1 df, $P < 0.0001$). In July, similar numbers were recorded in both types of habitat ($\chi^2 = 1.32$, 1 df, ns) but in August, more were taken in the crops ($\chi^2 = 31.94$, 1 df, $P < 0.001$). During September and October, similar numbers were recorded in both crop and edgegrowth sites ($\chi^2 = 0.02$, 1 df, ns - Sept; $\chi^2 = 0.10$, 1 df, ns - Oct). A comparison of syrphid distribution in different crops indicated that in May similar numbers were recorded in all four crops ($\chi^2 = 3.31$, 3 df, ns). In June, however, more were captured in the Brussels sprout and potato crops ($\chi^2 = 14.62$, 3 df, $P < 0.01$). In July and August, more syrphids were taken in the wheat than in any other crop ($\chi^2 = 124.65$, 3 df, $P < 0.001$ - July; $\chi^2 = 183.57$, 3 df, $P < 0.001$ - May) and, in September, more were recorded in the wheat and potato than in the Brussels sprouts ($\chi^2 = 18.46$, 3 df, $P < 0.001$). During October, similar numbers were recorded in both the potatoes and Brussels sprouts ($\chi^2 = 1.8$, 3 df, ns).

In the wheat, the equitability of the syrphid community was highest during June and lowest in July. During May and June, the community was dominated by *Platycheirus angustatus*, but in later months the dominant species was *Sphaerophoria scripta*. In the potatoes, equitability in the community was highest in July and lowest in October. The dominant species changed continuously: *P. angustatus* in May, *P. scutatus* in June, *Melanostoma mellinum*, *P. angustatus* and *P. albimanus* in July, *M. mellinum* again in August, and *P. albimanus* in September and October.

In the Brussels sprouts, equitability was also highest in July and lowest in October. During May and June, the dominant species in the syrphid community was *P. angustatus* and this gave way to *P. clypeatus* in July. *Sph. scripta* dominated during August and *P. albimanus* during September and October. In the syrphid community associated with the beans, equitability was highest during June and lowest in July. The dominant syrphid species were *P. angustatus* in May, *P. peltatus* in June and *Metasyrphus luniger* in July. In the edge-growth, the equitability of the syrphid community was highest in September and lowest in May. *P. angustatus* dominated the community during May and June, *M. mellinum* in July and August, *M. scalare* in September and *P. albimanus* in October.

2.4.3 Syrphid species phenology

The Malaise trap catches provided information on the activity patterns of adult syrphids during the 23-week study period: a basic assumption was that the numbers caught in the traps at a particular time reflected the level of activity of individual species at that time. The results presented here for individual syrphid species represent the total number of adult flies caught in the traps on five successive days each week. Estimates of abundance are relative and not absolute. It was pointed out earlier that some syrphid species may be captured more easily in the traps than others and thus the relative abundances of different species cannot be reliably compared. It was assumed, however, that the sampling 'bias' for a particular species remained constant throughout the study period and that fluctuations in weekly abundance reflect real changes in species phenology. Care should be taken in the interpretation of this phenological data: insect activity is influenced by prevailing weather conditions and low catches in the Malaise traps during periods of bad weather may thus give a misleading impression of a decline in numbers (see Chapter 3).

Figure 2.4 shows the number of syrphid adults caught during each week of the study period, The data are expressed in terms of the mean number of flies caught per trap since differences in the sowing and harvesting dates of individual crops dictated that not all eight traps could be in continuous operation throughout the study period. Two main peaks of syrphid activity occurred: the first in late May, the second during late July and August. The second peak was considerably larger than the first. The figure also shows the number of species recorded each week. Only species for which 5 or more individuals were captured each week are included in this graph. The number of species recorded follows a similar pattern to the number of individuals taken.

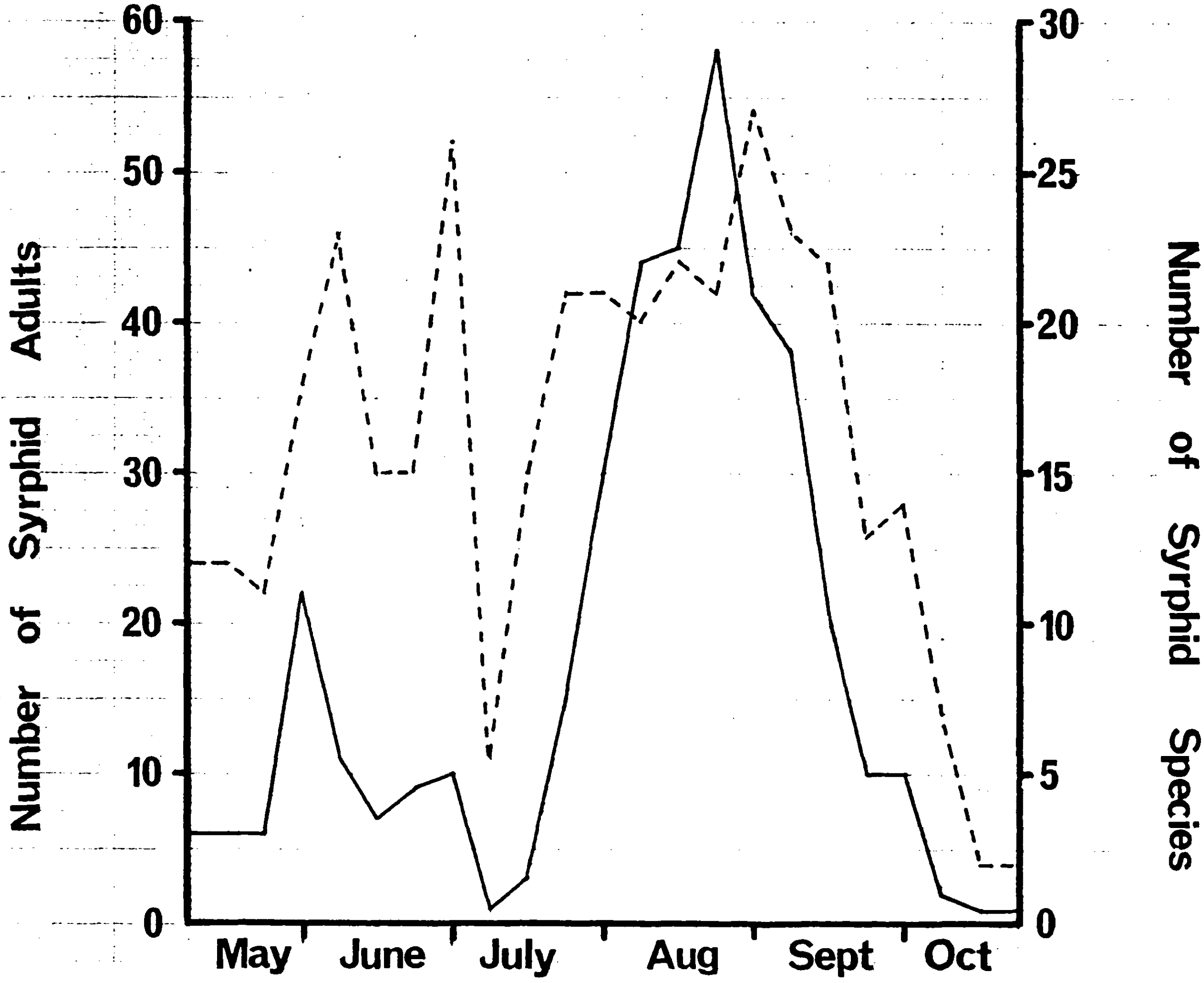
Table A6 (Appendix A) shows the number of individuals of each species caught during each week of the study period. The data suggests that discrete periods of activity occur in many species; these are conventionally interpreted as representing discrete generations in the life-cycle. Figure 2.5 a-n illustrate the activity patterns of some of the more abundant aphidophagous species recorded in this study and show the relative abundances of males and immature and gravid females. These results are compared with those obtained in previous studies on syrphid phenology in Table A7 (Appendix A). Dasysyrphus venustus and Chrysotoxum bicinctum L. both appear to be univoltine species with one main period of activity in early June and early August, respectively. These results for D. venustus are confirmed by Speight et al (1975) and Gilbert (1981a). Platycheirus albimanus, P. clypeatus, P. angustatus, Melanostoma mellinum, M. scalare and Meliscaeva cinctella Zett. all appeared to be bivoltine with two main periods of activity occurring during the study period. In each case, the two 'generations' were of dissimilar size and, with the exception of P. angustatus, the second was larger than the first. These patterns for P. peltatus, P. albimanus, P. clypeatus and M. mellinum have also been observed in Norway (Nielsen, 1971), West Germany (Claussen, 1980) and Britain (Pollard, 1971). The same patterns were recorded by

Figure 2.4: The number of adult syrphids caught per trap and the number of syrphid species recorded during each week of the study period

Key

•———• Number of adult syrphids caught per trap

•- - - -• Number of syrphid species


Number of Syrphid Adults
60
50
40
30
20
10
0
Number of Syrphid Species
30
25
20
15
10
5
0
May
June
July
Aug
Sept
Oct

Gilbert (1981a) in his study in Cambridge for all species except P. clypeatus; he reported only one generation for this species. In France, P. albimanus , P. clypeatus and M. mellinum are believed to have at least two generations (Goeldlin, 1974) and in East Germany, M. scalare is thought to be polyvoltine (Grosser and Klapperstück, 1977). The only other records relating to the phenology of Meliscaeva cinctella suggest that this species has four or five generations in West Germany (Schneider, 1948) but only one in Britain (Gilbert, 1981a). Sphaerophoria scripta also appeared to have two main periods of activity during the season. However, the second was considerably longer than the first. Large numbers of immature females were recorded in early June, late July and late August. This suggested that the species may in fact be trivoltine, with the second and third generations overlapping. These patterns are confirmed in other studies carried out in Britain (Bhatia, 1939; Rotheray, unpubl; Gilbert, 1981a) and in other parts of Europe (Bánkowska, 1964; Goeldlin, 1974; Grosser and Klapperstück, 1977).

Some species were continuously active throughout the entire study period: Metasyrphus corollae Fabr., Syrphus ribesii (L.), Platycheirus scutatus Meig. and Episyrphus balteatus all showed at least one main period of activity but it was difficult to interpret the observed activity patterns in terms of discrete generations. Reference to the literature indicates a wide range of reported phenologies for these four species. S. ribesii and P. scutatus are both recorded as having two or more generations in Britain (Bhatia, 1939; Pollard, 1971; Rotheray, unpubl) and in Western Europe (Goeldlin, 1974). The results from the present study suggest that at least two generations occur. Studies on E. balteatus suggest that this species is polyvoltine in the southern part of its European range but univoltine in the north. In central France, Gaumont (1929) calculated, on the basis of a 30-day life-cycle that seven generations a year were possible; Schneider (1948), working in Switzerland thought that four or five were more probable. In contrast, only one generation was recorded in the Halle region of East Germany (Grosser and Klapperstück, 1977), in Norway (Nielsen, 1971) and in Britain (Pollard, 1971; Rotheray, unpubl; Gilbert, 1981a). There is a considerable body of evidence which suggests that E. balteatus and several other syrphid species are capable of making large-scale migrations. Large 'swarms' of hoverflies have been recorded moving south in autumn through mountain passes in France and Switzerland (Lack and Lack, 1951; Snow and Ross, 1952; Gray *et al*, 1953; Burton and Owen, 1954; Williams *et al*, 1956; Aubert, 1962; 1964). The migrating species included *E. balteatus*, *Metasyrphus corollae*, *M. latifasciatus*, *Syrphus vitripennis* Meig., *Scaeva pyrastri* L., *Sc. selenitica*, *Melanostoma mellinum*, *Sphaerophoria scripta* and *Didea fasciata*. In the Himalayas, *E. balteatus* was observed moving north in March (Westmacott and Williams, 1954). The available evidence suggests that *E. balteatus* migrates northwards to Britain in the spring, breeds once and then makes a return flight south in the autumn, overwintering in the adult stage. The results of the present study appear to support this hypothesis. Gravid females were recorded during June, July and early August but females caught later in the season usually had undeveloped ovaries. The gravid individuals probably emerged from overwintering sites in Britain or migrated from the continent. These females give rise to a summer generation. Towards, the end of August adults of the next generation emerge. These mate, but the females do not mature their ovaries. Instead, they either migrate or seek overwintering sites. Some individuals may emerge in the spring and give rise to a small generation. A similar life-cycle would appear to be also true of *Metasyrphus corollae*. This species is reported to be polyvoltine in France (Goeldlin, 1974) but uni- or sometimes bi-voltine in East Germany (Grosser and Klapperstück, 1977) and Britain (Pollard, 1971; Rotheray, unpubl; Gilbert, 1981a). In the present study, gravid females were observed mainly during June and early July. Most of the females captured later in the season had immature ovaries. These results would seem to support the idea that *M. corollae* is principally a summer-occurring univoltine species in Britain with second generation adults remaining sexually immature and either overwintering in Britain to emerge in the spring or migrating to the continent.

It has been suggested that *E. balteatus*, at least, shows a phenological adaptation to latitudinal variation in climate. This phenomenon may also occur in other syrphid species with wide-ranging distributions, in which case the considerable variation in their reported phenologies may be explained.

Figure 2.5: Phenologies of some syrphid species

a) Dasysyrphus venustus
b) Chrysotoxum bicinctum
c) Melanostoma scalare
d) Platycheirus clypeatus
e) Platycheirus peltatus
f) Platycheirus albimanus

Key

░ - Immature females

☐ - Gravid females

▨ - Males

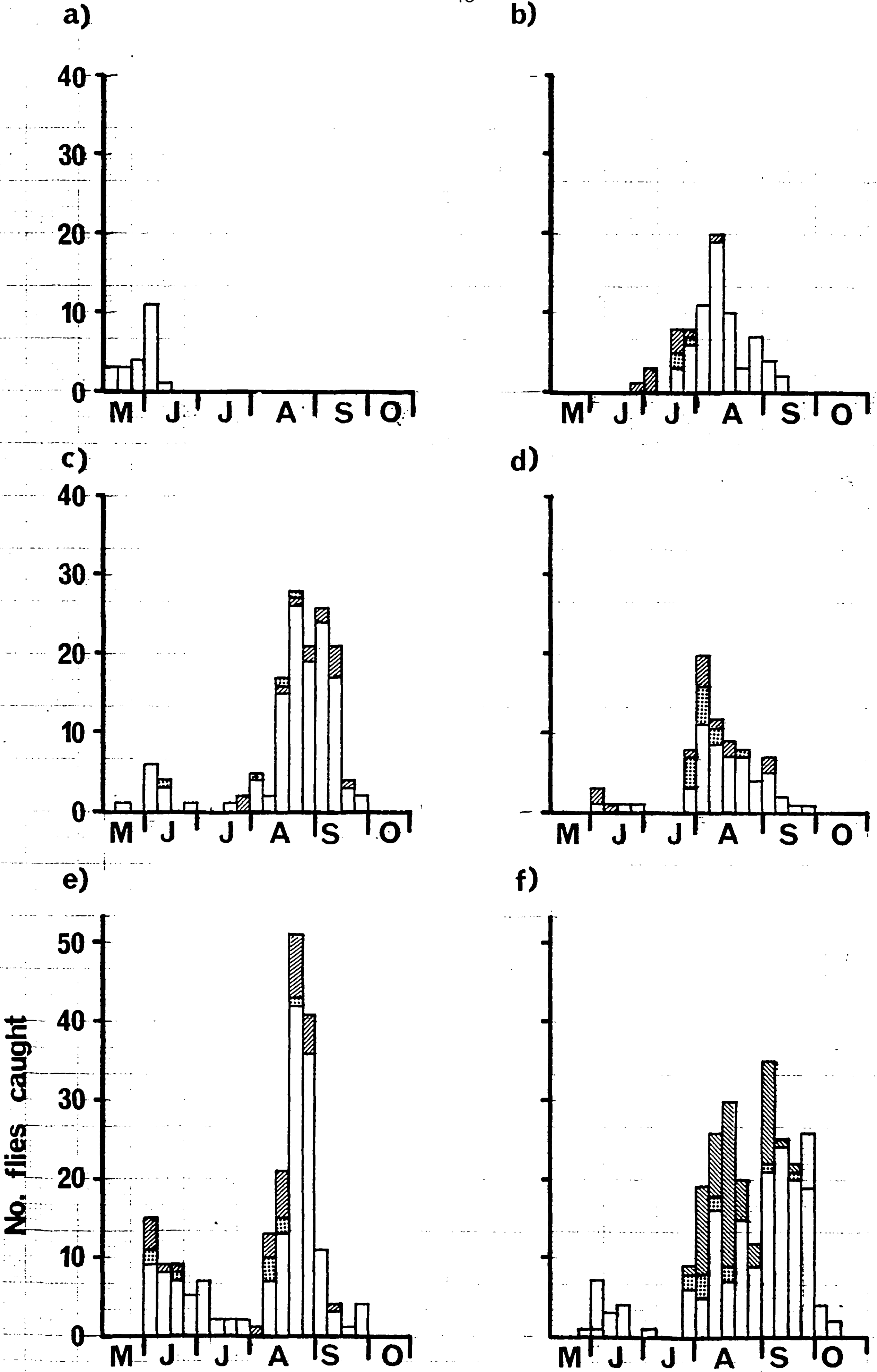

a)
b)
c)
d)
e)
f)
40
30
20
10
0
50
No. flies caught
M
J
J
A
S
O

Figure 2.5: continued

g) Melanostoma mellinum
h) Sphaerophoria scripta
i) Meliscaeva cinctella
j) Syrphus ribesii
k) Metasyrphus corollae
l) Episyrphus balteatus

Key

░ - Immature females

□ - Gravid females

▨ - Males

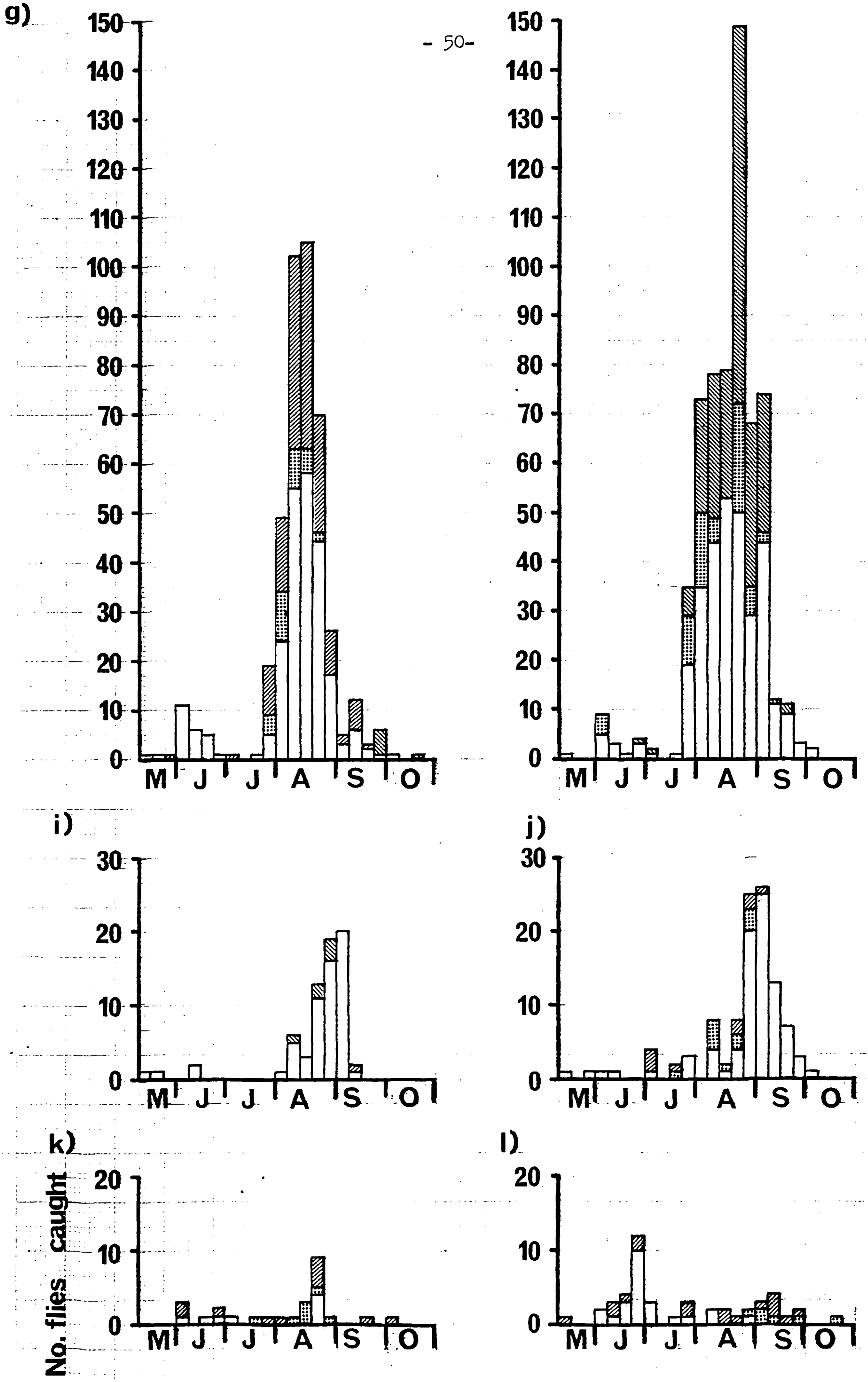

g)
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
M
J
J
A
S
O
i)
30
20
10
0
j)
k)
l)
No. flies caught

Figure 2.5: continued

m) Platycheirus angustatus

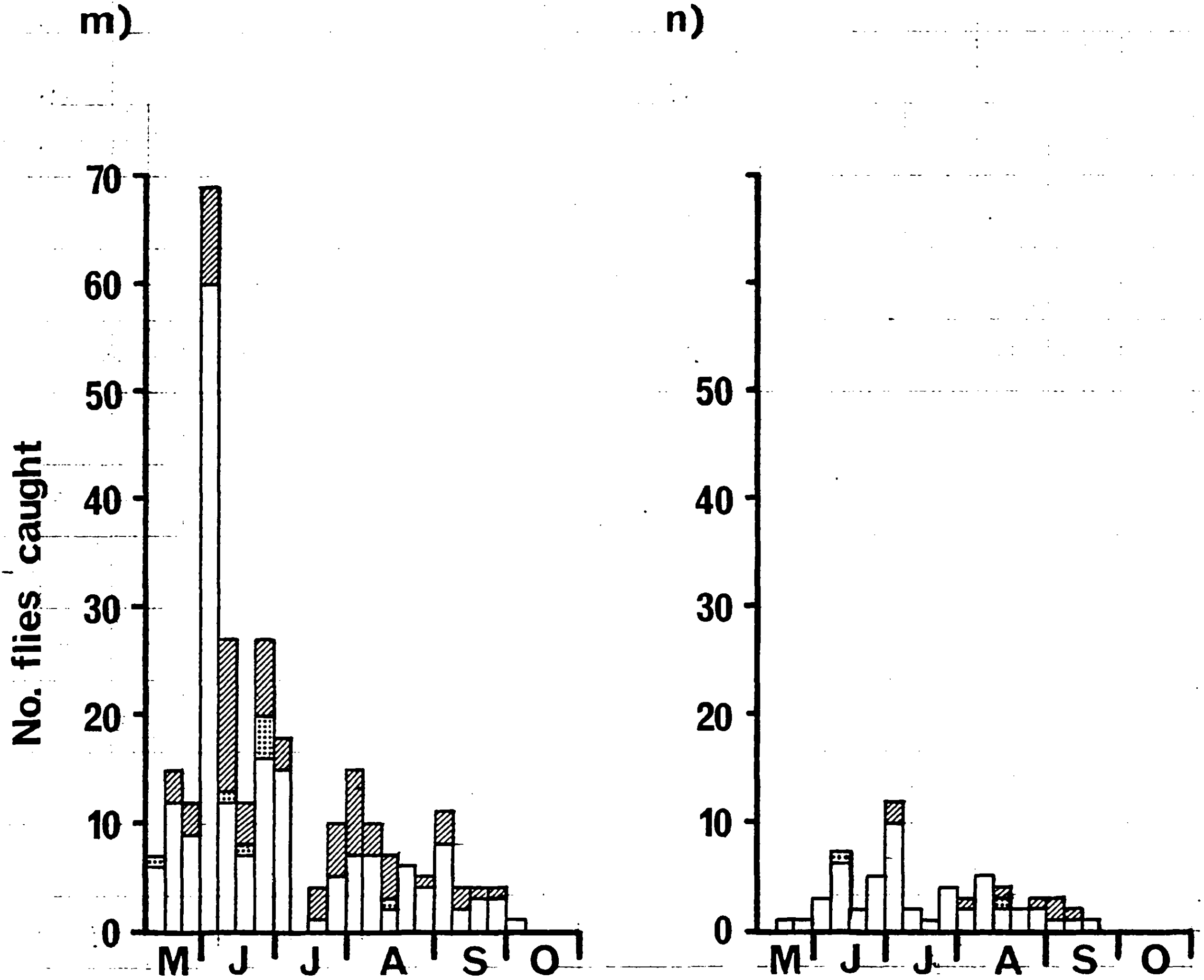
n) Platycheirus scutatus

<u>Key</u>

░ - Immature females

□ - Gravid females

▨ - Males


m)
n)
No. flies caught
0
10
20
30
40
50
60
70
M
J
J
A
S
O

Syrphids show a wide range of different phenological strategies. Some syrphid populations may be a mixture of several different voltine strategies: Dušek and Křístek (1967) demonstrated that populations of *Heringia heringi* (Zett.) and *Pipiza festiva* (Meig.) were partly univoltine and partly bivoltine. Hartley (1961) suggested that populations of *Myiatropa florea* L. were partly bivoltine and partly trivoltine. In this study, several bivoltine species occurred in which the two generations were of dissimilar size (eg *Platycheirus peltatus*, *P. albimanus*, *Melanostoma mellinum* etc). It has been suggested that these populations may also be partly univoltine and partly bivoltine (Gilbert, 1981a).

Syrphid phenology is conventionally interpreted in terms of the number of generations per year. Gilbert (1981a), however, has suggested that phenology may be better interpreted by considering the emergence patterns of the insect. These patterns are the primary cause of seasonal variations in the abundance of individual species. Emergence in many insects is delayed beyond the earliest physiologically possible date and this may result in an extended emergence curve for the population (Waldbauer, 1978). Individual differences in the degree of emergence may lead to emergence curves that are polymodal: bimodal, trimodal, or even more complex. The emergence of a single cohort may occur in this polymodal manner over an entire season, or even over several seasons. Polymodal patterns of emergence have been demonstrated in moths, butterflies, dragonflies, midges etc (Waldbauer,1978) and may also be common among the Syrphidae. In this particular study, syrphid phenology has been interpreted along conventional lines in terms of the number of generations recorded during the study period. *Melanostoma mellinum*, for example, was recorded as a bivoltine species with two discrete generations. According to Gilbert, the phenology of this species may be better interpreted in terms of a single generation or cohort which has two main emergence periods during the season: the population of *M. mellinum* thus has a bimodal emergence pattern. Similarly, the phenology of other syrphid species may be interpreted in terms of these polymodal emergence patterns. The extended phenological curves of *Syrphus ribesii*, *Episyrphus balteatus*, *Platycheirus scutatus* and

Metasyrphus corollae suggest a basic asynchrony in the emergence patterns of these populations.

2.4.4 Sex ratio

Table 2.5 shows the proportion of males recorded from the Malaise traps for some of the more abundant aphidophagous species. It is clear that in many species considerably more females were captured than males. This phenomenon may be explained in several ways: firstly, the natural sex-ratio may differ from the normal 1:1. This hypothesis may be discounted immediately on the basis of evidence from a five-week study in which different brassica crops were sampled at weekly intervals for syrphid eggs, larvae and pupae (see Chapter 4). The larvae and pupae were reared through in the laboratory and the sex ratio (expressed as the proportion of males) of the resulting adults are shown in Table 2.6. For all species, the natural ratio of males:females approximated to 1:1.

A second hypothesis is that the females of some species live longer than the males. If this hypothesis is correct, one would expect a progressive decline in the proportion of males caught during a single generation of the species. There was no clear evidence from the Malaise trap catches to support this hypothesis (see Figure 2.5a-n). Indeed, for many species, the proportion of males remained consistently low throughout each generation. Longevity studies carried out in the laboratory give conflicting results. Benestad (1970a) could find no significant difference in the longevity of male and female Metasyrphus corollae, whereas Tawfik et al (1974a) showed that the females lived longer. The longevity of male and female flies of both Merodon equestris (Doucette et al, 1942) and Mallota posticata Fabr. (Maier, 1978) has been shown to be similar. In contrast, laboratory-reared females of Paragus aegyptium Macq., Xanthogramma aegyptium Wied. and Sphaerophoria flavicauda Zett. live longer than the males (Tawfik et al, 1974b,c,d). In experiments on laboratory-reared E.balteatus flies, males lived longer than females (see Chapter 5). Maier and Waldbauer (1979a) noted that wing damage in field-caught Mallota posticata flies tended to be much greater in males than in females and attributed this to the increased time spent on the wing by the males when engaged in seeking mates and defending territories.

Table 2.5: Male mate-seeking strategies

Species	Number of flies ♂♂	♀♀	Proportion ♂♂	χ^2 (1 df)	Male mating -strategy	Location	Reference
Syrphus ribesii	9	97	0.08	73.06***	H,g	Near trees	Personal observation
					H,g,P	Near trees	Gilbert (1981a)
					H,g	Near trees	Rotheray (unpubl)
					P	Near trees	Carter (1919)
Metasyrphus corollae	11	15	0.42	0.62 ns	T	Flowers, crops	Personal observation
					T?	Near flowers	Gilbert (1981a)
					P		Schneider (1948)
Dasysyrphus venustus	0	22	0	22.00***	H	Woodland	Personal observation
Episyrphus balteatus	17	30	0.36	3.60 ns	H,s	Flowers, crops	Personal observation
					H,g	Near trees	Personal observation
					H,g	Near trees	Gilbert (1981a)
					H,g	Near trees	Rotheray (unpubl)
					H,g		Schneider (1948)
Meliscaeva cincta	7	61	0.10	42.88***			
Chrysotoxum bicinctum	9	68	0.12	45.22***	P	Woodland	Personal observation
Sphaerophoria scripta	227	377	0.38	37.25***	H,s/T	Flowers, crops	Personal observation
					T?	Flowers?	Gilbert (1981a)
					H,s	Grassland	Rotheray (unpubl)

Cont/. . .

Table 2.5: continued

Species	Number of flies		Proportion	χ^2 (1 df)	Male mating -strategy	Location	Reference
	♂♂	♀♀	♂♂				
Melanostoma mellinum	156	271	0.37	30.97***	H,T?	Trees, flowers, crops	Personal observation
Melanostoma scalare	13	128	0.09	93.79***	H,g H,g	Trees Trees, enclosed spaces	Personal observation Gilbert (1981a)
Platycheirus albimanus	71	175	0.29	43.97***	T T?	Flowers Flowers?	Personal observation Gilbert (1981a)
Platycheirus angustatus	74	194	0.28	53.73***	H	Near trees	Personal observation
Platycheirus clypeatus	13	64	0.17	33.78***	H,g H,g	Grassland Oviposition sites	Personal observation Gilbert (1981a)
Platycheirus peltatus	30	168	0.15	96.18***	H,g H,g	Trees, crops Oviposition sites	Personal observation Gilbert (1981a)
Platycheirus scutatus	8	53	0.13	33.20***	H,s	Grassland	Rotheray (unpubl)

Key H - Hovering P - Perching T - Patrolling s - singly g - groups

*** $p < 0.001$

Table 2.6: Sex-ratio of flies emerging from field-collected larvae and pupae

Species	Number of larvae and pupae	Number of flies		Proportion	χ^2 (1 df)	p
		♂♂	♀♀	♂♂		
Episyrphus balteatus	131	54	58	0.46	0.14	$p < 0.90$ ns
Sphaerophoria scripta	55	15	17	0.47	0.13	$p < 0.90$ ns
Syrphus ribesii	9	2	4	0.33	a	$p = 0.234$ ns
Metasyrphus luniger	2	2	-	1.00	b	
Platycheirus manicatus	17	5	7	0.42	a	$p = 0.193$ ns
Platycheirus albimanus	2	1	1	0.50	b	
Platycheirus peltatus	23	8	12	0.40	a	$p = 0.120$ ns
Melanostoma mellinum	28	10	6	0.63	a	$p = 0.12$ ns

a Exact probability of binomial calculated ($n < 25$)

b Numbers too low to permit statistical analysis

Flies with severely damaged wings rarely survive for long and thus an increased susceptibility to wing damage in males may well result in a shorter life-span under natural conditions. Conversely, it may be argued that increased flight activity in male flies might increase the probability of their capture in the Malaise traps. No attempt was made to age male flies caught in the traps and so there was no evidence to support or reject the hypothesis of early death in male flies.

A third explanation is that differences in the behavioural ecology of male and female flies result in males having a lower probability of being captured in the traps. Male syrphids exhibit a range of different mate-seeking strategies. Some species patrol potential feeding and/or oviposition sites and attack females visiting these sites (eg Eristalis tenax, E. arbustorum - Gilbert, 1981a;

Syritta pipiens - Collett and Land, 1975b). Others may perch on exposed leaves or branches and indiscriminately ambush passing insects in the hope that one is a female (eg *Epistrophe eligans* - Collett and Land, 1975a; *Helophilus* sp - Nielsen, 1966; *Syrphus ribesii* - Gilbert, 1981a). A third strategy is to hover either singly (eg *Eristalis pertinax* - Gilbert, 1981a) or in groups (*Platycheirus peltatus* - Gilbert, 1981a), often in sunspots close to trees, and chase after passing insects. A fourth strategy of finding mates has been observed in some males of *Xylota* species: the males often search while running over leaf surfaces (Gilbert, 1981a).

Males of one species may adopt different strategies, and individuals may also change strategy according to environmental conditions (Maier and Waldbauer, 1979b; Maier, 1980; Gilbert, 1981a). A detailed study of swarming behaviour in *Syrphus ribesii* has shown that male flies congregate at specific 'encounter-sites' early in the morning. Initially, they perch on vegetation and fly out at passing insects. As the temperature increases they switch to the hovering strategy (Gilbert, 1981a).

Observations on the male mate-seeking strategies of some of the more abundant species encountered in the present study are presented in Table 2.5 together with previous records of mate-seeking behaviour in these species.

The particular strategy adopted by a male syrphid can influence its chances of capture in the Malaise traps. Males of *Sphaerophoria scripta*, *Platycheirus albimanus* and *Metasyrphus corollae* were often to be seen 'patrolling' potential feeding and/or oviposition sites in crop and edgegrowth habitats. Both males and females of these three species tended to fly low down among the vegetation and therefore have an equal chance of entering the trap. Indeed, the ratio of males:females recorded in the traps approximated to 1:1.

Males of *Syrphus ribesii*, *Melanostoma scalare* and *Platycheirus peltatus* were frequently observed hovering in groups at the edge of nearby deciduous woodland. These groups or 'swarms' tended to occupy specific locations and were usually present throughout the day.

Interestingly enough, few females were observed at these sites. Male S. ribesii, M. scalare and P. peltatus were rarely seen in the crops and the number of males caught in the Malaise traps in crop and edgegrowth sites was accordingly very low.

Males of Episyrphus balteatus were also frequently observed hovering in swarms under trees, but solitary individuals were also found hovering near edgegrowth flowers and in the crops. Two Dasysyrphus venustus males were seen hovering in deciduous woodland, but no males of this species were recorded in the crops or adjacent edgegrowth.

Thus, it seems that there was a crude correlation between the particular mate-seeking strategy adopted by a male syrphid and the probability of it being captured in the Malaise traps. Males that actively patrolled feeding and oviposition sites in crop and edgegrowth habitats were more likely to be caught than males that congregated at localized encounter-sites which were often completely removed from the Malaise-trap sites.

2.4.5 Spatial distribution patterns of adult syrphids in crop and edgegrowth sites

It was established earlier (Section 2.4.2) that one main syrphid community operated within the study area, although the abundance of individual species sometimes varied considerably in different crop and edgegrowth sites. Table 2.7 shows the distribution of some of the more abundant species in crop and edgegrowth habitats. In this table, the study period has been divided into one eleven-week and one twelve-week period, corresponding to the periods before and after the bean crop was harvested. It is clear that several species showed a significant preference for either the crop or the edgegrowth habitat.

During spring and early summer, most syrphid species were equally active in both crop and edgegrowth sites. Exceptions included Platycheirus angustatus, Episyrphus balteatus and Melanostoma scalare which were all significantly more active in the edgegrowth. During

Table 2.7: Distribution of some syrphid species in crop and edgegrowth sites

Species	12.5.80 - 25.7.80				28.7.80 - 17.10.80			
	Number of flies		χ^2 (1 df)	p	Number of flies		χ^2 (1 df)	p
	crop	edge			crop	edge		
Syrphus ribesii	5	8	†	$p = 0.157$ ns	32	61	2.80	$p < 0.10$ ns
Metasyrphus corollae	7	2	†	$p = 0.070$ ns	10	7	†	$p = 0.117$ ns
Dasysyrphus venustus	13	9	†	$p = 0.119$ ns	-	-	-	-
Episyrphus balteatus	8	21	5.83	$p < 0.05$ *	10	8	†	$p = 0.167$ ns
Sphaerophoria scripta	26	30	0.29	$p < 0.90$ ns	371	177	136.41	$p < 0.001$***
Meliscaeva cinctella	2	2	†	$p = 0.375$ ns	45	19	19.48	$p < 0.001$***
Chrysotoxum bicinctum	7	13	†	$p = 0.074$ ns	18	39	3.03	$p < 0.10$ ns
Melanostoma mellinum	17	30	3.60	$p < 0.10$ ns	134	246	9.28	$p < 0.01$ **
Melanostoma scalare	4	11	†	$p = 0.042$*	14	112	52.28	$p < 0.001$***
Platycheirus albimanus	11	14	†	$p = 0.133$ ns	136	85	30.99	$p < 0.001$***
Platycheirus angustatus	47	154	56.96	$p < 0.001$***	8	59	27.07	$p < 0.001$***
Platycheirus clypeatus	5	9	†	$p = 0.122$ ns	23	40	1.08	$p < 0.50$ ns
Platycheirus peltatus	19	32	3.31	$p < 0.10$ ns	71	76	1.68	$p < 0.50$ ns
Platycheirus scutatus	21	18	0.23	$p < 0.90$ ns	11	11	†	$p = 0.168$ ns
Syritta pipiens	9	13	†	$p = 0.119$ ns	55	42	7.43	$p < 0.01$ **

† Exact probability of binomial calculated ($n < 25$)

*** $P < 0.001$

** $P < 0.01$

* $P < 0.05$

late summer and autumn, three species were taken more frequently in the edgegrowth (P. angustatus, M. mellinum and M. scalare) while a further four species (Sphaerophoria scripta, Meliscaeva cinctella, P. albimanus and Syritta pipiens) occurred predominantly in the crops.

Table 2.8 shows the distribution of the most common syrphid species in different crops. Again, the study period has been divided into two parts. In the early part of the season, most species were equally active in all four crops. Three exceptions occurred: Sph. scripta was significantly more active in the wheat than in any other crop, P. albimanus was most active in the potatoes and P. angustatus was taken more frequently in both the wheat and Brussels sprouts than in the other crops. Later on in the season, six species were significantly more active in the wheat than in other crops: these included Sph. scripta, Meliscaeva cinctella, Melanostoma mellinum, Syrphus ribesii, Chrysotoxum bicinctum and the non-aphidophagous species, Syritta pipiens. P. peltatus and P. clypeatus were both most active in the Brussels sprout crop while P. albimanus showed a significant preference for the potatoes.

These 'preferences' may well reflect the suitability of different crop and edgegrowth sites as feeding and/or oviposition sites for the adults of individual syrphid species and are discussed more fully in Sections 2.4.6, 2.4.7 and 2.5.

2.4.6 The relationship between syrphid activity and aphid distribution

The overwhelming abundance of species with an aphidophagous larval stage suggested that aphids might be an important source of larval food material. The following section examines the relationship between the adult syrphid activity and aphid distribution in crop and edgegrowth sites.

Wheat

The development of aphid and syrphid adult populations in the wheat crop is illustrated in Figure 2.6a. The aphid population was initiated in May by large numbers of immigrant alatae. There was

Table 2.8: Distribution of some syrphid species in different crops

Species	12.5.80 - 25.7.80					
	Number of flies caught				X^2 (3 df)	p
	W	P	Br	B		
Syrphus ribesii	1	-	3	1	a	
Metasyrphus corollae	2	2	3	-	a	
Dasysyrphus venustus	7	2	-	4	a	
Episyrphus balteatus	3	2	-	3	a	
Sphaerophoria scripta	22	2	2	-	49.70	***
Meliscaeva cinctella	-	-	1	1	a	
Chrysotoxum bicinctum	5	-	2	-	a	
Melanostoma mellinum	6	3	3	5	a	
Melanostoma scalare	-	-	1	3	a	
Platycheirus albimanus	2	3	6	-	a	
Platycheirus angustatus	14	8	17	8	15.79	**
Platycheirus clypeatus	-	-	4	1	a	
Platycheirus peltatus	3	4	9	3	5.20	ns
Platycheirus scutatus	1	11	6	3	10.81	*
Syritta pipiens	1	2	3	3	a	

Species	28.7.80 - 17.10.80					
	Number of flies caught				X^2 (2 df)	p
	W	P	Br	B		
Syrphus ribesii	23	8	1	nr	23.69	***
Metasyrphus corollae	6	2	2	nr	a	
Dasysyrphus venustus	-	-	-	nr	a	
Episyrphus balteatus	4	5	1	nr	a	
Sphaerophoria scripta	255	39	77	nr	215.04	***
Meliscaeva cinctella	40	5	-	nr	63.34	***
Chrysotoxum bicinctum	15	2	1	nr	20.34	***
Melanostoma mellinum	55	43	36	nr	4.13	ns
Melanostoma scalare	9	1	4	nr	a	
Platycheirus albimanus	36	64	36	nr	11.53	**
Platycheirus angustatus	6	1	1	nr	a	
Platycheirus clypeatus	2	1	20	nr	29.81	***
Platycheirus peltatus	18	10	43	nr	25.04	***
Platycheirus scutatus	5	-	7	nr	a	
Syritta pipiens	31	21	3	nr	21.26	***

<u>Key</u> W = wheat P = potato Br = Brussels sprout
B = beans

a Numbers too low to permit statitical analysis
nr no record
*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

a rapid rise to a population peak of about 21 aphids per shoot in late June, just after the crop had flowered. Numbers then began to decline rapidly and the aphid populations had collapsed entirely by the end of July. Predation by syrphid larvae and other natural enemies (notably coccinellids) was undoubtedly one of the major factors contributing to the decline of the aphid population. The most abundant aphid species recorded on the wheat shoots was Sitobion avenae (F.). Metapolophium dirhodum (Wlk.) was also found, but was much less common than S. avenae. Aphid populations also developed on weeds (mainly Veronica persica Poir., V. polita Fries, Matricaria chamomilla L., Ranunculus arvensis L.) growing in the lower canopy of the wheat crop. No formal sampling of these aphid populations (mainly Brachycaudus helichrysi Kalt.) was carried out. However, casual inspection of the weeds indicated that aphid populations developed in May and remained at low levels throughout the summer.

Syrphid adult activity in the wheat remained generally low during spring and early summer. A small peak of activity occurred in early June which coincided with the initial infestation of the crop by large numbers of alatae. Adult activity remained low during early July and then increased rapidly, reaching a peak in mid-August. Syrphid eggs first appeared in the crop in late May, and the larvae in early June, when the aphid population was approaching its peak. Eggs and larvae were recorded in the crop during June, July and early August. Pupae were found until the beginning of September.

Most of the syrphid eggs and larvae collected from wheat plants in June and early July were indentified as Episyrphus balteatus. Those collected in late July and early August were principally Sphaerophoria scripta. The adult activity patterns of these two species in the wheat crop are illustrated in Figures 2.6b. Few adult E. balteatus were captured in the wheat crop. This species occurred throughout most of the season but was most abundant in late June. Gravid females were recorded in the wheat during June and July but individuals observed thereafter invariably had undeveloped ovaries. E. balteatus is probably a univoltine species Britain and the immature adults recorded in August and September are probably newly-emerged individuals of the second, overwintering generation that completed its larval and pupal development within the wheat crop. *Sph. scripta* adults were active in the wheat crop during July and August, with peak activity occurring in mid-August. *Sph. scripta* was the most abundant species taken in the wheat representing 45% of all individuals captured. In this study, *Sph. scripta* was recorded as a trivoltine species with the second and third generations overlapping. Gravid females of the second generation first appeared in the wheat in mid-July when aphid populations on the wheat shoots were still fairly high. Eggs and larvae were recorded both on wheat plants and on weeds at this time. The aphid population collapsed two weeks later and few gravid females were observed thereafter. Oviposition in *Sph. scripta* is stimulated by the presence of aphids (Chandler, 1968b) and thus when aphid populations collapsed, the wheat crop would become unattractive as an oviposition site for gravid females. Large numbers of *Sph. scripta* adults occurred in the wheat in mid-August when aphid populations on the wheat shoots were very low. Most of the females recorded at this time had immature ovaries. These individuals probably represented the newly-emerged third generation which had completed its entire larval and pupal development within the wheat crop. The numbers of *Sph. scripta* adults recorded in the wheat declined rapidly during late August and it seemed likely that third generation adults emerging in this crop were dispersing elsewhere to find more suitable oviposition sites.

According to the Malaise trap data on syrphid adult numbers, *Melanostoma mellinum*, *Platycheirus albimanus* and *Meliscaeva cinctella* were the three most abundant species taken in the wheat after *Sph. scripta*. Interestingly enough, very few eggs and larvae of these three species were found on the wheat plants. Eggs and larvae of *Platycheirus* and *Melanostoma* species were, however, frequently collected from the weeds growing in the lower canopy layer of the wheat crop. These observations suggested that the activity of ovipositing females of *P. albimanus*, *Melanostoma mellinum* and possibly *Meliscaeva cinctella* also was associated primarily with the weeds in the wheat crop rather than the wheat plants *per se*. The adult activity patterns of these three species in the wheat is shown in Figure 2.6c.

Figure 2.6: Development of aphid and adult syrphid populations in the wheat crop

a) Patterns of aphid infestation and adult syrphid activity in the wheat crop

x——x Number of aphids per tiller

x - - -x Number of adult syrphids trapped (all species considered)

b) Activity patterns of *Sphaerophoria scripta* and *Episyrphus balteatus* in the wheat crop

●——● *Sphaerophoria scripta*

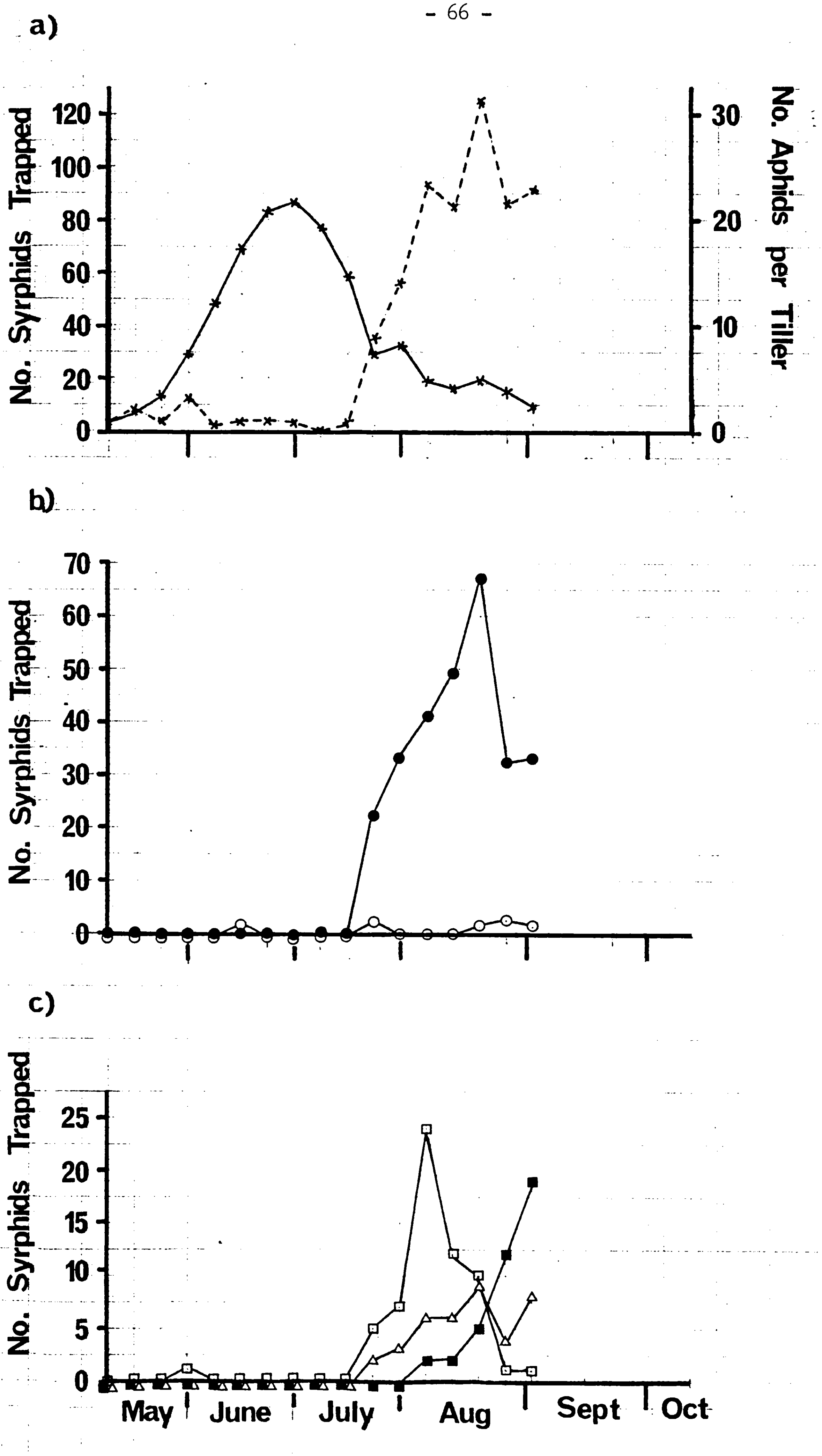
○——○ *Episyrphus balteatus*

c) Activity patterns of *Melanostoma mellinum*, *Meliscaeva cinctella* and *Platycheirus albimanus*

□——□ *Melanostoma mellinum*

■——■ *Meliscaeva cinctella*

△——△ *Platycheirus albimanus*


a)
No. Syrphids Trapped
120
100
80
60
40
20
0
No. Aphids per Tiller
30
20
10
0
b)
No. Syrphids Trapped
70
60
50
40
30
20
10
0
c)
No. Syrphids Trapped
25
20
15
10
5
0
May
June
July
Aug
Sept
Oct

Adults of all three species are active in the wheat during July and August, although the peak activity of individual species occurred at different times: *M. mellinum* in early August, *M. cinctella* and *P. albimanus* in late August/early September. The three species are all bivoltine and, in each case, it is the second generation that is active in the wheat crop.

Brussels sprouts

The development of aphid and syrphid adult populations in the Brussels sprouts in illustrated in Figure 2.7a. Aphid populations were initiated by immigrant alatae in early June and built up slowly to reach a small first peak in mid-June. The populations declined again during early July but then increased to give a second larger peak at the end of August. Numbers fell again at the beginning of September and then increased rapidly to reach a third peak in early October. *Myzus persicae* Sulz. was the dominant aphid species recorded during May, June and July, whereas *Brevicoryne brassicae* L. became the most abundant in August, September and October.

The syrphid adult populations showed three main peaks of activity: the first in early June, the second in early August and the third and largest peak in late August. Adult activity in the Brussels sprouts decreased dramatically at the end of August. Syrphid eggs were first observed in the crop at the beginning of June and peak oviposition occurred in early August. Syrphid larvae were first recorded in early June and become particularly numerous during August and September. The eggs and larvae collected in June, early July and September were identified as mainly *Platycheirus* species. Those found in late July and August were chiefly *Sphaerophoria scripta* with a few *Melanostoma mellinum*.

The adult activity patterns for the most abundant syrphid species recorded in the Brussels sprouts are shown in Figures 2.7 b and c. *M. mellinum* and *Sph. scripta* adults were mainly active in the crop during both spring and summer generations. Peak activity of *P. peltatus* occurred in late August, whereas that of *P. albimanus* occurred in late September.

Figure 2.7: Development of aphid and adult syrphid populations in the Brussels sprout crop

a) Patterns of aphid infestation and adult syrphid activity in the Brussels sprout crop

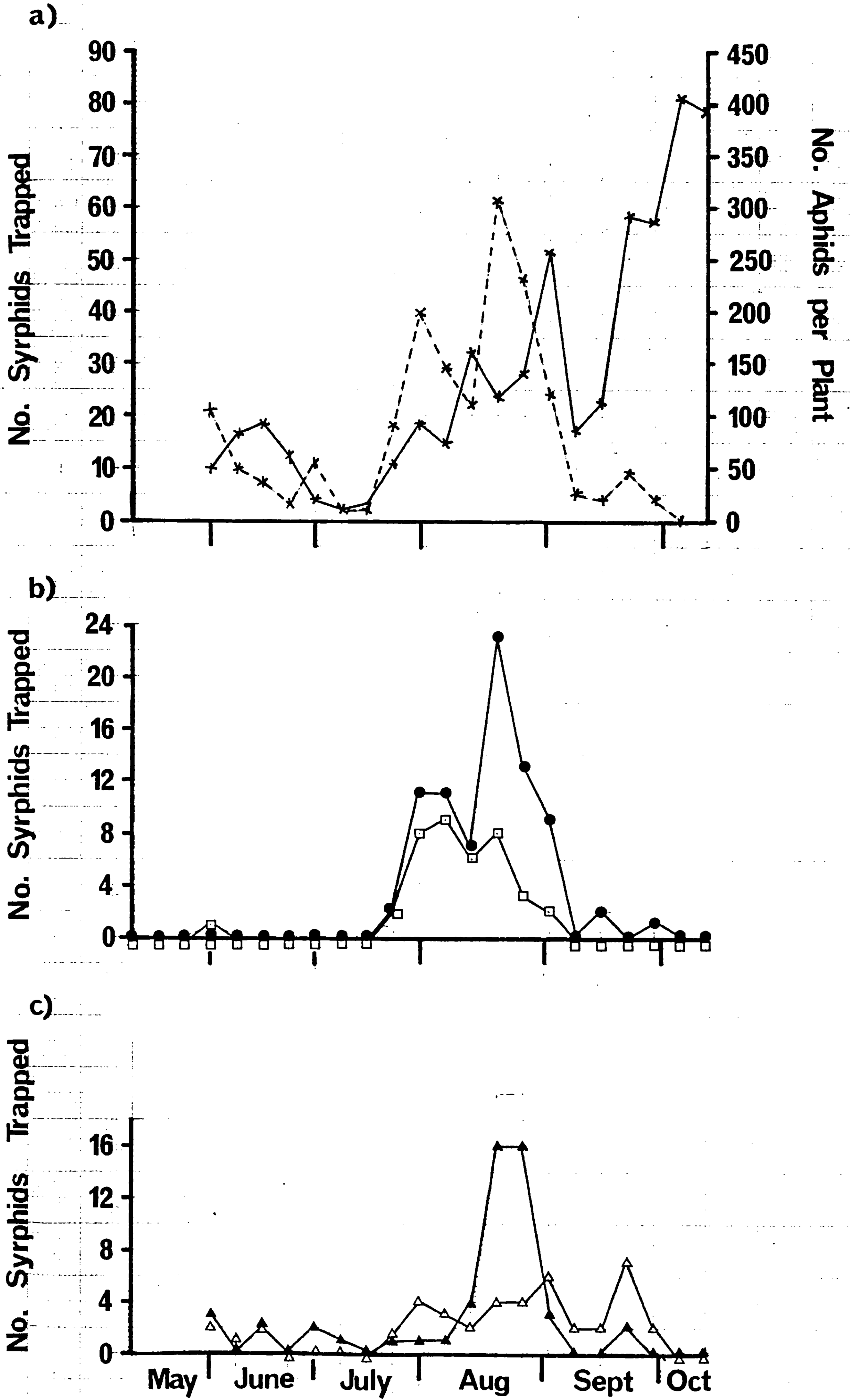
x——x Number of aphids per plant
x---x Number of adult syrphids trapped (all species considered)

b) Activity patterns of *Sphaerophoria scripta* and *Melanostoma mellinum* in the Brussels sprout crop

●——● *Sphaerophoria scripta*
□——□ *Melanostoma mellinum*

c) Activity patterns of *Platycheirus peltatus* and *Platycheirus albimanus* in the Brussels sprout crop.

▲——▲ *Platycheirus peltatus*
△——△ *Platycheirus albimanus*


a)
No. Syrphids Trapped
0
10
20
30
40
50
60
70
80
90
No. Aphids per Plant
0
50
100
150
200
250
300
350
400
450
b)
No. Syrphids Trapped
0
4
8
12
16
20
24
c)
No. Syrphids Trapped
0
4
8
12
16
May
June
July
Aug
Sept
Oct

The pattern of syrphid activity in the Brussels sprout crop was closely related to the development of aphid populations. Oviposition by Platycheirus species occurred in early June, shortly after the crop was planted. Aphid infestation was very low at this time. Gravid females of Platycheirus species have been frequently recorded ovipositing on plants that are only lightly infested with aphids or even entirely uninfested (Chandler, 1968b). The larval stage of Platycheirus species is believed to be only facultatively aphidophagous and can subsist on alternative non-aphid prey, if aphids are scarce. The larvae require few aphids to complete development and so these species are well-adapted to utilizing small aphid populations. Syrphid larvae were frequently observed feeding in aphid colonies and their activity evidently caused considerable reductions in aphid numbers. There was little doubt that predation by syrphid larvae was an important factor in keeping aphid populations low throughout most of the summer. Only in late September and October, when syrphid activity had declined, were aphid populations able to build up appreciably in the Brussels sprouts crop.

Potatoes

The development of aphid and adult syrphid populations in the potato crop is shown in Figure 2.8a. The general level of aphid infestation remained low throughout the crop growing season. Aphid populations began to build up in June and reached a peak in mid-July. Numbers then fell off rapidly and the population maintained a low level for the remainder of the season. The most abundant aphid species recorded were Myzus persicae Sulz., Macrosiphum solanifolii Ashm. and Aulacorthum solani Kalt.

As in the Brussels sprouts, the adult syrphid population showed three main peaks of activity. The first occurred in early June, the second in the middle of August, and the third in early September. Thereafter, syrphid activity in the potatoes declined rapidly thoughout September. Eggs were first observed in early June and were thereafter recorded throughout the season. Larvae first appeared in mid-June and were particularly abundant in mid-July and

Figure 2.8: Development of aphid and adult syrphid populations in the potato crop

a) Patterns of aphid infestation and adult syrphid activity in the potato crop

x——x Number of aphids per plant

x- - -x Number of adult syrphids trapped (all species considered)

b) Activity patterns of *Sphaerophoria scripta* and *Platycheirus albimanus* in the potato crop

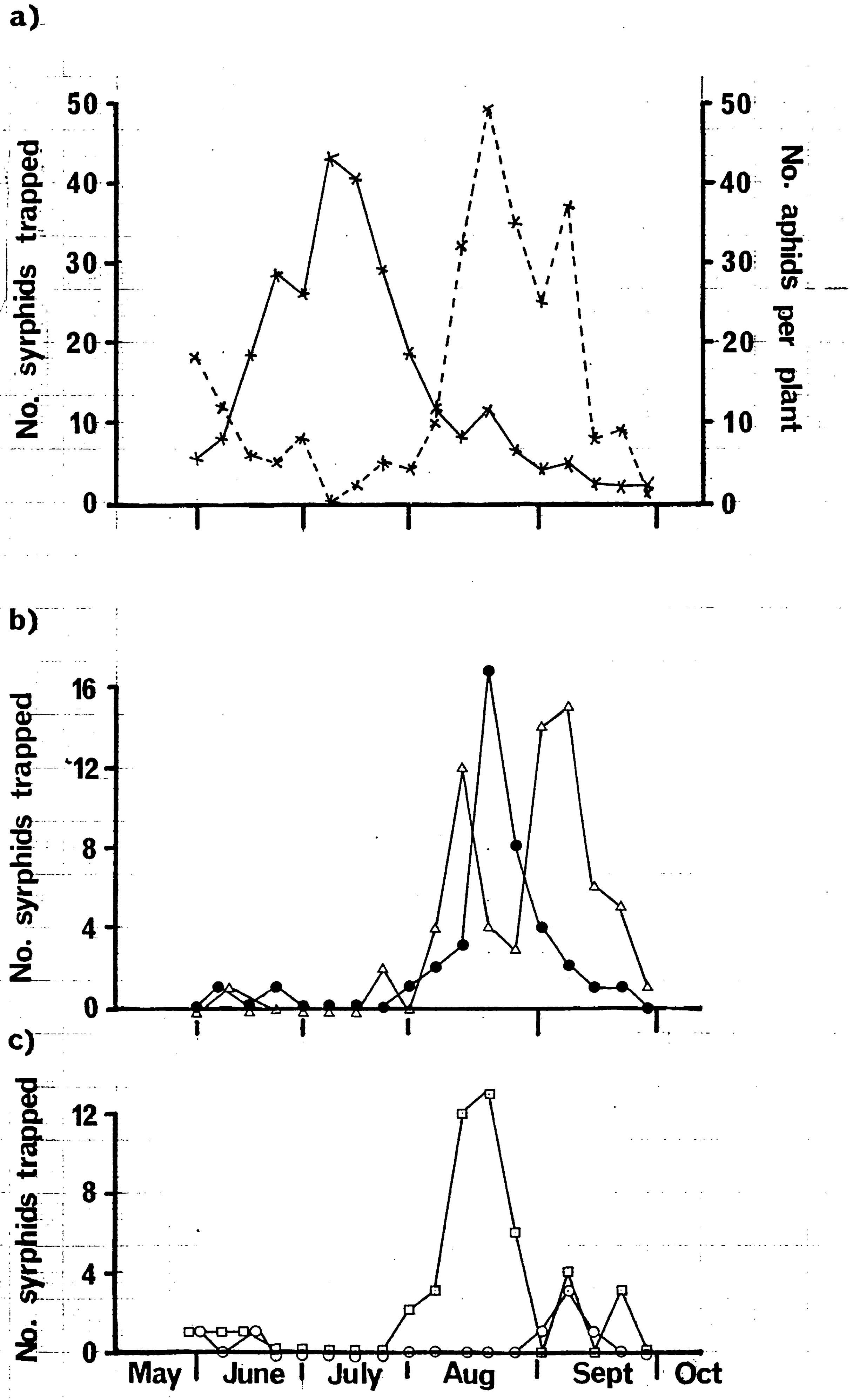
●——● *Sphaerophoria scripta*

△——△ *Platycheirus albimanus*

c) Activity patterns of *Melanostoma mellinum* and *Episyrphus balteatus* in the potato crop.

□——□ *Melanostoma mellinum*

○——○ *Episyrphus balteatus*


a)
No. syrphids trapped
0
10
20
30
40
50
No. aphids per plant
0
10
20
30
40
50
b)
No. syrphids trapped
0
4
8
12
16
c)
No. syrphids trapped
0
4
8
12
May
June
July
Aug
Sept
Oct

again in late August. Most immature stages collected from the potato plants were *Melanostoma* and *Platycheirus species*. Eggs and larvae of *E. balteatus* were found in June and those of *Sph. scripta* in early August. The adult activity patterns of some of these species are shown in Figures 2.8 b and c. Few *E. balteatus* adults were record in the potatoes during the entire season. Gravid females occurred in June and several immature individuals were captured in September. The most abundant *Platycheirus* species taken was *P. albimanus*.

Gravid females occurred throughout the season with two main peaks of activity in mid-August and early September, respectively. Gravid females of *Melanostoma mellinum* were also taken throughout the season with peak numbers being recorded in August. *Sph. scripta* was active mainly in August when gravid females of the second and immature individuals of the third generation were recorded.

Predation by syrphid larvae during June and July was a major feature contributing to the decline of the aphid population in late July. The continued activity of these larvae throughout the rest of the season helped to maintain the aphid population at a very low level.

Beans

The development of aphid and syrphid populations in the beans is shown in Figure 2.9a. Aphid population levels were consistently low throughout the crop growing season. The main aphid species present was *Aphis fabae* Scop.. Syrphid adult activity was correspondingly low with the number of syrphid adults recorded declining steadily until the crop was harvested in late July. Syrphid eggs and larvae were first observed in the crop in late May. These were identified to be principally *Platycheirus* and *Melanostoma* species. Figure 2.9b shows the adult activity patterns of the most abundant species taken in the beans, *P. angustatus*. This species was mainly active in the crop during May and June.

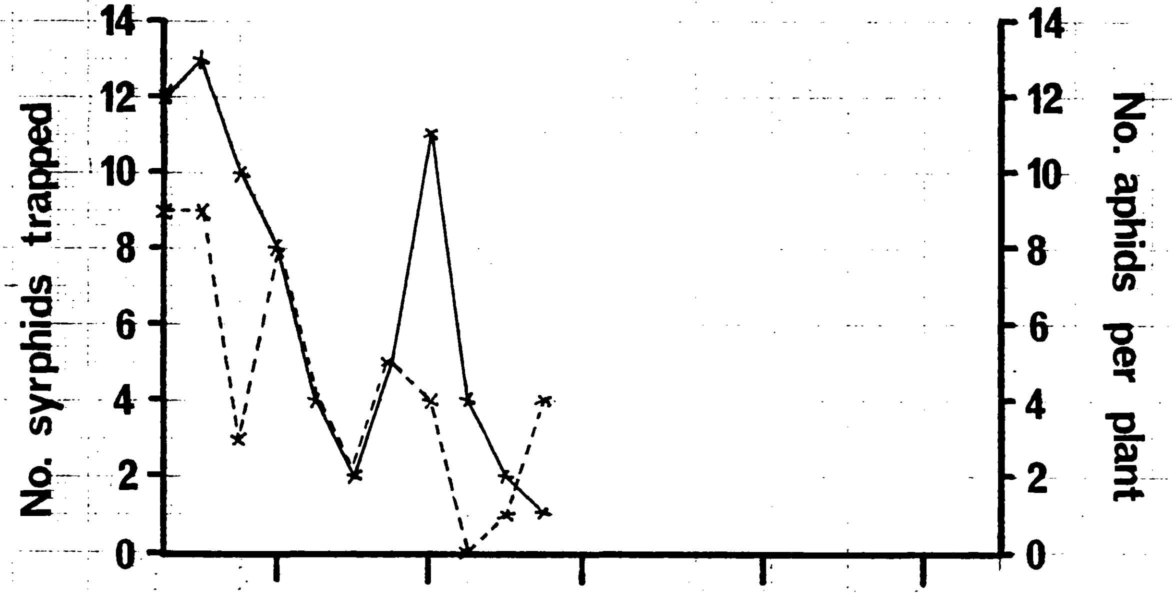
Figure 2.9: Development of aphid and adult syrphid populations in the bean crop

a) Patterns of aphid infestation and adult syrphid activity in the bean crop

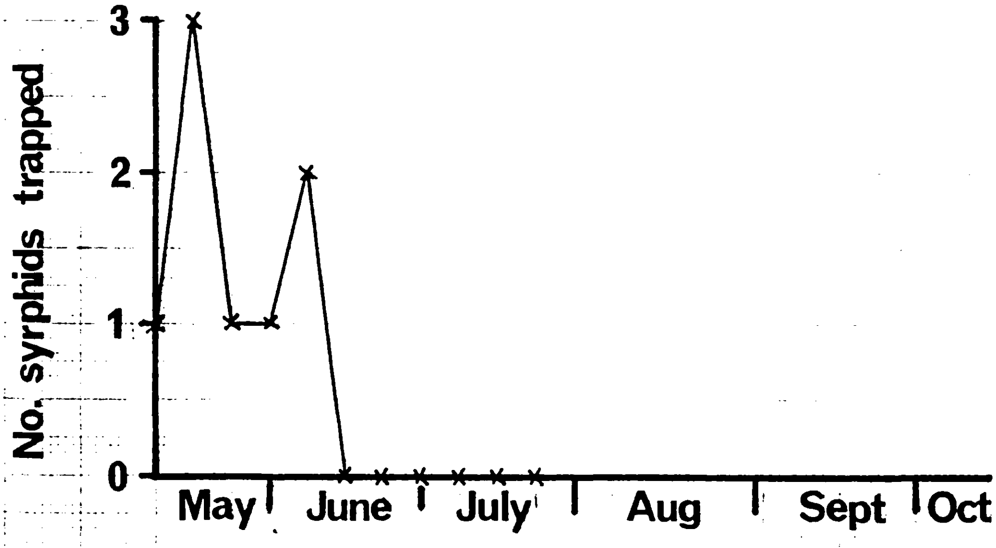
x——x Number of aphids per plant

x- - -x Number of adult syrphids trapped (all species considered)

b) Activity patterns of *Platycheirus angustatus* in the bean crop a)


No. syrphids trapped
14
12
10
8
6
4
2
0
No. aphids per plant
14
12
10
8
6
4
2
0

b)


No. syrphids trapped
3
2
1
0
May
June
July
Aug
Sept
Oct

Predation by syrphids and other natural enemies was an important factor keeping the aphid population in the beans at a very low level throughout the season.

In summary, adult syrphid activity and aphid abundance in the crops appeared to be closely related. In all crops, the development of aphid populations led to increased syrphid activity, and predation by syrphid larvae was important in reducing aphid numbers.

However, the effectiveness of syrphids in limiting aphid populations was often constrained by their phenology. Poor synchronization between aphid and syrphid populations sometimes enabled aphid populations to attain high levels when syrphid numbers were low. A mid-season lull in syrphid activity allowed aphid populations in the wheat and potatoes to reach high levels of infestation during June and early July. However, syrphid activity in these two crops increased again during late July and early August with the appearance of Sphaerophoria scripta, Melanostoma mellinum and Platycheirus albimanus and aphid populations soon began to decline. In the Brussels sprouts, syrphid activity was largely responsible for maintaining aphid populations at a low level throughout the spring and summer. In September, however, when syrphid numbers were low, aphid populations increased rapidly.

Syrphid activity in the edgegrowth

No formal sampling of aphid populations in the edgegrowth flora was carried out. However, several crude assessments of aphid levels on a range of edgegrowth plants were made at regular intervals throughout the study period. This enabled a very general view of the relationship between syrphid activity and aphid abundance to be obtained.

The general pattern of syrphid activity in the edgegrowth is illustrated in Figure 2.10. Two main peaks of syrphid activity occurred: the first in June and the second in August. During May and June, syrphid activity in the edgegrowth was concentrated in the

Figure 2.10: Development of adult syrphid populations in the edgegrowth

a) Activity patterns of adult syrphids in the edgegrowth (all species considered)

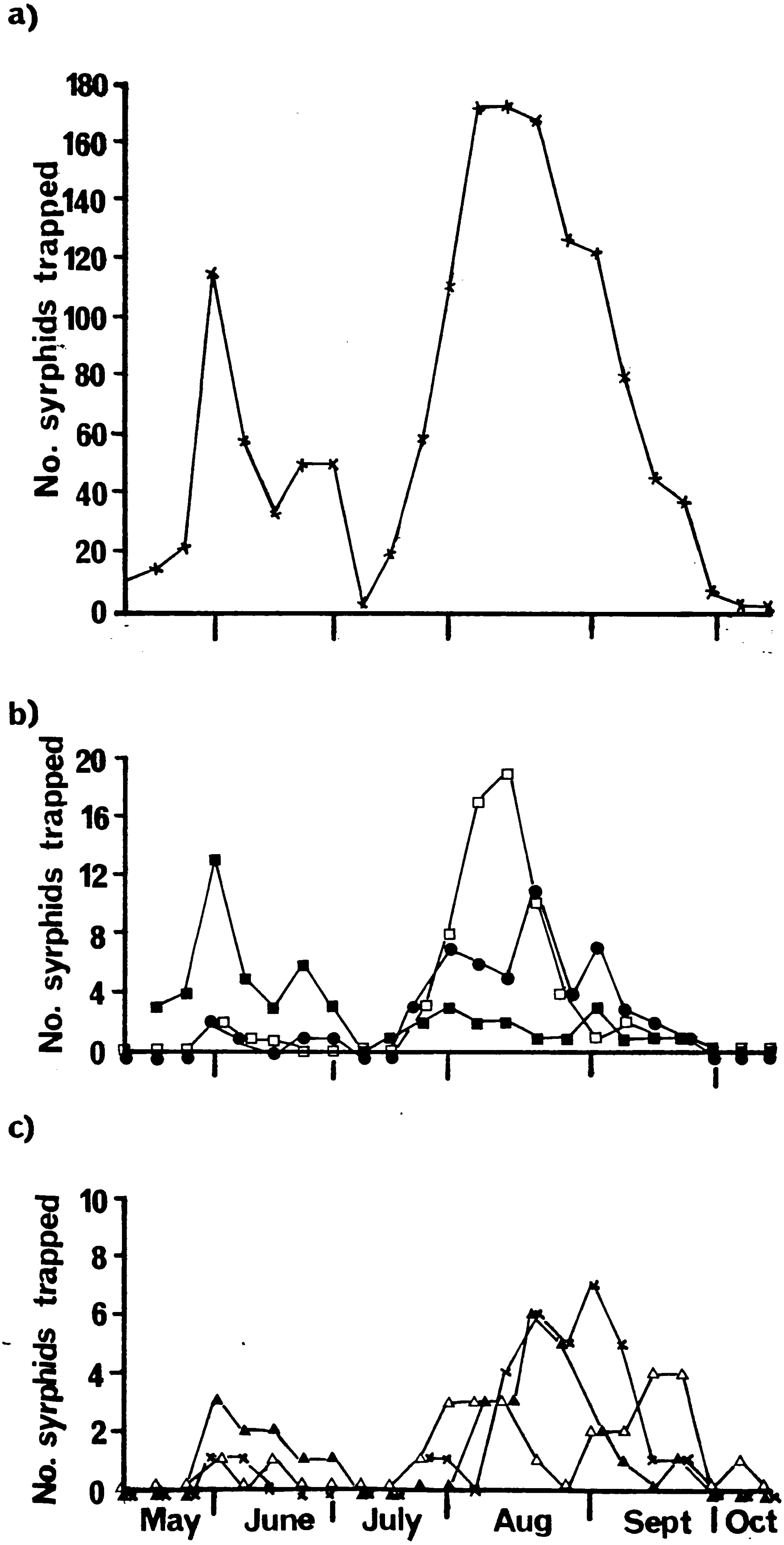
b) Activity patterns of Platycheirus angustatus, Melanostoma mellinum and Sphaerophoria scripta

■——■ Platycheirus angustatus
□——□ Melanostoma mellinum
•——• Sphaerophoria scripta

c) Activity patterns of Platycheirus albimanus, Platycheirus peltatus and Melanostoma scalare

△——△ Platycheirus albimanus
▲——▲ Platycheirus peltatus
x——x Melanostoma scalare

The figures show the total number of flies caught in four edgegrowth traps


a)
No. syrphids trapped
0
20
40
60
80
100
120
140
160
180
b)
No. syrphids trapped
0
4
8
12
16
20
c)
No. syrphids trapped
0
2
4
6
8
10
May
June
July
Aug
Sept
Oct

immediate vicinity of several flowering broom bushes (Cytisus scoparius (L.) Link) which were heavily infested with the aphids Acyrthosiphon spartii (Koch) and Aphis sarothamni Fransson. These bushes have been previously shown to be extremely attractive to adult syrphids, both as a feeding and as an oviposition site (Dixon, 1959). In early July, aphid populations on the broom bushes had fallen to very low levels, mainly due to heavy predation by syrphid larvae. Aphid populations on other edgegrowth plants were also low at this time and syrphid adult activity in the edgegrowth dropped off accordingly. During July, aphid populations started to build up on a variety of herbaceous plants and grasses and a corresponding increase was observed in syrphid activity. During August, high levels of aphid infestation were observed on flowering Heracleum sphondylium L. and large numbers of adult syrphids were frequently observed feeding and ovipositing on this particular plant. In September and October, aphid levels on herbaceous plants and grasses in the edgegrowth declined and there was a corresponding decline in syrphid adult activity.

Figure 2.10 b and c show the activity patterns of the dominant (Platycheirus angustatus, Melanostoma mellinum and Sphaerophoria scripta) and subdominant (P. albimanus, M. scalare and P. peltatus) species in the edgegrowth. Gravid females of all five species were recorded throughout most of the study period although peak activity of individual species occurred at different times: P. angustatus in June; Sph. scripta in early August; M. mellinum and P. peltatus in late August; M. scalare in late August/early September and P. albimanus in early August and September.

2.4.7 The relationship between syrphid activity and the distribution of adult food resources

It had been hoped to examine the effect of the distribution of adult and larval food resources on syrphid activity independently of each other. Unfortunately this was not possible: feeding and oviposition sites frequently occurred in close proximity and adult syrphids were often observed both feeding and ovipositing on the same plant (eg on *Cytisus scoparius* and on *Heracleum sphondylium*). The Malaise trap catches give no indication as to the precise nature of the syrphid activity in a particular site.

The importance of flower feeding in adult syrphids has already been discussed (see Section 2.1). During spring, the only flowers present were found in the edgegrowth and this may well have been a contributing factor in concentrating syrphid activity in edgegrowth sites at this time. Later on in the summer, flowering weeds were abundant in the wheat crop, this may have contributed to the overwhelming attraction of the wheat to adult syrphids as compared to other crops. Indeed, it is noteworthy that adults of several non-aphidophagous species (eg *Eristalis* spp) were taken more frequently in the wheat than in the other crops and these flies may well have been utilizing the wheat crop as a feeding site.

2.4.8 The use of the Malaise trap for measuring syrphid activity

It now seems timely to discuss the Malaise trap as a tool for sampling adult syrphid activity. The advantages of the trap as a passive, non-attractant sampling technique that can operate continuously both night and day have already been discussed (Section 2.3.3).

The results presented in this study show that the trap does not give an unbiassed estimate of the abundance of different syrphid species. Some species prefer to fly at a particular height above the ground when searching for feeding (Gilbert, 1981a) or oviposition (Chandler, 1968d) sites and this will influence their probability of entering the trap: species that fly low down in the vegetation (eg *Sphaerophoria scripta*) are more likely to be caught than those that fly some distance above the ground (eg *Eristalis* spp). Differences in the behavioural ecology of male and female flies of some species have also been shown to give misleading impressions of a biassed sex-ratio.

In this study, it was assumed that the sampling bias for a particular species remained constant and that long-term changes in the numbers of an individual species reflect actual changes in species phenology and population size. However, care should be taken in the interpretation of this phenological data as periods of inclement weather result in low syrphid activity and this may give a misleading impression of a decline in numbers.

The height of the trap remained fixed and could not be adjusted for changes in crop height. Care was taken to ensure that the vegetation in the immediate vicinity of the trap was kept at a low level. However, it is still possible that changes in the height of the vegetation surrounding the traps influence trap captures.

One main disadvantage of the Malaise trap in monitoring insect activity is that the catches give no indication as to the precise nature of the activity. Frequently, feeding and oviposition sites occurred in close proximity to each other and it was thus impossible to differentiate between feeding and oviposition activities in a particular site on the basis of the Malaise trap catch.

2.5 GENERAL DISCUSSION AND CONCLUSIONS

This chapter has examined the spatial and temporal distribution patterns of the adult syrphid communities associated with four annual crops and with the adjacent natural habitats. One main syrphid community operated within both crop and edgegrowth habitats and this was dominated by species with an aphidophagous larval stage.

There was a considerable amount of indirect evidence to suggest that the syrphid activity was closely related to the distribution of aphids. In the spring, aphids were common on trees and woody shrubs in the edgegrowth but aphid populations in the crops were very low. During the early summer, aphids migrated to secondary annual hosts in the crops and aphid populations in the edgegrowth declined. The spatial and temporal distribution patterns of adult syrphids in crop and edgegrowth sites showed a similar seasonal shift. Two main periods of syrphid abundance occurred: the first in the spring and the second in the summer. In the spring, syrphid activity was concentrated in the edgegrowth but in the summer, most syrphids were active in the crops. The mid-season lull in syrphid activity corresponded to the period when aphids were migrating from primary to secondary hosts and overall aphid numbers in both crop and edgegrowth sites were low.

The spatial distribution patterns of individual syrphid species were constrained mainly by their phenology. Spring-occurring species (eg Epistrophe nitidicollis, Episyrphus balteatus and Meligramma cincta) were all more active in the edgegrowth whereas species that occurred mainly in the summer (eg Sphaerophoria scripta, Meliscaeva cinctella) were taken more frequently in the crops. Chandler (1968d) showed that some syrphid species search for oviposition sites at a particular height above the ground and these 'preferred' searching-zones often reflect the time of year when a species occurs. For example, the spring-occurring species Epistrophe eligans prefers to search at a height of 1-2 m above the ground and is thus well adapted for locating aphid colonies on trees and shrubs. In contrast, the summer-occurring species, Sphaerophoria scripta has a preferred searching height of a few centimetres above ground level and so is better adapted for searching out aphid colonies on annual and perennial herbs.

Some syrphid species were more active in some crops than in others. (eg Sph. scripta in wheat, Platycheirus albimanus in potatoes). Such 'preferences' for a particular crop may reflect differences in the suitability of different aphid species as larval food material. Three factors may be important here: 1) the suitability of different aphid species for larval development; 2) the relative ease of capture of different aphid species by syrphid larvae; and 3) the foraging efficiency of syrphid larvae on different aphid host plants.

Studies on feeding in aphidophagous syrphid larvae have concentrated mainly on larval voracity, ie the number of aphids required to complete development (eg Bombosch, 1963; Yakhontov, 1966; Benestad, 1970b;

Tawfik et al, 1974a; Růžička, 1975; Barlow, 1979; Polak, 1980; Cornelius and Barlow, 1980). Růžička (1975) showed that some aphid species are toxic and that the larvae can exert some sort of prey selection to avoid such deadly prey (Růžička, 1976). The larvae of the most common species recorded in the present study are all reported to be polyphagous. However, there is considerable scope for a study relating larval development on different aphid species to the particular aphid species preferred by ovipositing females. A second factor is the efficiency with which syrphid larvae can capture different aphid species. Some aphids (eg Drepanosiphum platanoides (Schrank.) respond to the presence of a predator by walking away (Kennedy, 1966), while other (eg Brevicoryne brassicae) remain sedentary. Again, there has been very little work relating ease of capture of different aphid species by the larvae to oviposition site selection by the adult female. The final factor to consider is the foraging efficiency of syrphid larvae on different aphid host plants. Rotheray (unpubl) has shown that the efficiency with which larvae can locate their aphid prey can vary considerably on different substrates. It seems possible that foraging efficiency is influenced by the spatial complexity of the host plant, although there is little experimental evidence to confirm or reject this hypothesis.

From a biocontrol point of view, the effectiveness of syrphid predators in limiting aphid populations in annual crops is restricted by their phenology. In the present study, aphid populations in the crops built up rapidly when syrphid activity was low (ie in early summer and again in the autumn). However, as soon as syrphid numbers started to increase, a corresponding decline occurred in aphid numbers. A succession of syrphid species occurred in each crop throughout the summer with the most abundant species occurring at different times. Predation by syrphid larvae was a significant factor contributing to the decline of aphid populations in the wheat crop and was responsible for maintaining low aphid populations in both the potato and Brussels sprout crops throughout the summer.

CHAPTER 3

THE EFFECT OF CLIMATE ON THE DIEL PERIODICITY OF SYRPHID FLIGHT

3.1 INTRODUCTION

The timing or periodicity of insect activity is determined by both endogenous and exogenous factors. The endogenous components include innately-controlled rhythms, cycles and phases; the influence of these factors on insect activity will be discussed in more detail in Chapter 5. The exogenous factors are chiefly temperature, light intensity, humidity and wind velocity, and these often act by imposing thresholds which limit the duration of the activity (Corbet, 1966). The purpose of this chapter is to examine the effects of these climatic factors on the diurnal activity patterns of syrphid flies.

Different authors claim different diel periodicities for syrphids. Unimodal patterns for syrphid activity near flowers have been reported with peaks occurring in the early morning (Nielsen, 1966, for *Helophilus*; Stelleman and Meeuse, 1976; Grosser, 1979, for *Metasyrphus corollae* and *Episyrphus balteatus*; Morse, 1981, for *Melanostoma mellinum* and *Toxomerus marginatus*); mid-morning (Kikuchi, 1962, 1965b, for *Eristalis* spp; Kormann, 1972; Maier and Waldbauer, 1979a); or around midday (Lewis and Taylor, 1964, for flight activity in several species; Gilbert, 1981a). Kikuchi (1962, 1965b) reported a unimodal mid-morning activity peak for dominant *Eristalini* species visiting *Chrysanthemum* flowers, but a bimodal, early morning/late afternoon peak for the subdominant Syrphini. Schneider (1958) recorded that *Scaeva pyrastri* adults flew distances of 1-2 km to visit flower fields in mountain valleys but returned nightly to alpine spruce forests. A similar pattern of movement was observed by Rotheray (unpubl) in South Wales: syrphids flew out from their overnight resting sites close to woodland to feed in meadows during the day and then returned to the woods again in the evening.

Differences in reported periodicities are due mainly to different activities being observed or to microclimatic factors. Temperature is often considered to be the most important factor influencing syrphid activity. Syrphids tend to avoid high temperatures and will often rest during the hottest parts of the day (Zimina, 1957b; Bánkowska, 1964; Nielsen, 1966) or move to cooler places (Kikuchi, 1965a; Nielsen, 1966; Maier and Waldbauer, 1979a). Midday rests often explain the bimodal periodicities reported for syrphids feeding at flowers (Zimina, 1957b; Bánkowska, 1964; Willmer, 1983). Maier and Waldbauer (1979a) have described the diurnal activity patterns of six syrphid species living in an Illinois sand area. During the morning flies of both sexes were active at flowers in open areas. As the temperature rose and humidity declined, the flies moved into a nearby oak-hickory forest where hygrothermal conditions were more favourable. In the afternoon, females oviposited in rot-cavities in trees, and males defended mating territories around these larval habitats. On days when the temperature in the forest was less than 29 °C, a single peak of oviposition activity was observed. However, when the temperature exceeded 29 °C, the activity curve became bimodal, the mid-afternoon lull corresponding to the hottest part of the day. Similarly, the oviposition activity of Eristalis tenax has been shown to have a unimodal peak during moderate weather but a bimodal peak in hot weather (Campan, 1973). Bánkowska (1961, 1964) reported that different species have different optimal temperatures for flight activity.

Light intensity is also important: direct sunshine can elevate the body temperature and this effect can override the inhibition of activity by low air temperatures. Katô (1943) demonstrated that E. tenax can forage at air temperatures as low as 5 °C if the sun is shining and the radiant temperature exceeds 15 °C. Kikuchi (1965a) showed that the numbers of E. tenax and E. cerealis visiting Chrysanthemum flowers were directly related to solar radiation.

Relative humidity has also been considered to have a significant influence on syrphid activity (Bânkowska, 1964; Stollar, 1968; Grosser and Klapperstück, 1977), but its effects are difficult to separate from those of temperature.

Grosser and Klapperstück (1977) found that wind speeds of up to 3.67 ms^{-1} did not affect syrphid flight activity. However, Goffe (1951), observed syrphids feeding at flowers in gale-force winds in Scotland. Grosser and Klapperstück (1977) reported that cloud cover, slight mist and light rain did not affect the number of syrphids caught in yellow water traps but constant rain or fog suppressed flight activity.

These patterns may all be explained in terms of the hygothermal balance of the animal. Most insects are considered to be ectotherms relying on passive heat exchange with the environment to determine their body temperature (May, 1979; Casey, 1981; Willmer, 1982a, 1983). Heat exchange consists mainly of radiative heat gain and convective heat loss (May, 1979). Radiative heat gain is influenced by the radiation intensity together with the surface area, absorptivity, colour and pilosity of the insect cuticle; convective heat losses are proportional to some fractional power of the wind velocity (Digby, 1955; Casey, 1981). Willmer (1982b) showed that the heat budgets of different insects affected the timing of their appearance at a resting site. A later study (Willmer, 1983) showed that the pattern of visits to Tilia and Heracleum flowers by various insects, including syrphids, was largely determined by the insects' thermal requirements and the restrictions imposed by avoidance of overheating.

Several insect groups, including syrphids (Heinrich and Pantle, 1975), can regulate their body temperature by behavioural and/or endothermic means (May, 1979). Many authors have noted that syrphids are highly heliotropic and invariably avoid shade. Syrphus adults can elevate their thoracic temperature more than 10 °C above the ambient temperature by a combination of sun-basking and shivering and are therefore able to fly at low temperatures (Heinrich and Pantle, 1975). Endothermic warm-up is energetically very costly in insects of this size and shivering is probably only used as a reserve mechanism enabling the flies to warm up in shade in the early morning; behavioural thermoregulation by sun-basking essentially eliminates the need for endothermy under many conditions. Behavioural and/or endothermic thermoregulation probably accounts for the presence of syrphids at flowers very early in the morning (Nielsen, 1966; Stelleman and Meeuse, 1976; Grosser, 1979; Morse, 1981).

Thermoregulation has been shown to be an important factor in the mating success of male syrphid flies (Heinrich and Pantle, 1975; Gilbert, 1981a). Male Syrphus flies aggregate at 'encounter sites' early in the morning to meet unmated females or females whose store of sperm need replenishing. The males utilize two strategies for catching a mate: either they sit on exposed foliage and fly out at passing insects, or they hover, often in patches of sunlight. Early on in the day, males are confined to the perching strategy because, in energetic terms, it is too costly to hover; instead, they maintain their body temperature at a high level, ready for instant take-off, by endothermic shivering. As the air temperature rises, they switch to the hovering strategy: this is assumed to be advantageous because hoverers can reach a passing female more quickly than can perchers. Body size is important in determining reproductive success: larger males can become flight-active at lower temperatures than small males and the earliest males on the wing probably mate with most of the available females.

Another factor that may influence the activity patterns of syrphid flies is the availability of food resources. Several studies have related insect visiting patterns to the pattern of pollen (Maier and Waldbauer, 1979a) and nectar secretion (Heinrich, 1976, 1981; Corbet et al, 1979a; Corbet and Willmer, 1981). However, while insect activity patterns are directly related to climatic factors, it is also known that nectar production (Shuel, 1955; Percival, 1965) and nectar concentration (Corbet et al, 1979a, b) are dependent on temperature and humidity so that separating the two phenomena is inherently difficult. Willmer (1983) showed that the pattern of visits to Heracleum and Tilia flowers by various insects, including syrphids, was not related to the net amount of nectar available. However, insect activity and nectar concentration were both highly correlated with radiation and this suggested that insects may be foraging for maximally convenient rewards. Most syrphids visited the flowers when the nectar was relatively concentrated, viscous and difficult to imbibe. There is little published data available on the efficiency with which flies can extract and digest nectar solutions of different concentrations. However, flies can feed on very concentrated solutions or dry substances by adopting a spit-and-lap technique but this is wasteful of time and possibly also of fluid. Willmer concluded that the foraging patterns of syrphid flies were determined largely by thermal costs and restrictions, with rewards taking a secondary role.

Several studies have shown that the basic response to environmental factors may be modified by interactions with other species. Kikuchi (1962, 1965b) reported a unimodal, mid-morning activity peak for the dominant Eristalini species visiting Chrysanthemum flowers, but a bimodal, early morning-late afternoon peak for the subdominant Syrphini. When the dominant species were excluded from the flowers, the bimodal periodicity was transformed into a unimodal one with peak activity occurring around midday. Morse (1981) examined the interaction between bumblebees (Bombus spp) and syrphid flies (Melanostoma mellinum and Toxomerus marginatus (Say)) visiting pasture rose (Rosa carolina L.). Dominance interactions were of the order: bumblebees > Melanostoma > Toxomerus. On all occasions when bumblebees approached and landed on flowers where syrphids were already present, the latter were displaced: Toxomerus rapidly returned to the flower once the bee had left but Melanostoma always flew away. By affecting Melanostoma activity in this way, bumblebees inadvertently favoured Toxomerus. When bumblebees were excluded from the flowers, the amount of time spent foraging by Melanostoma increased by 41%, but for Toxomerus, foraging activity increased by only 4%.

These interactions may explain the timing of visits to pasture rose flowers by different insects. Melanostoma adults arrived very early in the morning, often before sunrise; they arrived significantly earlier than both the bumblebees and Toxomerus, their activity peaked earlier and their numbers started to decline as numbers of the other insects started to increase. The early time of arrival by Melanostoma may well be a mechanism to reduce the amount of competitive interference from bumblebees, thereby increasing foraging efficiency. There was no significant difference in the visiting patterns of bumblebees and Toxomerus; the latter could forage more efficiently in the presence of bumblebees than in the presence of Melanostoma alone.

3.2 MATERIALS AND METHODS

3.2.1 Monitoring the diel periodicity of syrphid flight

Syrphid flight activity was monitored using Malaise traps sited in wheat, bean, potato and Brussels sprout crops and in the natural habitats immediately adjacent to these crops (see Chapter 2). Eight traps were operated for 24 h each day and for five days each week from May to October 1980. During June, the traps were sampled four times daily between the hours of sunrise and sunset. The day was divided up into four periods of approximately four hours duration: sunrise - 0900 h, 0900 - 1300 h, 1300 - 1700h, and 1700 h - sunset. All times are GMT unless otherwise stated. During August and early September, three traps were sampled five times daily at 2½ h intervals: sunrise - 0800 h, 0800 h - 1030 h, 1030 - 1300 h, 1300 - 1530 h and 1530 h - sunset. (Times of sunrise and sunset for each week in June, August and September are given in Table B1, Appendix B). On each sampling occasion, care was taken to ensure that all insects caught during the previous period had entered the collecting bottle and were included in the sample.

Analysis of the Malaise trap samples enabled the diurnal flight patterns of some syrphid species to be determined. The abundance of some species fluctuated considerably over a period of several weeks. To avoid the complicating issue of changing phenology, analysis of the diel periodicities of these species was therefore restricted to periods when the population level remained relatively constant. The number of days included in the analysis for a single species ranged from 9-30 days.

3.2.2 Studying the effect of climatic factors on the diel periodicity of syrphid flight

The effect of climate on syrphid activity patterns was studied over seven days in August and September 1980 (dates given in Table 3.1). The number of adult syrphids caught in the Malaise traps at $2\frac{1}{2}$ h intervals between the hours of sunrise and sunset was recorded as described above. The ambient conditions of temperature, relative humidity, radiation, wind velocity, and rainfall at the study site were measured continuously. The maximum, minimum and mean values for each climatic parameter, together with the variance were calculated for each $2\frac{1}{2}$ h period; the mean values are tabulated in Tables B2 - B8 (Appendix B).

3.2.3 Measurement of climatic factors

Temperature

Temperature was measured using maximum and minimum thermometers at a height of 1 m above the ground. The thermometers were enclosed within a louvered wooden shelter (standard Stevenson's screen) to protect them from direct solar and reflected radiation. The accuracy of the thermometer readings was ± 0.5 °C.

Humidity

Relative humidity was measured continously by a Meteorological Office hair hygrograph. The accuracy of the instrumentation was ± 5%

Radiation

Three measures of radiation were made:

1) Total solar radiation

Total incoming solar radiation was measured by a thermopile pyranometer (Kipp type).

2) Net radiation flux at the soil surface

The net flux of radiant energy into and out of the soil was measured by disc-shaped thermal flux plates. A differential thermopile connects the top and bottom parts of the sensing plates and determines the temperature drop across a known thermal impedance. Syrphids are often observed basking in the sun on the ground or on foliage: the net radiation flux at the soil surface gives some indication of the radiant energy perceived by a syrphid resting on the ground.

3) Net radiation flux at a height of 1 m above the ground

The net flux of incoming and outgoing radiation at a height of 1 m above the ground was measured by a Meteorological Office net pyrradiometer Mk 8. The sensing element is essentially a coiled wire winding formed from constanton wire with one half of each turn copper-plated, so forming two diametrically-opposite sets of thermojunctions. This measure of radiation gives some indication of the net radiant energy perceived by a syrphid perched at a height of 1 m above the ground.

Wind velocity

The wind velocity at a height of 2 m above the ground was measured by a three cup anemometer. The rate of rotation of the cups is a quadratic function of the wind velocity and of certain geometric design features of the cups.

Rainfall

The amount and duration of rainfall during each 2½ h period was measured using a tilting siphon rain gauge.

The instruments measuring temperature, humidity and rainfall were fitted with pen recorders operating on a daily clock. Wind velocity and radiation readings were recorded at one-minute intervals on a Kent Mark 3M/MVM 12 point millivolt recorder.

3.3 RESULTS AND DISCUSSION

3.3.1 Diel periodicity of syrphid flight

The relationship between time of day and syrphid activity for seven days in August and September 1980 is illustrated in Figure 3.1. All species are considered together. The graph indicates a basic circadian pattern of activity with fly numbers low in the early morning. Maximum activity occurred around midday and in the early afternoon with numbers declining again during late afternoon. Chi-square analysis confirmed a highly significant difference in fly numbers at different times of day ($\chi^2 = 57.40$, 1 df, $p < 0.001$). The graph also shows that the number of flies caught during a particular time period varied considerably on different days and this suggested that time of day alone was not a good predictor of net activity.

Table 3.1 compares the number of male and female flies caught at different times of day. There was no significant difference in the activity patterns of the two sexes ($\chi^2 = 2.06$, 1 df, ns). More females were caught in the traps than males overall ($\chi^2 = 97.34$, 1 df, $p < 0.001$). Possible reasons for this female-bias in the Malaise trap catches have already been discussed in section 2.4.4.

The flight periodicities of some of the more abundant aphidophagous species are illustrated in Figures 3.2 - 3.9. Most species first become active after 0800 h. The activity patterns of Sphaerophoria scripta (Figure 3.2) and Syrphus ribesii (Figure 3.3) both conformed to the general pattern described above. Individuals of both species first become active after 0800 h, but only appreciably so after about 1030 h. Maximum activity of S. ribesii occurred between 1030 and 1300 h, whereas Sph. scripta was mainly active between 1300 and 1530 h. There was a rapid decline in the activity of both species during the late afternoon. The flight periods of Platycheirus peltatus (Figure 3.4) and P. angustatus (Figure 3.5) were more extended with activity occurring throughout the day after 0800 h. Again, both species showed peak activity in the late morning/early afternoon. A few individuals of P. albimanus (Figure 3.6) were caught

Figure 3.1: The relationship between time of day and syrphid activity

The figure shows the average number of flies trapped at different times of day during a seven-day period in August and September 1980 (with standard error bars)

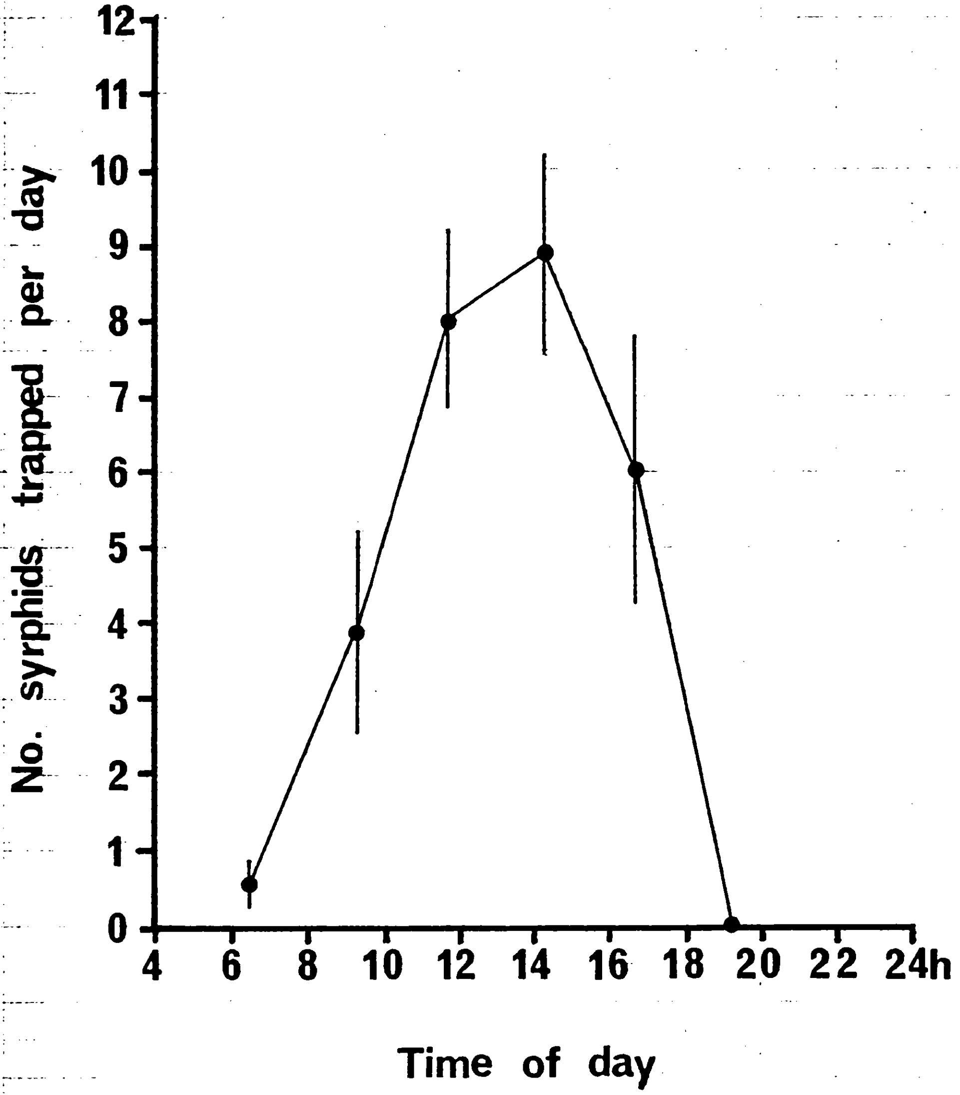
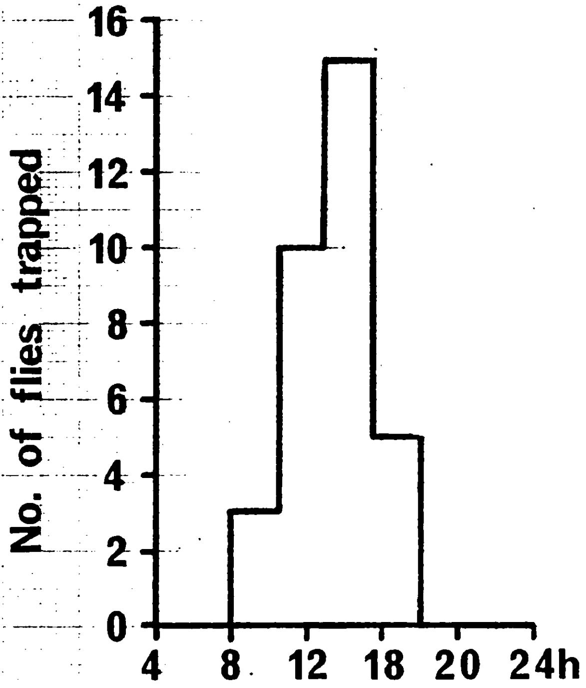

No. syrphids trapped per day
12
11
10
9
8
7
6
5
4
3
2
1
0
4
6
8
10
12
14
16
18
20
22
24h
Time of day

Figure 3.2: Diel flight periodicity of Sphaerophoria scripta

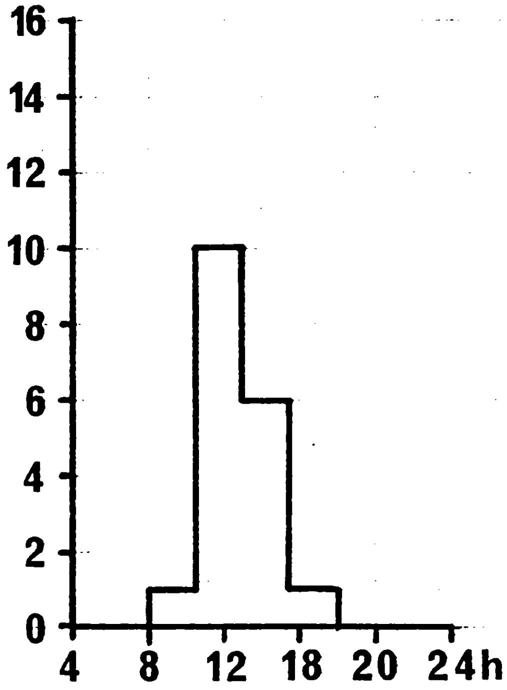
Figure 3.3: Diel flight periodicity of Syrphus ribesii

Figure 3.4: Diel flight periodicity of Platycheirus peltatus

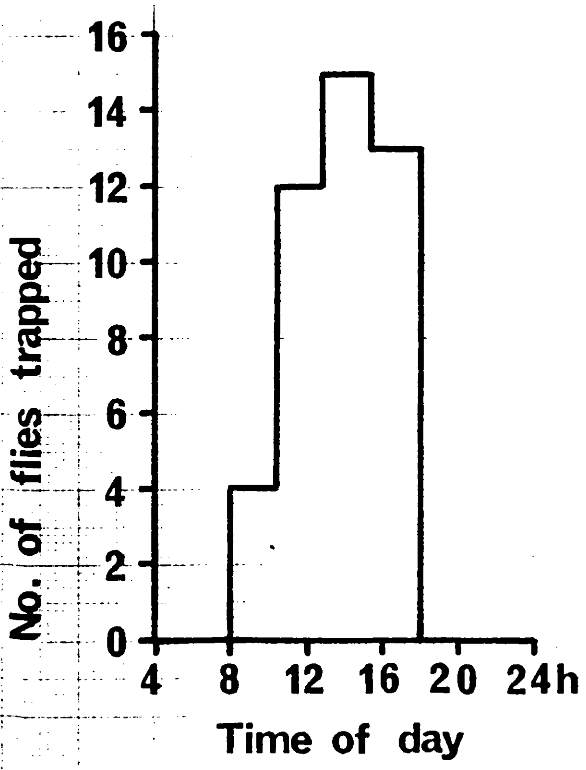
Figure 3.5: Diel flight periodicity of Platycheirus angustatus



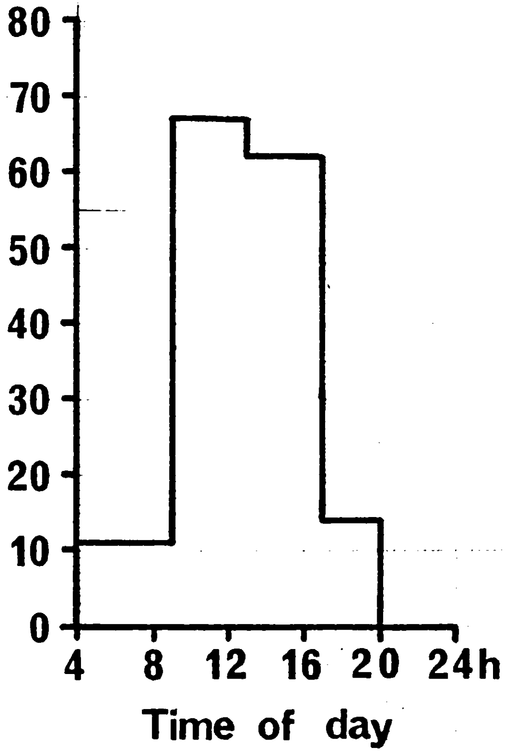
Sph. scripta



S. ribesii



P. peltatus



P. angustatus

Figure 3.6: Diel flight periodicity of Platycheirus albimanus

Figure 3.7: Diel flight periodicity of Episyrphus balteatus

Figure 3.8: Diel flight periodicity of Melanostoma scalare

Figure 3.9: Diel flight periodicity of Melanostoma mellinum

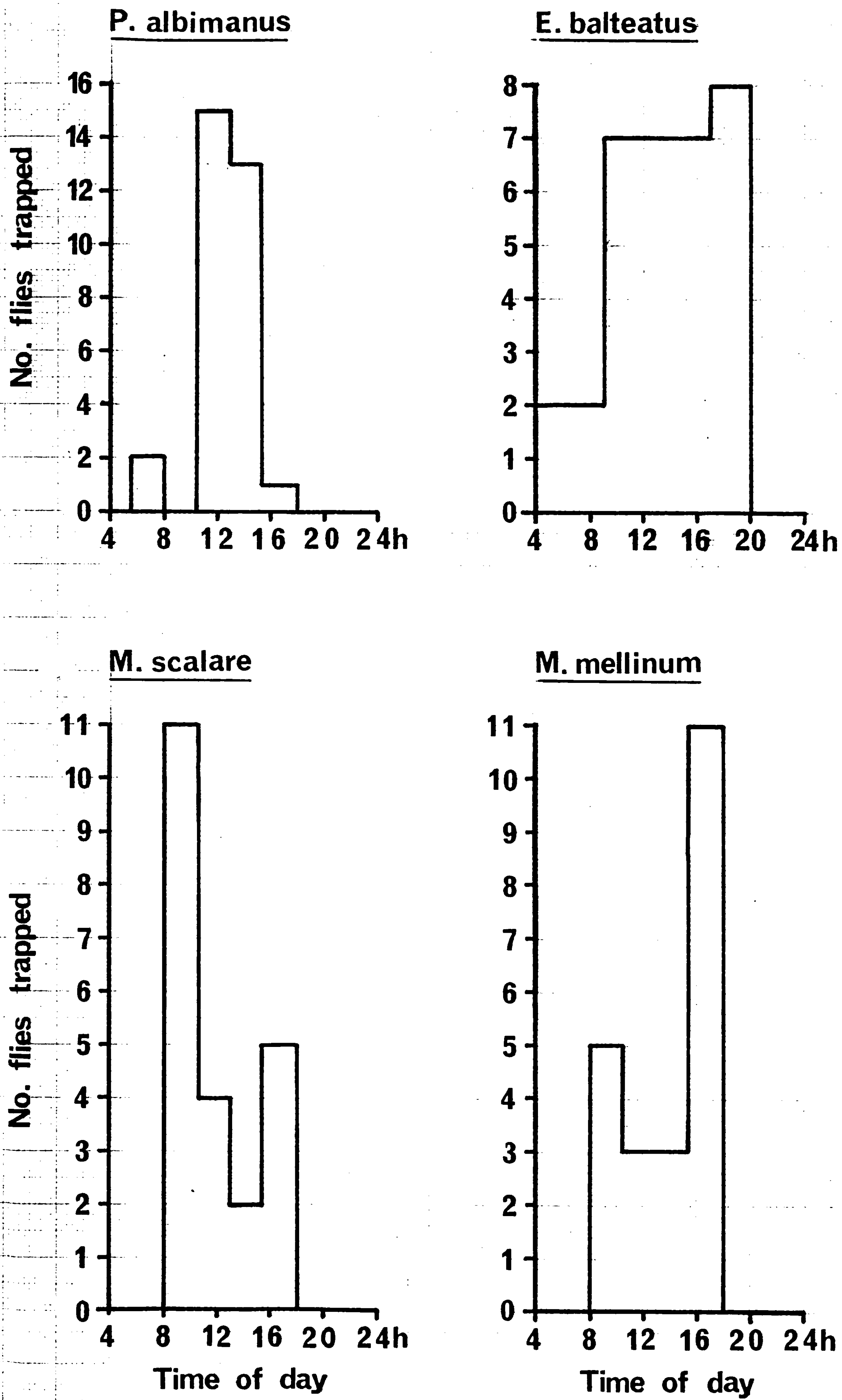

P. albimanus
No. flies trapped
0
2
4
6
8
10
12
14
16
4
8
12
16
20
24h
E. balteatus
0
1
2
3
4
5
6
7
8
4
8
12
16
20
24h
M. scalare
No. flies trapped
0
1
2
3
4
5
6
7
8
9
10
11
4
8
12
16
20
24h
Time of day
M. mellinum
0
1
2
3
4
5
6
7
8
9
10
11
4
8
12
16
20
24h
Time of day

Table 3.1: The number of male and female flies caught at different times of the day during a seven day period

Date	Number of flies caught at different times of day									
	Sunrise -0800		0800-1030		1030-1300		1300-1530		1530-Sunset	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
25.8.80	-	-	-	4	2	9	-	5	-	6
26.8.80	-	1	2	8	2	9	4	7	-	12
27.8.80	-	2	-	-	1	4	3	11	1	11
28.8.80	-	-	-	2	-	7	2	7	2	3
4.9.80	-	-	-	3	-	3	-	9	-	1
5.9.80	-	-	-	1	1	9	1	3	-	1
6.9.80	-	-	2	5	2	7	1	9	1	4
Total	-	3	4	23	8	48	11	51	4	38

before 0800 h, but maximum activity for this species occurred around midday. Episyrphus balteatus (Figure 3.7) usually became active after 0900 h and remained so throughout the day; this species showed no distinct peak in activity during the day. After 0800 h the two Melanostoma species were active throughout the day, although M. scalare (Figure 3.8) occurred principally in the early morning between 0800 h and 1030 h, whilst M. mellinum (Figure 3.9) was most active in the late afternoon. Due to the low numbers of males caught, it was not possible to statistically compare the diurnal flight patterns of males and females of individual syrphid species.

3.3.2 Effect of climatic factors on the diel periodicity of syrphid flight

Figures 3.10 and 3.11 compare syrphid activity patterns on a cool dull day (5 September) with a warm dry day of steady high radiation (26 August). These two days are representative of the other days studied. It is clear that prevailing climatic conditions

Figure 3.10: Diurnal activity patterns of syrphid flies on September 5 (dull) together with the ambient climatic conditions

a) The number of flies trapped at different times of day

b) Ambient conditions of temperature and relative humidity at different times of day

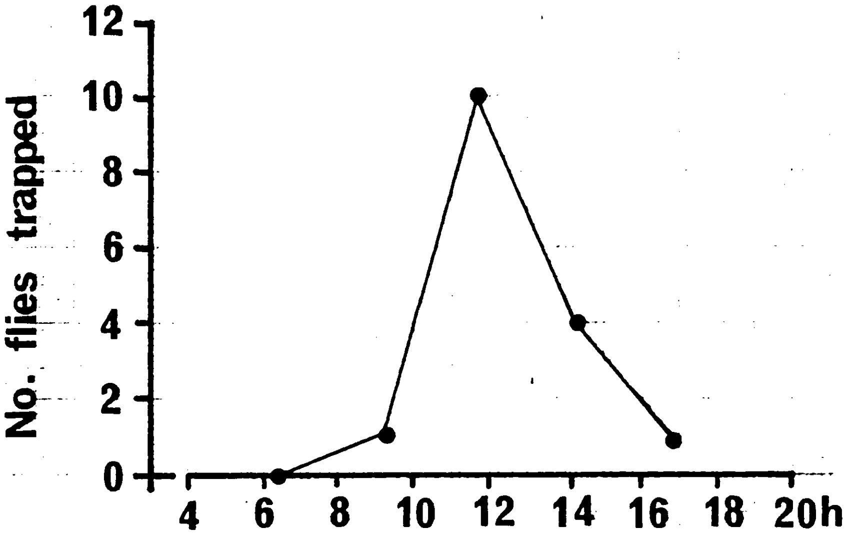
●——● Temperature
○——○ Relative humidity

c) Ambient conditions of radiation, wind velocity and rainfall at different times of day

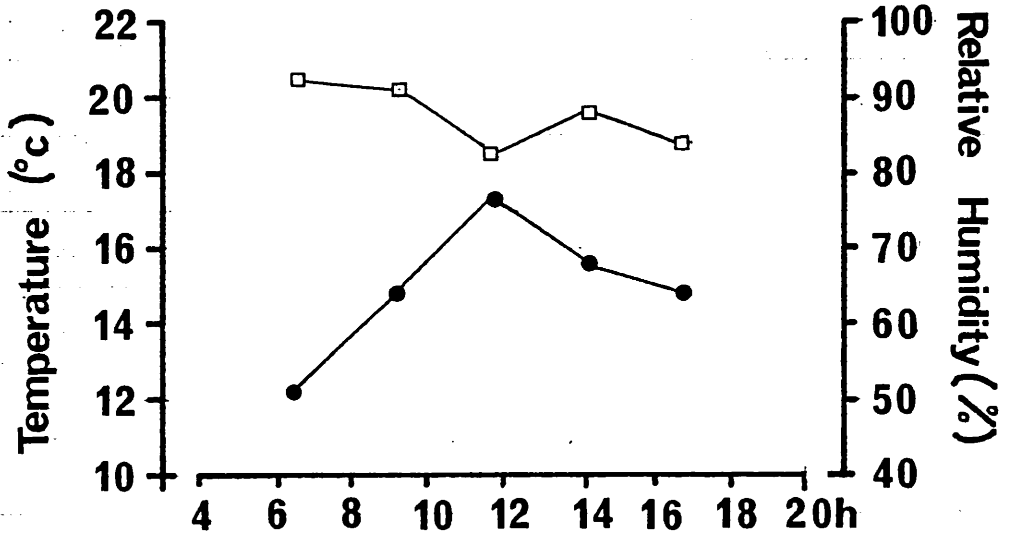
▲——▲ Radiation
■——■ Wind velocity
△——△ Rainfall

September 5

a)



b)



c)

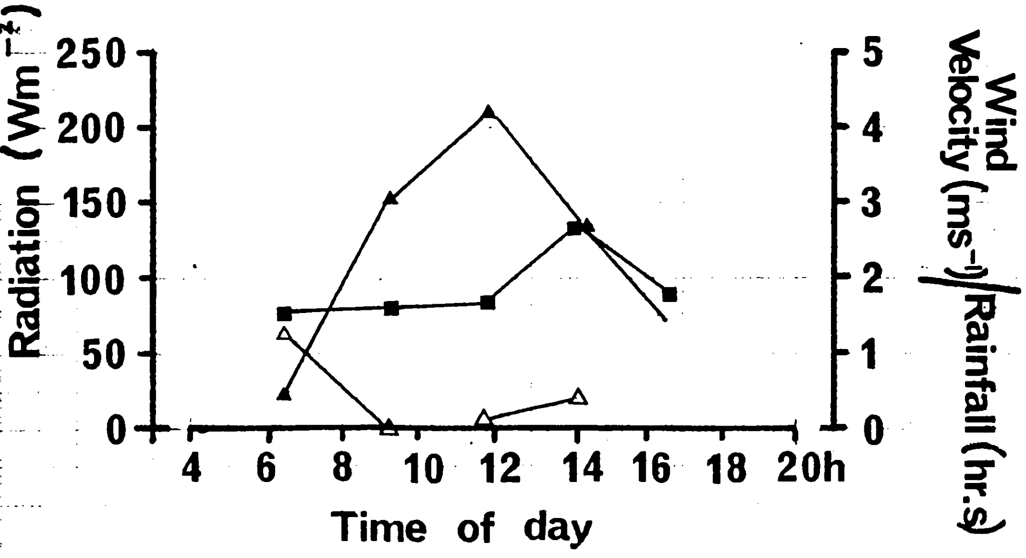


Figure 3.11: Diurnal activity patterns of syrphid flies on August 26 (sunny) together with the ambient climatic conditions

a) The number of flies trapped at different times of day

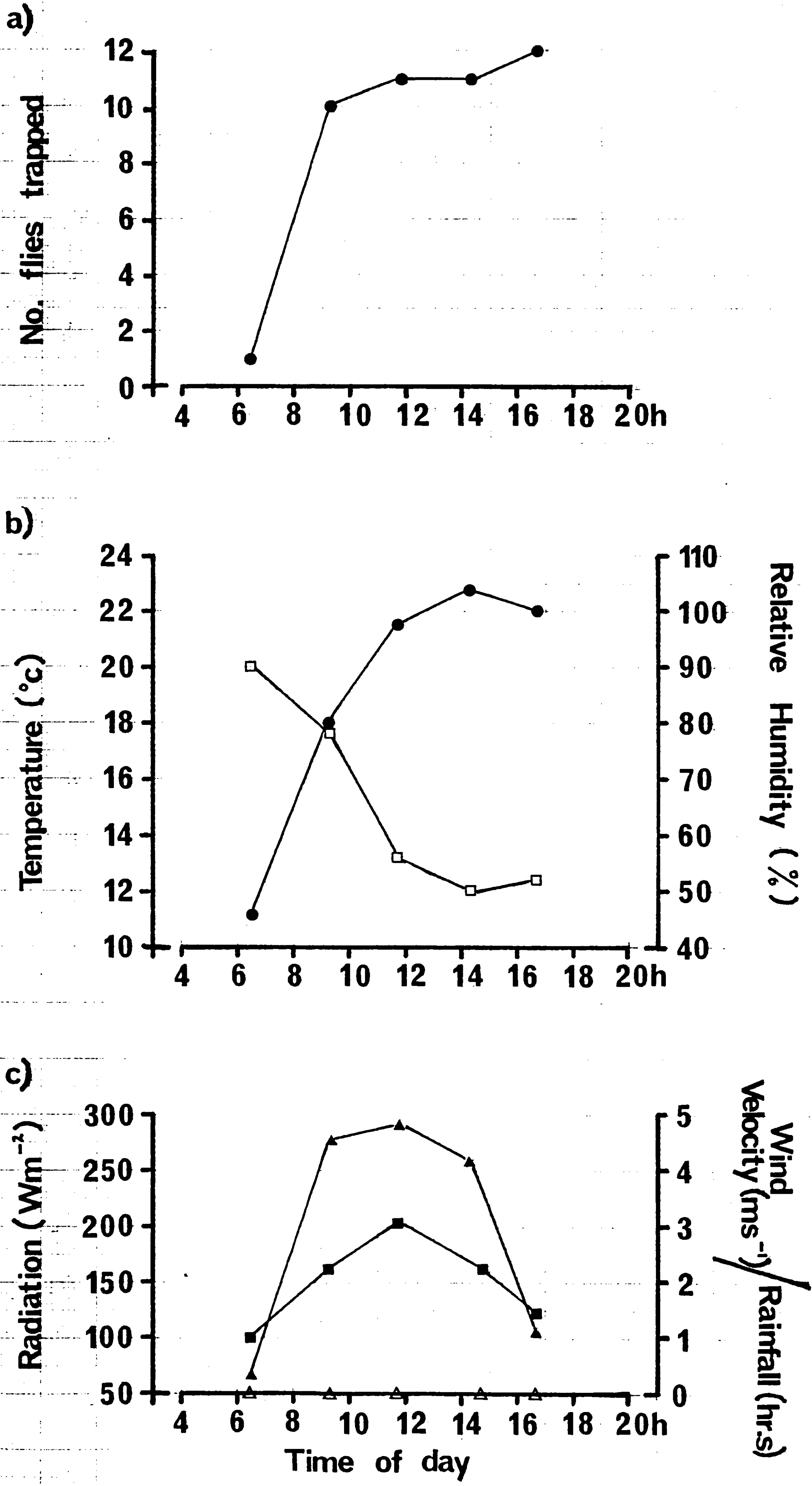
b) Ambient conditions of temperature and relative humidity at different times of day

●——● Temperature
○——○ Relative humidity

c) Ambient conditions of radiation, wind velocity and rainfall at different times of day

▲——▲ Radiation
■——■ Wind velocity
△——△ Rainfall

August 26


a)
No. flies trapped
0
2
4
6
8
10
12
4
6
8
10
12
14
16
18
20h
b)
Temperature (°c)
10
12
14
16
18
20
22
24
Relative Humidity (%)
40
50
60
70
80
90
100
110
4
6
8
10
12
14
16
18
20h
c)
Radiation (Wm⁻²)
50
100
150
200
250
300
Wind Velocity (ms⁻¹)/Rainfall (hr.s)
0
1
2
3
4
5
4
6
8
10
12
14
16
18
20h
Time of day

influence both the duration and amplitude of syrphid flight activity: more syrphids were active on warm sunny days and for longer periods of time than on cool overcast days. Thus both climatic and temporal patterns interact to determine net activity.

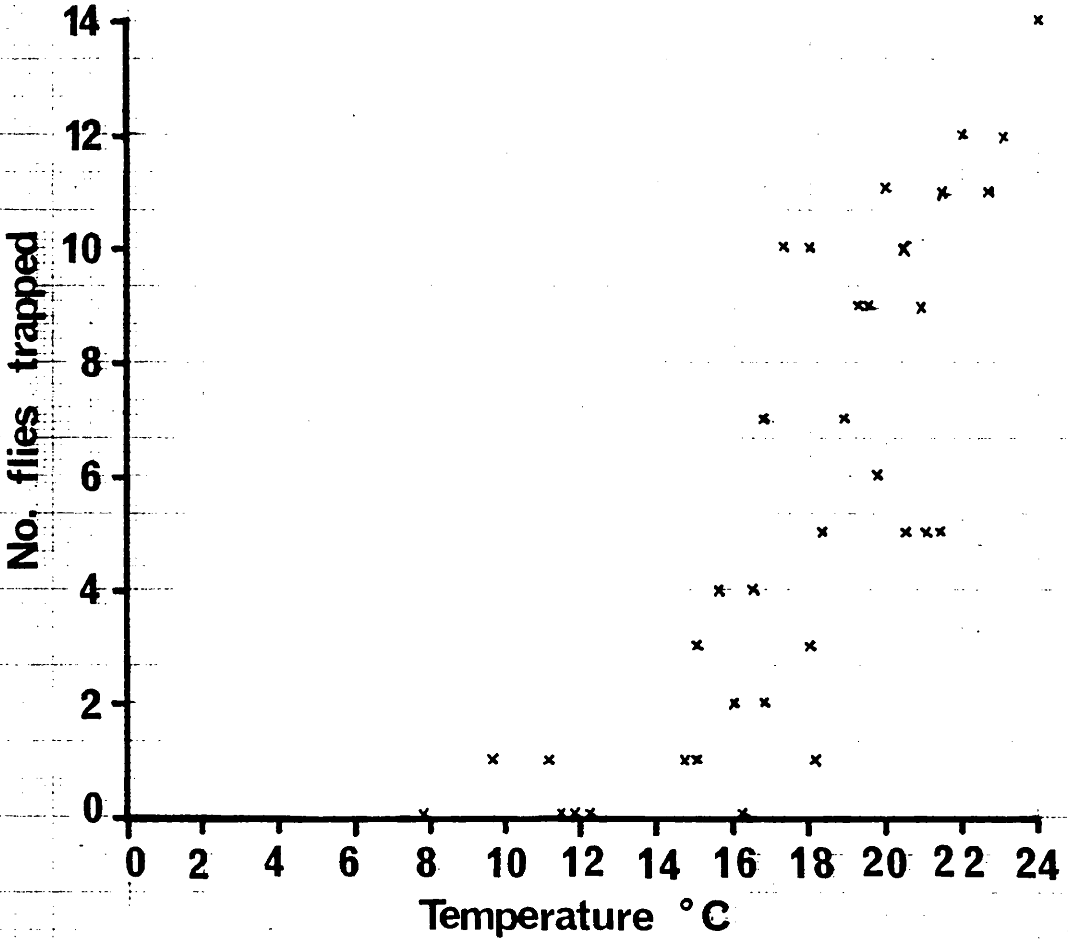
The relationship between temperature and syrphid numbers is illustrated in Figure 3.12. The results for seven days have been pooled. Fly numbers increased steadily from an initial temperature threshold of approximately 15 °C. There was no evidence of an upper critical temperature above which flight activity was inhibited (although presumably such an effect would occur if ambient temperatures became sufficiently high). Syrphid numbers showed similar characteristics in relation to radiation (Figure 3.13), wind velocity (Figure 3.14) and, inversely, to relative humidity (Figure 3.15). Wind velocities of up to 3.06 ms^{-1} did not appear to adversely affect syrphid activity. However, the wind velocity during each $2\frac{1}{2}$ h period could be highly variable and it is possible that syrphids fly between 'gusts'. The relationship between rainfall (hours) and syrphid numbers is shown in Figure 3.16. There was very little rain during the study period. However, the graph does indicate that prolonged periods of rainfall depress syrphid activity.

Linear regression analysis was initially applied to the pooled data to determine the relationship between individual climatic factors and the number of adult syrphids caught in the traps. The results are presented in Table 3.2. Syrphid numbers were significantly correlated with temperature, relative humidity, radiation and wind velocity. Of the three measures of radiation, syrphid activity was most highly correlated with the net radiation flux at the soil surface. However, it is difficult to determine the precise conditions which an insect perceives or responds to: temperature, humidity and radiation were themselves highly correlated (Table 3.3).

Multiple linear regression analysis was applied to the pooled data, using all combinations of variables. The model shown in Table 3.4

Figure 3.12: The relationship between temperature and syrphid activity

Figure 3.13: The relationship between radiation and syrphid activity


No. flies trapped
0
2
4
6
8
10
12
14
0 2 4 6 8 10 12 14 16 18 20 22 24
Temperature °C

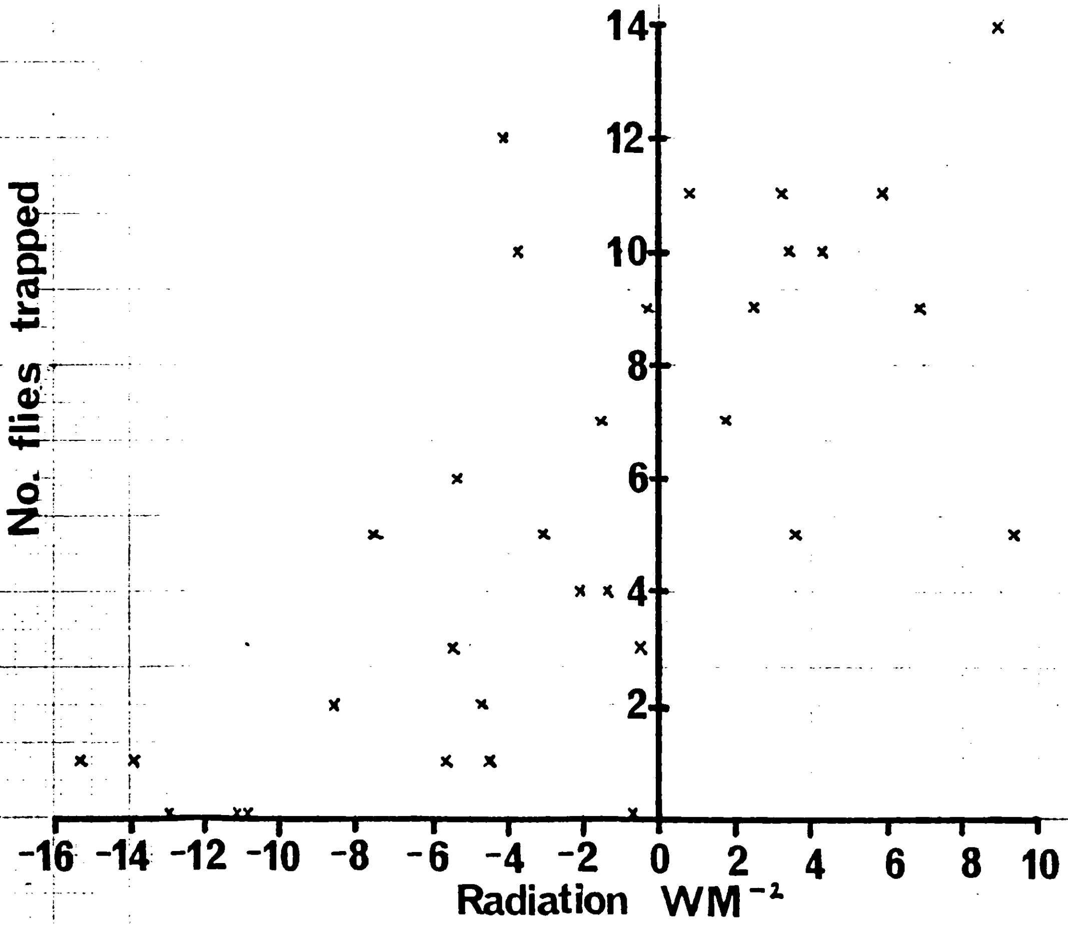
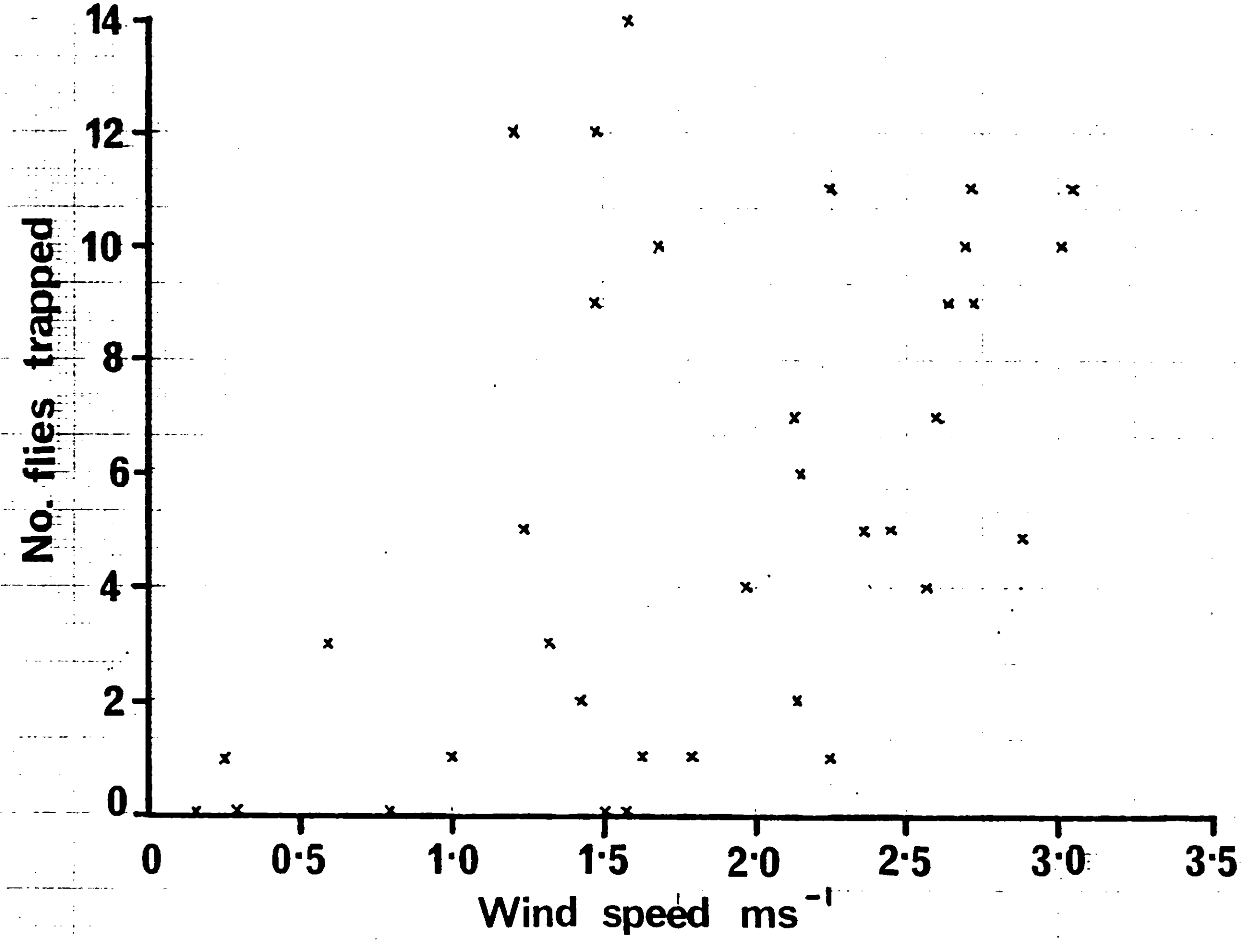

No. flies trapped
2
4
6
8
10
12
14
-16 -14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10
Radiation WM⁻²

Figure 3.14: The relationship between wind speed and syrphid activity

Figure 3.15: The relationship between relative humidity and syrphid activity


No. flies trapped
14
12
10
8
6
4
2
0
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
Wind speed ms⁻¹

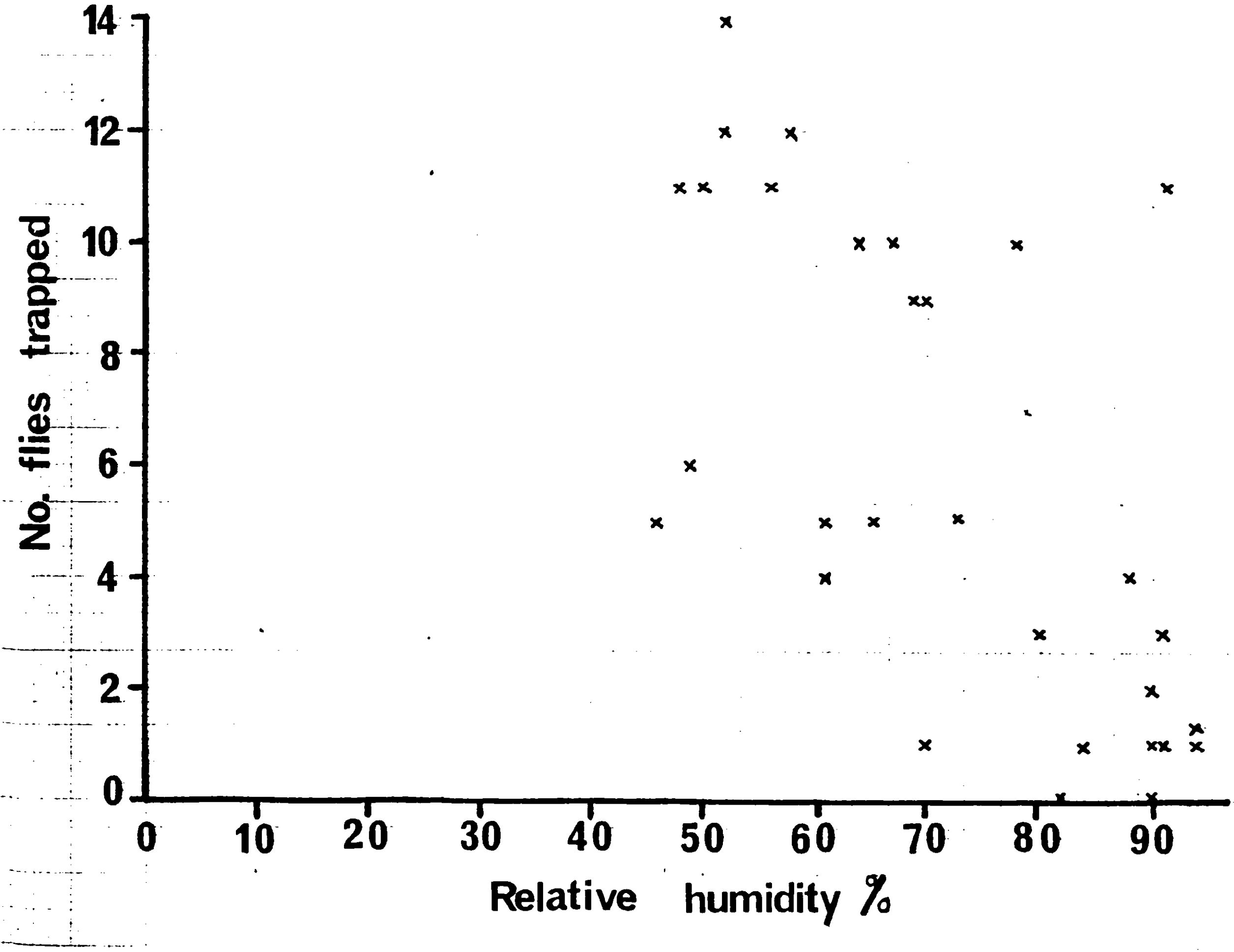

No. flies trapped
14
12
10
8
6
4
2
0
0
10
20
30
40
50
60
70
80
90
Relative humidity %

Figure 3.16: <u>The relationship between rainfall (hours) and syrphid activity</u>

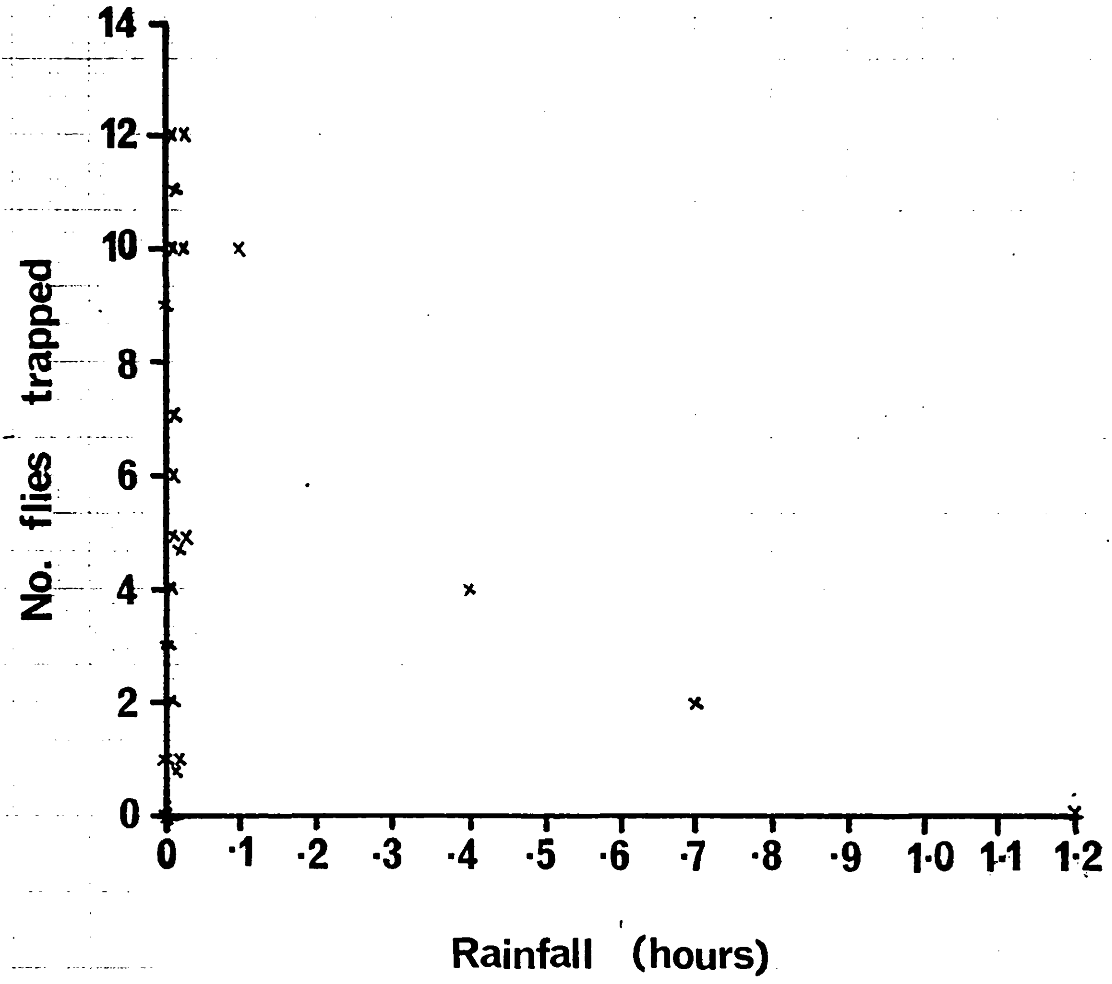

14
12
10
8
6
4
2
0
No. flies trapped
0
·1
·2
·3
·4
·5
·6
·7
·8
·9
1·0
1·1
1·2
Rainfall (hours)

Table 3.2: Linear Regression Analysis of the relationship between different climatic factors and the number of adult syrphids caught in Malaise traps

Factor	r	Regression Equation	F-value
Temperature	0.80	$Y = -10.0 + 0.89X$	62.22 ***
Relative humidity	-0.70	$Y = 19.9 - 0.20X$	34.52 ***
Net radiation flux at soil surface	0.71	$Y = 6.70 + 0.47X$	35.02 ***
Net radiation flux 1 m above ground	0.56	$Y = -35.7 + 0.11X$	16.33 ***
Total incoming solar radiation	0.57	$Y = 1.20 + 0.02X$	17.70 ***
Wind velocity	0.47	$Y = 0.62 + 2.69X$	10.44 **
Rainfall	-0.19	$Y = 5.78 - 4.70X$	2.35 ns

*** $p < 0.001$

** $p < 0.01$

resulted in the best fit of the data and accounted for 61.8% of the variance; each term was fitted in the order shown in the table. Temperature was shown to be the most important climatic factor influencing syrphid activity and accounted for a significant amount of the variance. The significance of individuals terms depends on the foregoing terms in the model. Thus, radiation and relative humidity would have been more significant had they not been so highly correlated with temperature.

Table 3.3: Correlation matrix for different climatic factors

	Temperature	Relative humidity	Net radiation flux at soil surface	Net radiation flux 1 m above ground	Total incoming solar radiation	Wind velocity	Rainfall
Temperature	1.00						
Relative humidity	-0.82	1.00					
Net radiation flux at soil surface	0.82	-0.65	1.00				
Net radiation flux 1 m above ground	0.53	-0.51	0.84	1.00			
Total incoming solar radiation	0.56	-0.62	0.82	0.95	1.00		
Wind velocity	0.58	-0.48	0.55	0.44	0.31	1.00	
Rainfall	-0.23	0.32	-0.20	-0.34	-0.31	0.41	1.00

Table 3.4: Multiple Linear Regression Analysis of the relationship between climatic factors and the number of syrphids caught in Malaise traps

The regression equation is:

$$Y = -42.1 + 0.89X_1 - 0.02X_2 - 0.21X_3 + 0.09X_4 + 0.01X_5 - 0.09X_6 + 0.62X_7$$

where Y = Number of syrphids captured in Malaise traps
X_1 = Temperature (°C)
X_2 = Relative humidity (%)
X_3 = Net radiation flux at soil surface (Wm^{-2})
X_4 = Net radiation flux at 1 m above ground (Wm^{-2})
X_5 = Total incoming solar radiation (Wm^{-2})
X_6 = Wind velocity (ms^{-1})
X_7 = Rainfall (hours)

The Regression Components

Factor	Coefficient	Standard deviation (SD) of coefficient	T-ratio = Coefficient/SD
	-42.14	± 33.16	-1.27
Temperature	0.89	± 0.39	2.29
Relative humidity	- 0.02	± 0.07	0.38
Net radiation flux at soil surface	- 0.21	± 0.27	-0.78
Net radiation flux 1 m above ground	0.09	± 0.09	1.05
Total incoming solar radiation	- 0.01	± 0.02	-0.23
Wind velocity	- 0.09	± 0.80	-0.11
Rainfall	0.62	± 2.40	0.26

The standard deviation of Y about the regression line is ± 2.69 with 27 degrees of freedom

Analysis of Variance

Source of variation	df	SS	MS	F-ratio
Regression	7	449.29	64.19	8.87 ***
Residual	27	195.39	7.24	
Total	34	644.69		

*** $p < 0.001$

Table 3.4: continued

Further Analysis of Variance

Source of variation	df	SS	MS	F-ratio
Regression	7	449.29	64.19	8.87 ***
Temperature	1	421.23	421.23	58.21 ***
Relative humidity	1	5.94	5.94	0.89 ns
Net radiation flux at soil surface	1	6.44	6.44	0.89 ns
Net radiation flux 1 m above ground	1	8.03	8.03	1.11 ns
Total incoming solar radiation	1	7.16	7.16	0.99 ns
Wind velocity	1	0.01	0.01	0.002 ns
Rainfall	1	0.49	0.49	0.07 ns

3.3.3 Temperature thresholds for flight activity

The most important factor influencing the amplitude of flight activity in heterogenous syrphid populations was shown to be temperature. If it is assumed that each species has a temperature threshold above which it becomes flight-active, it should be possible to predict the appearance of a species from a knowledge of the ambient air temperature.

In Figures 3.17 - 3.22 the data have been sorted according to temperature and the percentage of occasions when flight occurred at t °C is shown. It is clear that different species have different temperature thresholds, above which they become active. Platycheirus peltatus usually became active once the ambient air temperature had exceeded 13 °C (Figure 3.17). A few individuals of P. albimanus were recorded at 11 °C, but this species was mainly active at temperatures above 15 °C (Figure 3.18). Episyrphus balteatus was flight-active at temperatures as low as 9 °C (Figure 3.19). Four of the smallest species recorded: Melanostoma mellinum, M. scalare

Sphaerophoria scripta and *P. angustatus* were all active at temperatures above 15 °C (Figures 3.20 - 3.23).

There was a crude correlation between threshold temperature and body size with the larger species (eg *E. balteatus*) active at lower temperatures than the smaller species (eg *Melanostoma* spp). An inexplicable exception to this general rule was *Syrphus ribesii* which was only recorded as flight-active at temperatures exceeding 17 °C (Figure 3.24). This anomalous result may be due to the low number of individuals caught during the seven-day study period and on which this temperature threshold was based.

Strictly speaking, the threshold temperatures should be calculated using the maximum (for lower threshold) and minimum (for upper threshold) temperature values for each 2½ h period. However, when the number of insects captured is relatively low and the length of each time-period is relatively long, the probability of an individual insect becoming active in response to an instantaneous maximum or minimum temperature value is small and so it is permissible to use the mean value for each period (Taylor, 1963).

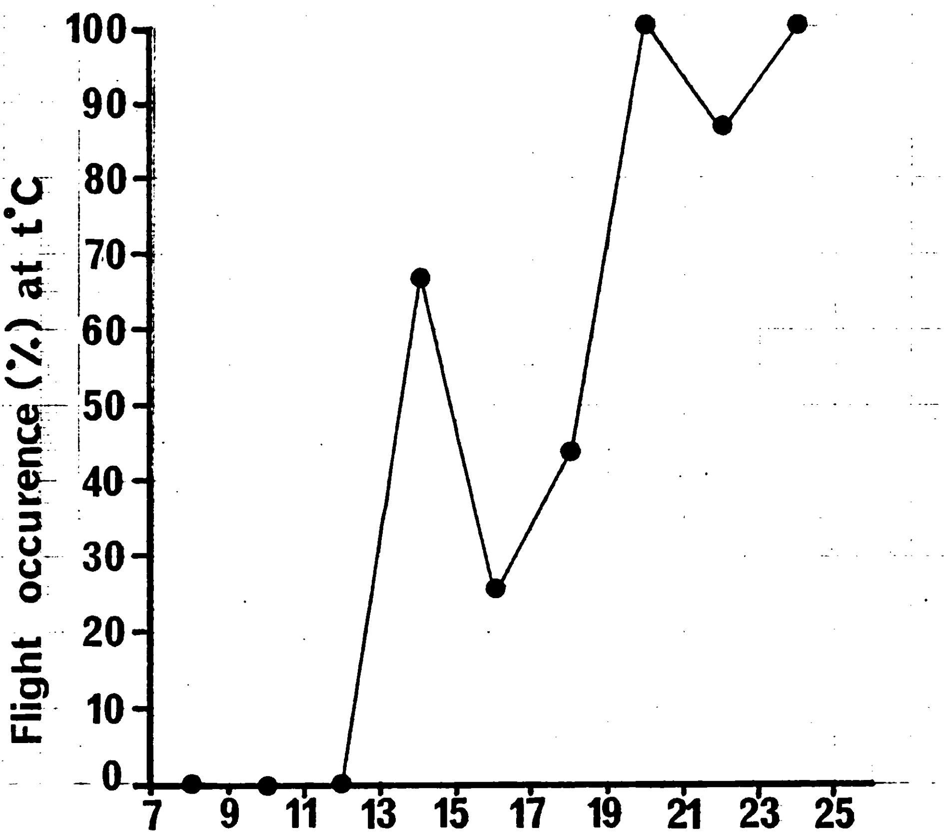
The accuracy of these threshold temperatures depends on the sensitivity of the trapping technique. The Malaise trap has been shown to act selectively: species that tend to fly low down in the vegetation are more likely to enter the trap than species that normally fly some distance above the ground (see section 2.4.8). Thus the temperature thresholds determined for species such as *Sphaerophoria scripta*, *Platycheirus* and *Melanostoma* spp are probably more reliable than those for *Episyrphus balteatus* and *Syrphus ribesii*.

Figure 3.17: The relationship between temperature and flight activity in Platycheirus peltatus

The Y-axis shows the percentage of occasions on which flight activity was recorded at t °C

Figure 3.18: The relationship between temperature and flight activity in Platycheirus albimanus

P. peltatus



P. albimanus

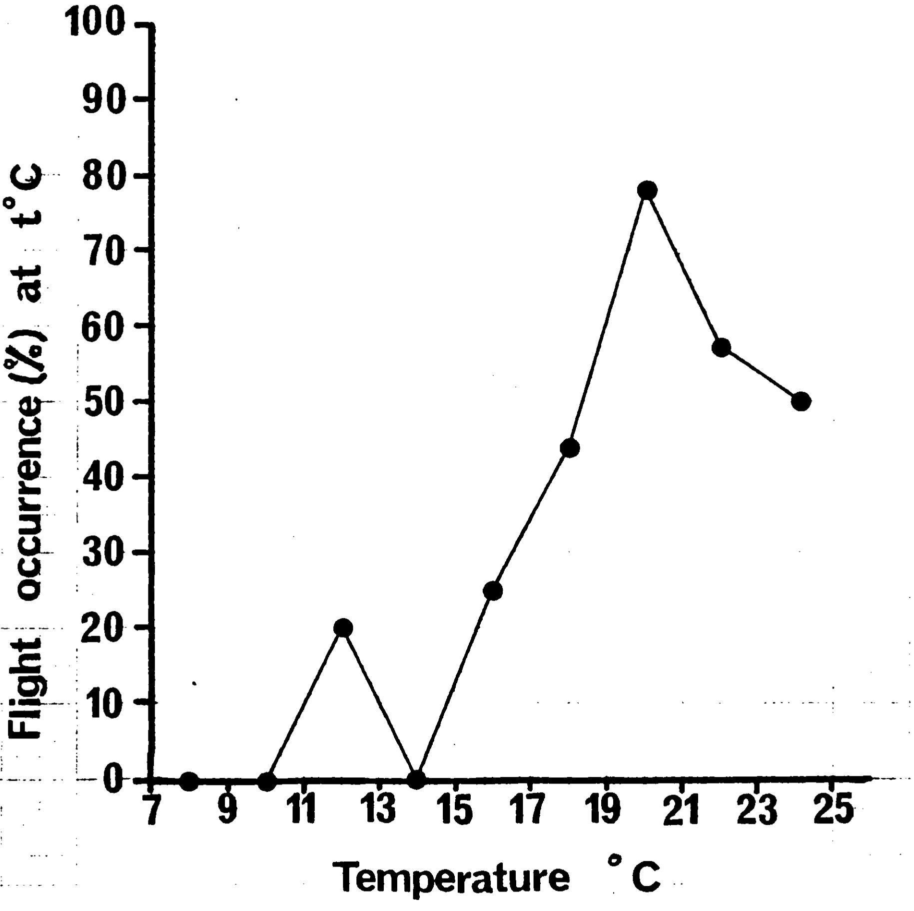
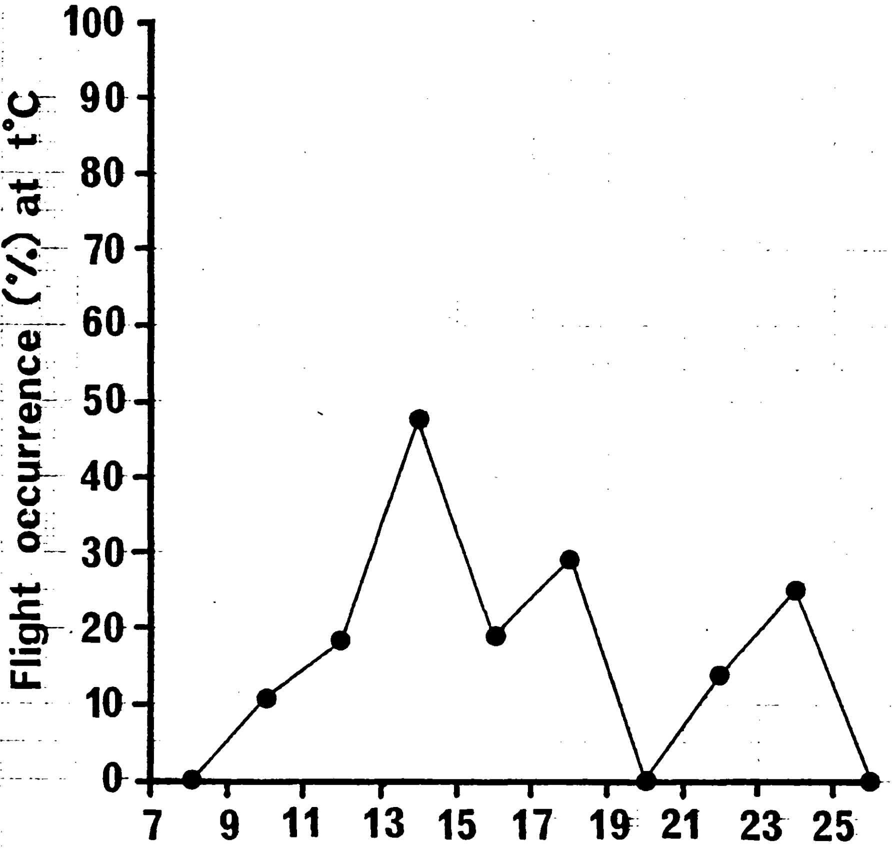


Figure 3.19: The relationship between temperature and flight activity in Episyrphus balteatus

Figure 3.20: The relationship between temperature and flight activity in Melanostoma mellinum

E. balteatus



M. mellinum

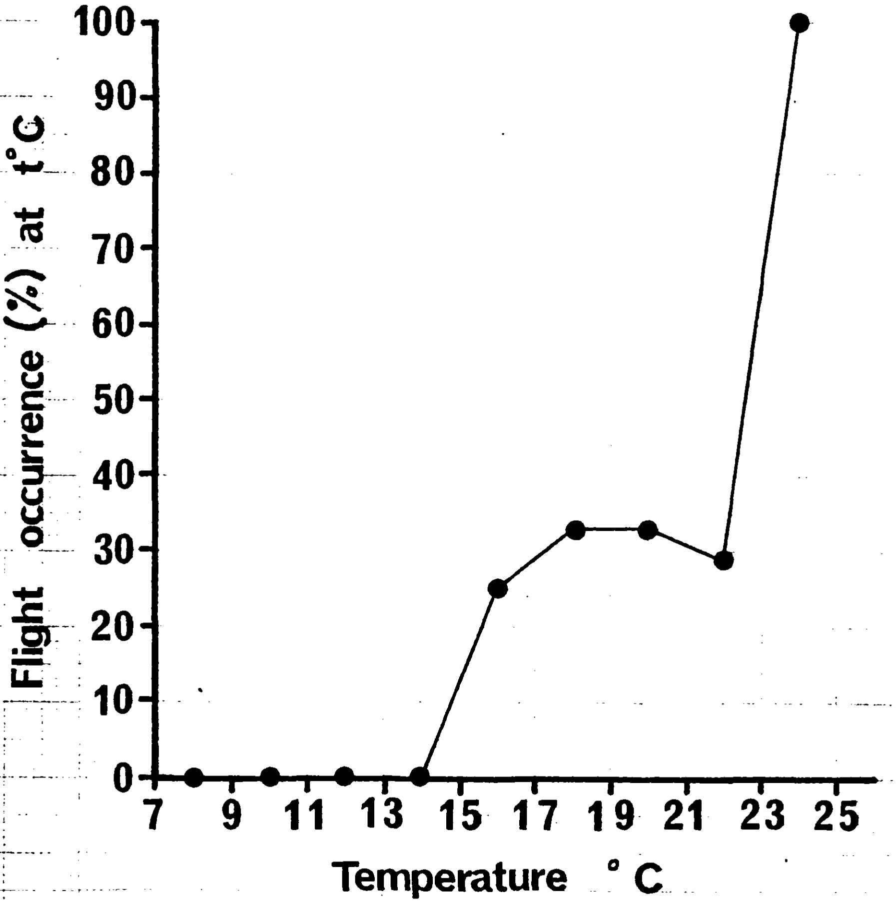
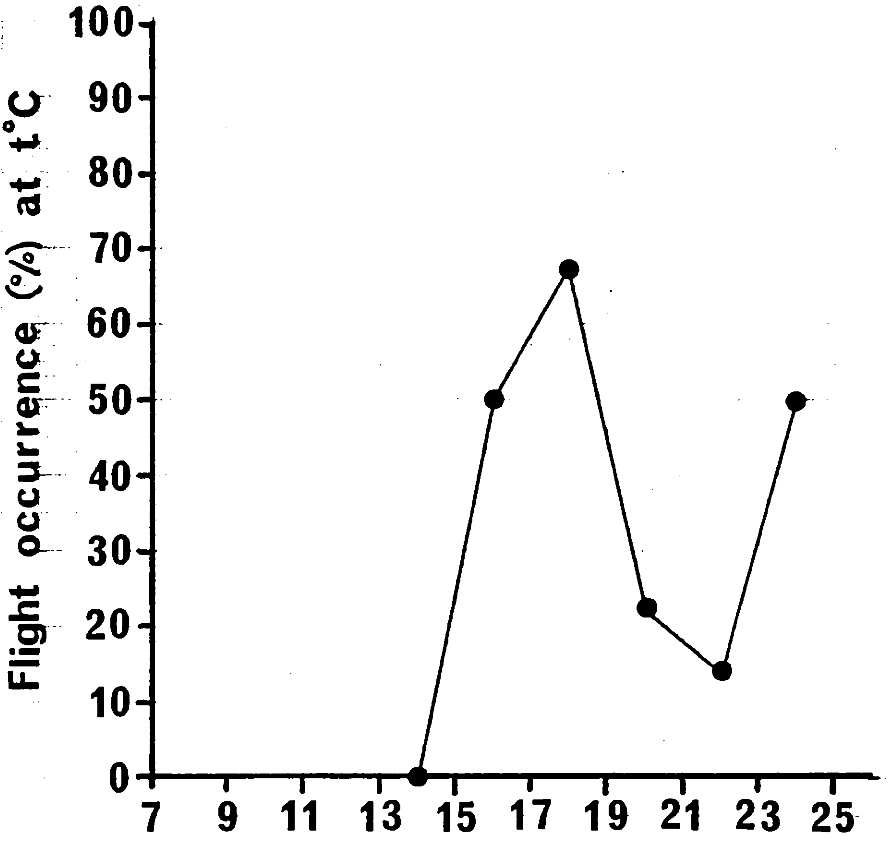


Figure 3.21: The relationship between temperature and flight activity in Melanostoma scalare

Figure 3.22: The relationship between temperature and flight activity in Sphaerophoria scripta

M. scalare



Sph. scripta

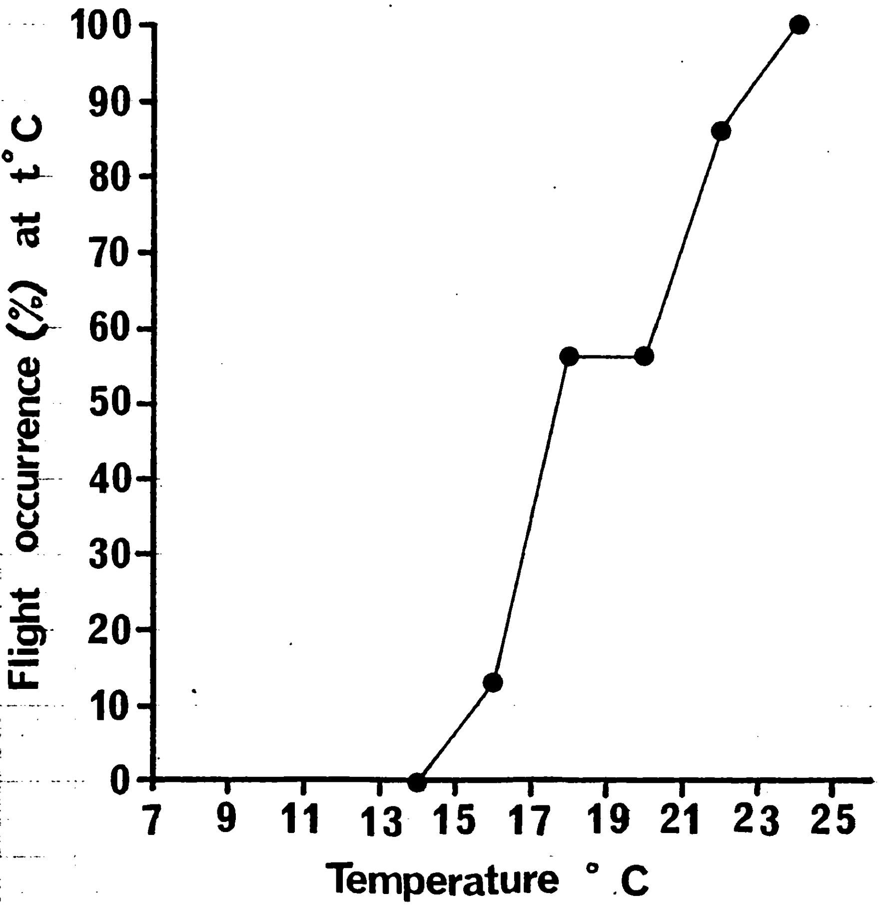
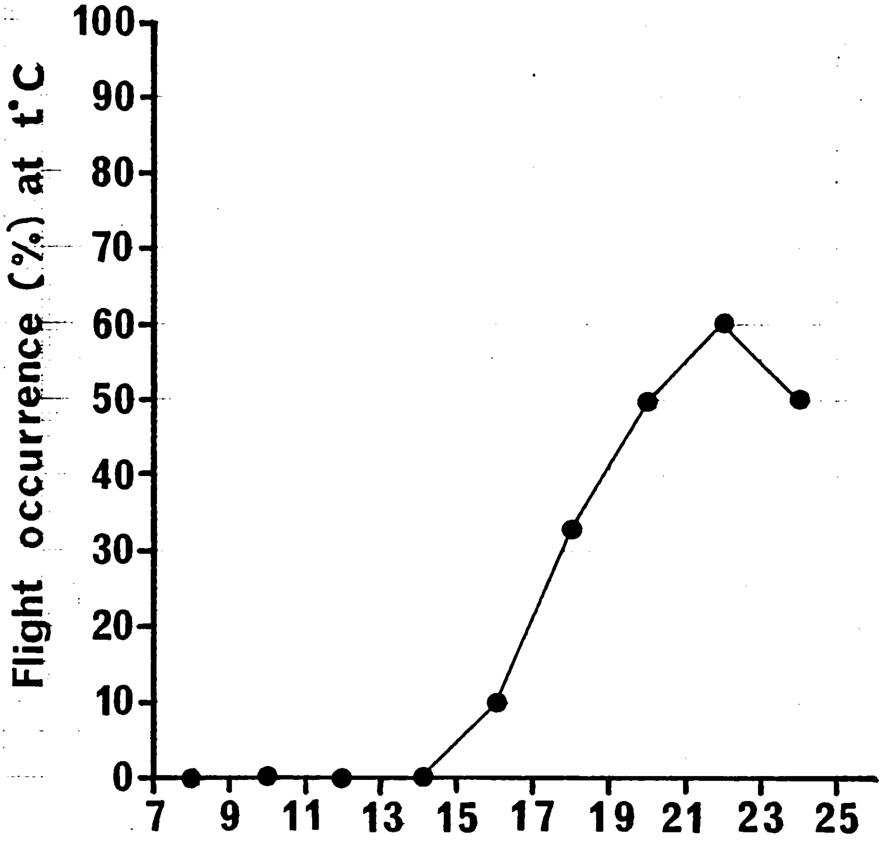


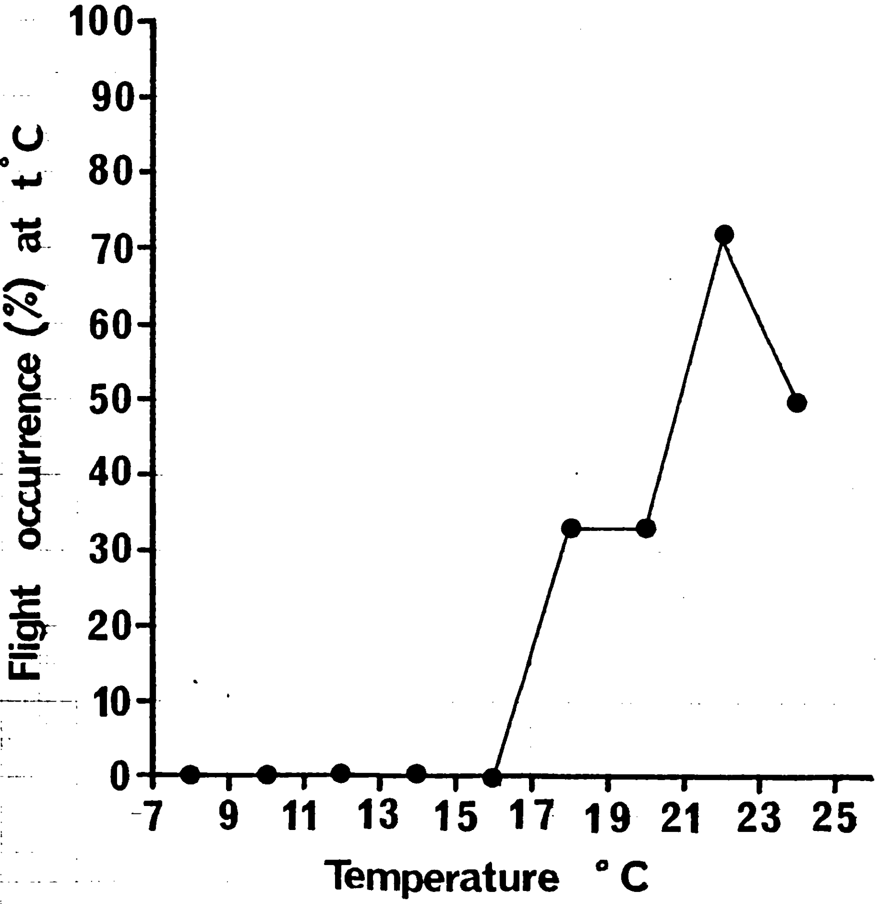
Figure 3.23: The relationship between temperature and flight activity in Platycheirus angustatus

Figure 3.24: The relationship between temperature and flight activity in Syrphus ribesii

P. angustatus



S. ribesii



3.4 GENERAL DISCUSSION AND CONCLUSIONS

The diel periodicity of syrphid flight activity was determined using Malaise traps. Most species showed the same basic diurnal flight patterns with peak activity occurring around midday. The relationship between climate and syrphid activity was considered: multiple linear regression analysis demonstrated that temperature was the most important climatic factor influencing fly activity. Temperature thresholds for flight activity in different syrphid species were determined. There was a crude correlation between temperature threshold and body size with the larger species becoming active at lower temperatures than the smaller species.

The diurnal activity patterns of syrphid flies are determined largely by the insect's hygrothermal requirements and the restrictions imposed by avoidance of overheating (Willmer, 1983). What are the implications in relation to the foraging patterns of syrphid flies? Clearly, the amount of time available for foraging will be limited, especially when conditions for flight activity are unfavourable.

Studies on butterflies have shown that climatic factors can have an important effect on oviposition by influencing both search time and egg deposition patterns. Most butterflies are inactive during overcast, windy or rainy conditions and use part of the time during favourable flight periods for feeding. Energy losses due to respiration may occur during warm but unfavourable flight conditions even though butterflies are not active (Janzen, 1973; Janzen and Wilson, 1974). Unfavourable flight conditions may result in a low realized fecundity due to a reduction in the time available for finding oviposition sites (Courtenay, 1982). However, some butterflies can compensate for reduced rates of oviposition during periods of adverse weather by increasing the rate of egg deposition (either on an hourly or daily basis) during subsequent favourable flight periods (Erhlich and Gilbert, 1973; Gossard and Jones, 1977). It is not known if female syrphids can similarly compensate for reduced oviposition during periods of adverse weather. Laboratory studies have shown that gravid syrphid females can retain mature eggs for a period of several weeks in the absence of suitable oviposition sites (Dixon, 1959; Lyon, 1965, 1968).

The advantages and disadvantages of the Malaise trap as a tool for monitoring syrphid activity have already been discussed in Section 2.4.8. It is possible to use the trap catches to determine thresholds (eg temperature) for flight activity. However, the accuracy of these thresholds depends on the sensitivity of the trap in catching different syrphid species. The trap catches give no clear indication as to the precise nature of the syrphid activity. Feeding and oviposition sites frequently occurred in close proximity both to each other and to the traps, and it was therefore difficult to determine if the flies caught in a particular trap had been foraging for food or oviposition sites. The large number of gravid females caught in the trap suggested that the trap catches may be good indicators of oviposition activity. Evidence to support this hypothesis comes from a later study (described in Section 4.3), in which Malaise traps were used to monitor adult syrphid activity close to aphid-infested potted Brussels sprout plants placed in different habitats. The number of gravid females caught in the traps correlated well with the observed egg-laying patterns recorded on the sprout plants.

CHAPTER 4

OVIPOSITION PATTERNS OF APHIDOPHAGOUS SYRPHIDS IN BRASSICA CROPS

4.1 INTRODUCTION

Many authors have reported that aphidophagous syrphids lay their eggs close to aphid colonies (eg Banks, 1953; Bombosch, 1962; Dixon, 1959; George, 1957; Heiss, 1938; Hughes, 1963; Metcalf, 1916; Sundby, 1966; Wadley, 1931). A few studies have noted the occasional egg on uninfested plants (Metcalf, 1916; Heiss, 1938; Dunn, 1949). Schneider (1948) believed such eggs to be sterile, but Chandler (1968a) later showed that some aphidophagous species lay many fertile eggs on aphid-free plants. Chandler (1968a, b, c) considered that aphidophagous species oviposit in response to a combination of aphid- and plant-associated stimuli. Some species respond primarily to the aphid factors whereas others respond mainly to plant stimuli. Chandler termed these two groups 'aphidozetic' and 'phytozetic', respectively. Aphidozetic species tend to lay single eggs close to aphid colonies and rarely oviposit on uninfested plants. The larvae of such species tend to be obligate entomophages. In contrast, phytozetic species frequently lay their eggs in batches of two or more and will often oviposit on plants that are aphid-free. Phytozetic larvae tend to be only facultatively entomophagous and have often been recorded feeding on non-aphid food: Davidson (1922) reported that Melanostoma obscurum larvae developed more rapidly on decaying chickweed than on aphids. He also observed that young larvae of Allograpta obliqua were able to sustain themselves on a diet of plant material. Rotheray (unpubl) successfully reared larvae of Melanostoma scalare on Acer pseudoplatanus L. leaf litter. Hamrum (1966) recorded Metasyrphus and

Allograpta larvae feeding on healthy brassica plant tissue. Thus aphids may represent only one source of food for phytozetic syrphid larvae.

The oviposition behaviour of Metasyrphus corollae, an aphidozetic species, has been particularly well studied in the laboratory (Bombosch, 1962; Bombosch and Volk, 1966; Peschken, 1965; Sanders, 1979, 1980, 1982; Volk, 1964). Oviposition in this species is stimulated by a complex pattern of olfactory, visual and mechanical stimuli. Olfactory stimuli are the most effective and may induce considerable oviposition even in the absence of the other stimuli. It has been shown that aphids and their liquid exudation (including cornicle secretion and honeydew) emanate an odour that releases oviposition behaviour in M. corollae. The active components of the odour are apparently present only in low concentrations. The chemical nature of these compounds has not yet been identified but they are volatile, mostly lipophilic, and can be absorbed in barium hydroxide solution and liberated again by acidifying (Volk, 1964). In the absence of aphid stimuli, gravid M. luniger females can retain mature eggs for a period of several weeks (Dixon, 1959). Lyon (1965) observed that gravid females of both M. corollae and Episyrphus balteatus can resorb their eggs if denied suitable oviposition sites. Mechanical stimuli from the substrate surface are important in determining the actual site of oviposition: in the presence of the appropriate aphid stimulus, M. corollae shows a significant preference for rugose surfaces, crevices and corners (Bombosch and Volk, 1966). Visual stimuli from the aphids also influence oviposition behaviour: Chandler (1966) demonstrated that gravid E. balteatus females laid more eggs on bean plants (Vicia faba Scop.) infested with a pink form of Acyrthosiphon pisum than a green form. If the shoots of plants infested with the green form were painted with red or white dots, as many eggs were laid as on plants infested with the pink aphid. However, if red bands were painted on the leaves of plants infested with the green aphid, no increase in the number of eggs laid occurred. Chandler concluded that the syrphids were attracted by a specific optical pattern resembling aphids.

Colour orientation by adult syrphids searching for food has been reported by Ilse (1949), Parmenter (1952), Schneider (1958) and Volk (1964). They found that syrphids are attracted to yellow. Studies on the attractiveness of different coloured water-traps showed that blue was the most attractive colour followed by white and yellow (Sol, 1966). Sanders (1982) demonstrated that colour and illumination can influence oviposition behaviour in gravid M. corollae females: in binary choices, ovipositing females preferred a black to a white monochromatic environment. Their choice was governed by the colour of the model and not by the contrast between the model and its background; black models within a black background were highly attractive. Dixon (1959) found that gravid M. luniger females laid more eggs on green poles than on black or white poles. The colour of the substrate has also been shown to influence the height preferences of caged E. balteatus females (Chandler, 1968e): a grass or green paper substrate stimulated oviposition at 30 cm, but bare soil or brown, silver or yellow substrates inhibited this preference except when a green margin was present.

The relative importance of plant and aphid stimuli in influencing oviposition behaviour varies considerably between species. Chandler (1968a) showed that young gravid females of the aphidozetic species E. balteatus did not oviposit on uninfested sprout plants. However, as the females aged, there was a gradual loss in restraint and subsequently a loss in discrimination which promoted oviposition in the absence of the effective aphid stimulus. Chandler concluded that the importance of the aphid stimulus relative to the plant stimulus declined as the females aged. In contrast, Platycheirus peltatus, a phytozetic species showed a much more positive response to the aphid host-plant per se and young gravid females oviposited freely on uninfested plants. P. peltatus females laid ten times as many eggs on uninfested waxy sprout plants than on a glossy-leaved variety whereas M. luniger showed little or no preference (Chandler, 1968). These results suggest that plant factors can exert a major influence on the oviposition behaviour of phytozetic syrphid species, but have little or no effect on the responses of aphidozetic species.

Plant background has also been demonstrated to influence oviposition behaviour in some syrphid species. The studies on the effect of substrate colour on syrphid oviposition have already been discussed. Peschken (1965) concluded that ovipositing *M. corollae* females were not influenced by the height of the plant stand or by the size of the plots. However, the flies preferred dense stands of ground for optimal oviposition although fallow areas were preferred when searching for food. Peschken suggested that negative phototaxis was the main orientation mechanism guiding females to the oviposition site. Smith (1976) showed that syrphid oviposition on sprout plants surrounded by weedy or weed-free background varied according to the species: *Melanostoma* spp laid more eggs on plants surrounded by weeds than on plants surrounded by bare soil, whereas *Platycheirus* spp oviposited preferentially on sprout plants growing in the weed-free background. Oviposition by *E. balteatus* females on sprouts in a weedy or weed-free background changed during the season in accordance with changes in the distribution of aphids.

Quantitative studies on the relationship between aphid infestation and syrphid oviposition give conflicting results. Banks (1953) found a positive correlation between the number of syrphid eggs laid on bean shoots (*Vicia faba* Scop.) and the number of aphids present although very heavy aphid infestations were avoided. Dixon (1959) observed that eggs were laid very close to *Acyrthosiphon spartii* Koch on broom (*Sarothamnus scoparius* L.) and that more eggs were laid the larger the aphid colony. In contrast, van Emden (1963) found no correlation between the number of syrphid eggs laid on Brussels sprout plants infested with *Brevicoryne brassicae* L. and the number of aphids present; nor did Bombosch (1963) in relation to colony size of *Aphis fabae* on sugar beet (*Beta vulgaris*), except at very high levels of aphid infestation. Chandler (1968a, b) demonstrated a basic dichotomy in the oviposition responses of aphidozetic and phytozetic species: oviposition by the former group is closely related to the number of aphids on a plant whereas oviposition by phytozetic species is largely independent of aphid density.

The following chapter examines the oviposition patterns of the syrphid community associated with brassica crops. The relative importance of aphid and plant factors on the egg-laying patterns of different syrphid species is determined and an attempt is made to evaluate the effect of these patterns on the survival of the larvae.

4.2 THE EFFECT OF APHID POPULATION SIZE AND CROP TYPE ON SYRPHID OVIPOSITION PATTERNS

4.2.1 MATERIALS AND METHODS

The effect of aphid population size and crop type on syrphid oviposition patterns was monitored in seven brassica crops: white cabbage (cv Langedijk 3-Starkwinter), red cabbage (cv Meteor Original), Chinese cabbage (cv pe-tsai), cauliflower (cv All The Year Round), Brussels sprouts (cv Winter Harvest), radish (cv Cherry Belle) and swede (cv Acme). The experiment was carried out at Silwood Park during a five-week period in August and September 1981 when syrphid oviposition is normally substantial.

All crops were initially grown in cold frames and were transplanted to the field as seedlings in early June. A diagram of the plot layout is given in Figure 4.1.

Twenty plants in each crop were selected at random and labelled. These plants were thereafter inspected at weekly intervals and the following information recorded:-

1) Number of aphids per plant.
   All apterous aphids were included in the count but alate and mummified aphids were excluded. Seven categories of aphid infestation were defined and these are listed in Table 4.1.
2) Number of syrphid eggs per plant (unhatched eggs only)
   a) Total number of eggs per plant
   b) Number of single eggs per plant
   c) Number of batched eggs per plant

The term 'batch' was applied when a number of eggs were laid side by side, presumably by one female during a single oviposition. Eggs laid end to end or near to, but not touching one another, were not considered to be batched.

d) The size of each egg batch, together with the number of batches per plant.

3) The distance between each egg and the nearest aphid (mm) for distances up to 25 mm. All eggs laid at a distance greater than this or on uninfested plants were included in a single category (25+ mm). (Brussels sprout crop only).

4) Number of syrphid larvae per plant

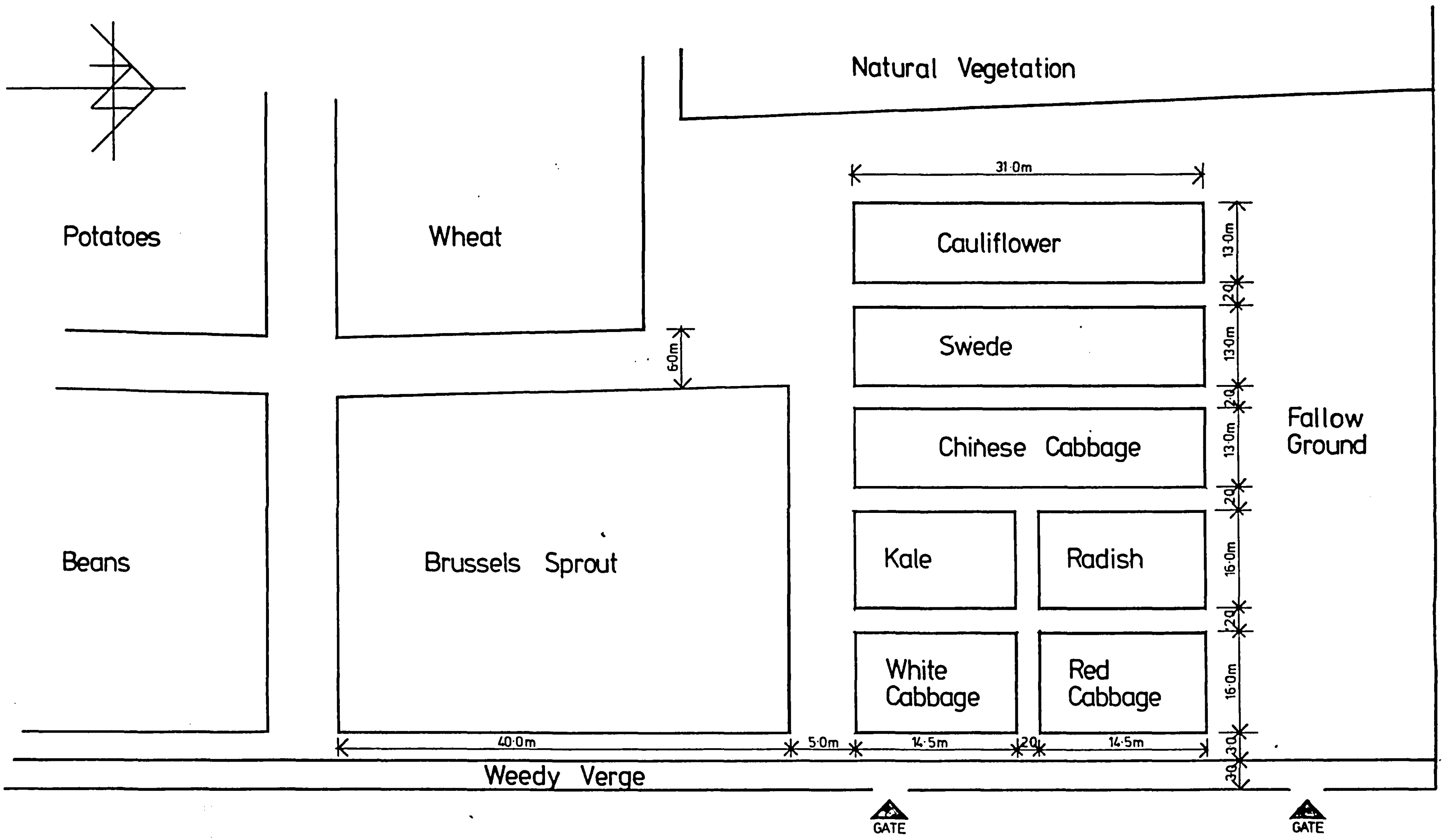
5) Number of syrphid pupae per plant

Table 4.1: Categories of aphid infestation

Category	Estimate of aphid numbers
1	0
2	1 - 50
3	51 - 100
4	101 - 200
5	201 - 400
6	401 - 800
7	801 - 1600

All syrphid eggs, larvae and pupae were removed from the plants and transferred to the laboratory for identification. Eggs were stored in Pampel's Fluid (6 parts 35% formaldehyde, 15 parts 95% ethanol, 2 parts glacial acetic acid and 30 parts distilled water) prior to identification. Eggs were identified using Chandler's (1968d) egg key: this proved satisfactory for most syrphid species although it was sometimes difficult to distinguish between the eggs of certain closely-related Syrphus and Platycheirus species.

Figure 4.1: <u>Diagram to show the layout of different brassica crops</u>


Natural Vegetation
31·0m
Potatoes
Wheat
Cauliflower
13·0m
2·0
Swede
13·0m
6·0m
2·0
Chinese Cabbage
13·0m
Fallow Ground
2·0
Beans
Brussels Sprout
Kale
Radish
16·0m
2·0
White Cabbage
Red Cabbage
16·0m
40·0m
5·0m
14·5m
2·0
14·5m
3·0
3·0
Weedy Verge
GATE
GATE

Syrphid larvae were identified using Dixon's (1960) key and by rearing through to the imaginal stage in the laboratory. Syrphid pupae were all identified by rearing through to the adult stage.

4.2.2 RESULTS AND DISCUSSION

4.2.2.1 Patterns of aphid infestation

Aphid numbers in each crop were determined at weekly intervals during August and early September as described in Section 4.2.1. Table 4.2 shows the mean number of aphids per plant recorded weekly for each crop. Seven categories of aphid infestation were defined and the number of plants in each category are given in Table C1 (Appendix C) for each sample occasion. The results indicate that the general level of aphid infestation in all crops remained low, (usually 1-50 aphids per plant), throughout the five-week period. This was particularly true of the swede, radish and Chinese cabbage crops where many plants remained entirely aphid-free throughout. The greatest range of aphid infestations occurred in the cauliflower and Brussels sprout crops where aphid numbers ranged from 0-1600 aphids per plant.

Table 4.2: The number of aphids per plant recorded on each sample date

Crop	Mean number of aphids per plant on each sample date (± SE)				
	4.8.81	11.8.81	18.8.81	25.8.81	1.9.81
Cauliflower	77.6 ±44.0	72.3 ±33.8	79.4 ±23.8	117.1 ±40.5	141.5 ±75.9
Brussels sprout	331.7 ±97.3	311.4 ±76.9	317.8 ±92.6	395.6 ±95.9	275.8 ±74.4
White cabbage	19.1 ± 4.9	24.6 ± 7.6	59.5 ±18.8	46.1 ±13.1	46.1 ±17.5
Red cabbage	69.5 ±11.5	68.5 ±20.7	25.3 ± 5.2	25.8 ± 4.3	21.0 ± 4.4
Chinese cabbage	10.9 ± 5.2	8.2 ± 3.6	11.9 ± 4.8	13.0 ± 5.4	11.3 ± 6.1
Swede	14.6 ± 4.4	5.0 ± 1.6	3.9 ± 1.6	9.4 ± 2.5	6.4 ± 2.6
Radish	2.0 ± 1.6	5.7 ± 4.7	5.7 ± 3.3	11.2 ± 5.5	5.3 ± 4.2

The main aphid species recorded in all crops was *Brevicoryne brassicae* L. although a few *Myzus persicae* individuals were also found.

4.2.2.2 Patterns of syrphid oviposition

Eggs laid by twelve aphidophagous syrphid species were collected from the brassica crops during August and early September. Table 4.3 shows the number of eggs laid by each species during the five-week period (results for all seven crops are combined here). The four most abundant species recorded were *Episyrphus balteatus*, *Platycheirus peltatus*, *Melanostoma mellinum* and *Sphaerophoria scripta*; collectively, these species accounted for 62% of all eggs laid. *E. balteatus* and *P. clypeatus* oviposited consistently throughout the five-week period, although eggs of the former species were most abundant during the first two weeks of August. *P. manicatus* and *M. mellinum* laid most of eggs in early August whereas *Sph. scripta* laid predominantly during mid-August. *P. peltatus* oviposited chiefly during mid-late August. Eggs of *P. albimanus*, *P scutatus*, *Metasyrphus luniger*, *M. corollae*, *Syrphus ribesii* and *Melanostoma scalare* were recorded mainly during late August and early September. Thus, there was some degree of temporal separation in the peak oviposition periods of different syrphid species.

Some syrphid species tend to lay eggs singly whilst others lay in batches of two or more eggs. Table 4.4 summarizes the egg-laying habits of the species encountered in this particular study. *Sph. scripta*, *S. ribesii*, *Metasyrphus luniger*, *M. corollae*, *P. manicatus*, *P. albimanus* and *P. scutatus* all laid single eggs. *E. balteatus* usually laid eggs singly, but occasionally batches of between two and four eggs were collected. *P. peltatus*, *Melanostoma mellinum* and *M. scalare* tended to lay their eggs in batches of two or three although some single eggs were also recorded. *P. clypeatus* also laid eggs in batches, the batch size ranging from 2-6 eggs.

Laying eggs in batches is a reproductive tactic that occurs in a wide range of different insect groups. Batch-laying in aphidophagous syrphids is generally believed to be a mechanism that ensures survival

Table 4.3: The number of eggs laid by different syrphid species on five sample dates in August and September 1981

Syrphid species	Number of eggs laid on each sample date											
	4.8.81		11.8.81		11.8.81		25.8.81		1.9.81		Total	
	No	%	No	%	No	%	No	%	No	%	No	%
Episyrphus balteatus	220	32.0	176	26.7	81	10.6	143	16.8	110	15.8	730	20.0
Sphaerophoria scripta	2	0.3	105	15.8	271	35.4	94	11.0	1	0.1	472	12.9
Syrphus ribesii	1	0.1	13	2.0	25	3.3	150	17.7	126	18.1	315	8.6
Metasyrphus luniger	2	0.3	-	-	3	0.4	29	3.4	26	3.7	60	1.6
Metasyrphus corollae	-	-	-	-	-	-	10	1.2	8	1.2	18	0.5
Platycheirus manicatus	154	22.4	93	14.1	52	6.8	5	0.6	-	-	304	8.3
Platycheirus peltatus	16	2.3	28	4.2	242	31.6	201	23.7	100	14.4	587	16.1
Platycheirus clypeatus	38	5.5	48	7.3	22	2.9	38	4.4	49	7.1	195	5.3
Platycheirus albimanus	32	4.7	17	2.6	10	1.3	96	11.3	119	17.1	274	7.5
Platycheirus scutatus	-	-	11	1.7	3	0.4	25	2.9	37	5.3	76	2.1
Melanostoma mellinum	220	32.0	168	25.5	54	7.1	24	2.8	11	1.6	477	13.0
Melanostoma scalare	3	0.4	1	0.2	2	0.3	34	4.0	108	15.5	148	4.0
Total	688	100%	659	100%	765	100%	849	100%	695	100%	3656	100%

Table 4.4: The egg-laying habits of the syrphid species encountered in this study

Syrphid species	Number of eggs laid			Number of batches of stated size					
	Total	Single	Batched	2	3	4	5	6	6+
Episyrphus balteatus	730	651	79	19	11	2	-	-	-
Sphaerophoria scripta	472	472	-	-	-	-	-	-	-
Syrphus ribesii	315	315	-	-	-	-	-	-	-
Metasyrphus luniger	60	60	-	-	-	-	-	-	-
Metasyrphus corollae	18	18	-	-	-	-	-	-	-
Platycheirus manicatus	304	304	-	-	-	-	-	-	-
Platycheirus albimanus	274	274	-	-	-	-	-	-	-
Platycheirus scutatus	76	76	-	-	-	-	-	-	-
Platycheirus peltatus	588	57	531	60	63	39	12	1	-
Platycheirus clypeatus	195	-	195	24	12	21	3	2	-
Melanostoma mellinum	476	36	440	97	62	15	-	-	-
Melanostoma scalare	148	2	146	32	22	4	-	-	-

of at least one member of the batch. If food resources are scarce, then the first-emerged larvae can cannibalise the remaining batch members and thus sustain itself in its further search for prey. A search of the literature yielded little information on the extent to which cannibalism occurs in the field among batch-laying syrphid species.

Many Coccinellid species also lay their eggs in batches and egg and/or larval cannibalism may be common. Laboratory studies have shown that 25% of the eggs of *Harmonia axyridis* (Pallas) (Kawai, 1978), and 31 and 43% of those deposited by *Liodalia flavomaculata* (De Geer) and *Cheilomenes lunata* (F.), respectively (Brown, 1972) were eaten. Levels of over 90% cannibalism have been recorded for *Hippodamia convergens* (Guerin-Meneville) (Kirby and Ehler, 1977). The extent to which sibling cannibalism occurs is unclear. In species where the hatching process lasts several days (eg *Coccinella septempunctata* L. and *Propylea quattuordecempunctata* L.), cannibalism of unhatched eggs and newly-hatched larvae by other larvae from the same batch may be common (Dean, 1983). However, Mills (1982) reported that while up to 33% of *Adelia bipunctata* L. eggs were eaten, this was due only to cannibalism by larvae and adults dispersing from other egg-batches.

Newly emerged Coccinellid larvae are initially inefficient in capturing aphids, even if they encounter them (Dixon A. F. G., 1959; Brown, 1972), and cannibalism can be beneficial for the survival of the young of *A. bipunctata* (Banks, 1956) and *C. septempunctata* (Dimetry, 1974). Banks (1953) has shown that the nutritive value of one coccinellid egg to a first-instar coccinellid larva is equivalent to three aphids.

An interesting hypothesis has been advanced by Courtenay (1983) to explain the batch-laying tactic. He compared the realized fecundities of a range of insect species (Lepidoptera, Hymenoptera, Diptera and Hemiptera) which lay their eggs singly or in batches. He found that the batch-laying species showed a much higher realized fecundity than species that laid eggs singly. Low realized fecundity may arise for a number of reasons, perhaps the most important being scarcity of food resources (Benson *et al*, 1975), inhibition of flight activity by poor weather (Courtenay, 1982), and pre-reproductive death of females. Batch-laying species need locate fewer food plants than species with an equivalent potential fecundity which lay their eggs singly. As a consequence of this shortened searching period, batch-laying females may be less likely to be influenced by unfavourable weather conditions and pre-reproductive mortality than females that lay eggs singly.

4.2.2.3 Sampling of syrphid larvae and pupae

A full list of the syrphid larvae and pupae collected from the seven brassica crops during the five-week study period is given in Tables 4.5 and 4.6, respectively. Most of the larvae were first instars and had probably hatched from eggs laid before or after each sample date or from eggs that had escaped detection during sampling. The most abundant species recorded overall in both larval and pupal stages was E. balteatus.

Table 4.5: Syrphid larvae recorded from brassica crops in August and September 1981

Syrphid species	Number of larvae recorded							Total	Total as % of all larvae recorded
	C	BS	WC	RC	CC	S	R		
Episyrphus balteatus	31	33	10	17	6	7	-	104	46.4
Sphaerophoria scripta	6	17	2	9	4	5	-	43	19.2
Syrphus ribesii	2	6	-	-	1	-	-	9	4.0
Metasyrphus luniger	-	1	-	1	-	-	-	2	0.9
Metasyrphus corollae	-	-	-	-	-	-	-	-	-
Platycheirus manicatus	6	3	3	1	2	-	-	15	6.7
Platycheirus albimanus	-	1	1	-	-	-	-	2	0.9
Platycheirus scutatus	-	-	-	-	-	-	-	-	-
Platycheirus peltatus	1	3	3	4	5	6	-	22	9.8
Platycheirus clypeatus	-	-	-	-	-	-	-	-	-
Melanostoma mellinum	5	11	4	3	2	2	-	27	12.1
Melanostoma scalare	-	-	-	-	-	-	-	-	-
Total	51	75	23	35	20	20	-	224	100

Key C - cauliflower; BS - Brussels sprout; WC - white cabbage; RC - red cabbage; CC - Chinese cabbage; S - swede; R - radish

Table 4.6: Syrphid pupae recorded from brassica crops in August and September 1981

Syrphid species	Number of pupae recorded							Total	Total as % of all pupae recorded
	C	BS	WC	RC	CC	S	R		
Episyrphus balteatus	7	3	3	5	4	3	2	27	62.8
Sphaerophoria scripta	2	5	2	1	1	1	-	12	27.9
Syrphus ribesii	-	-	-	-	-	-	-	-	-
Metasyrphus luniger	-	-	-	-	-	-	-	-	-
Metasyrphus corollae	-	-	-	-	-	-	-	-	-
Platycheirus manicatus	1	-	1	-	-	-	-	2	4.7
Platycheirus albimanus	-	-	-	-	-	-	-	-	-
Platycheirus scutatus	-	-	-	-	-	-	-	-	-
Platycheirus peltatus	-	-	-	1	-	-	-	1	2.3
Platycheirus clypeatus	-	-	-	-	-	-	-	-	-
Melanostoma mellinum	-	1	-	-	-	-	-	1	2.3
Melanostoma scalare	-	-	-	-	-	-	-	-	-
Total	10	9	6	7	5	4	2	43	100

Key C - cauliflower; BS - Brussels sprout; WC - white cabbage; RC - red cabbage; CC - Chinese cabbage; S - swede; R - radish

It is interesting to compare the relative abundances of different syrphid species in the egg, larval and pupal stages (see Tables 4.3, 4.5 and 4.6). E. balteatus accounted for only 20.0% of all eggs collected, but for 46.4% of all larvae and 62.8% of all pupae recorded. In contrast, P. peltatus accounted for 16.1% of all eggs collected, but only 9.8% of all larvae and for only 2.3% of all pupae recorded. No larvae or pupae of Metasyrphus corollae, P. scutatus, P. clypeatus, or Melanostoma scalare were collected. What causes these changes in the relative abundance of different syrphid species at different stages in the life-cycle? There are several possible explanations:

1) Inter-specific differences in the survivorship of eggs and /or early larval instars;
2) Inter-specific differences in larval behaviour resulting in the larvae of some species being sampled more readily than others;
3) inter-specific differences in larval competitiveness.

These various hypotheses will be discussed more fully in Section 4.4

4.2.2.4 The effect of aphid population size on the number of syrphid eggs laid per plant

The relationship between aphid population size and the total number of syrphid eggs laid per plant is illustrated in Figures C1 a-g (Appendix C). A one-way analysis of variance was applied to this data and the results are summarized in Table 4.7. In all crops, the number of eggs laid per plant increased significantly with increasing aphid density.

Earlier on, a distinction was made between syrphid species that tend to lay their eggs singly and those that lay eggs in batches. Figures C2 a-g (Appendix C) illustrate the effect of aphid population size on the number of single eggs laid per plant. A one-way analysis of variance confirms that there is a significant increase in the number of eggs laid in response to increasing aphid density (Table 4.8). This pattern was repeated in all crops.

The relationship between aphid density and the number of batched eggs per plant is shown in Figures C3 a-g (Appendix C). Here, the results are less clear-cut: a one-way analysis of variance showed that there were significant differences in the number of eggs laid per plant

Table 4.7: The effect of aphid density on the total number of syrphid eggs laid per plant

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	4.46 ±0.47	7.57 ±2.40	12.09 ±1.53	15.43 ±3.14	19.33 ±2.19	19.00 ±4.00
Brussels Sprout	*	10.08 ±1.34	10.63 ±1.07	16.92 ±2.53	21.50 ±3.31	23.50 ±2.20	25.55 ±3.66
White Cabbage	0.67 ±0.29	4.77 ±0.50	8.75 ±0.92	12.00 ±1.27	13.67 ±2.73	*	*
Red Cabbage	1.00 ±0.45	1.51 ±0.20	2.35 ±0.40	3.40 ±1.29	5.50 ±3.50	*	*
Chinese Cabbage	1.19 ±0.28	4.63 ±0.85	6.44 ±1.08	*	*	*	*
Swede	0.94 ±0.27	3.19 ±0.42	5.00 ±0.00	*	*	*	*
Radish	0.48 ±0.15	2.55 ±0.59	3.50 ±0.92	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	2066.6 1989.9	344.4 21.4	16.10	0.001
Brussels Sprout	Among groups Within groups	5 94	3784.1 6838.2	756.8 72.7	10.40	0.001
White Cabbage	Among groups Within groups	4 95	827.1 1413.3	206.8 14.9	13.90	0.001
Red Cabbage	Among groups Within groups	4 95	55.59 311.16	13.90 3.28	4.24	0.01
Chinese Cabbage	Among groups Within groups	2 97	371.92 914.27	185.96 9.43	19.73	0.001
Swede	Among groups Within groups	2 97	133.86 628.89	66.93 6.48	10.32	0.001
Radish	Among groups Within groups	2 97	84.84 224.95	42.42 2.32	18.29	0.001

In this and subsequent tables of this type * denotes that no plants were recorded in this aphid infestation category

Table 4.8: The effect of aphid density on the number of single eggs laid per plant

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	1.29 ±0.20	6.86 ±2.42	9.36 ±1.44	13.29 ±2.92	16.67 ±3.18	19.00 ±4.00
Brussels Sprout	*	4.42 ±0.60	5.97 ±0.66	10.42 ±1.39	16.08 ±2.31	20.00 ±1.76	22.36 ±3.25
White Cabbage	0.67 ±0.29	2.44 ±0.37	3.00 ±0.72	7.67 ±0.85	11.67 ±2.19	*	*
Red Cabbage	0.60 ±0.40	1.05 ±0.15	1.70 ±0.32	3.40 ±1.29	5.50 ±3.50	*	*
Chinese Cabbage	0.78 ±0.25	1.81 ±0.27	3.22 ±0.52	*	*	*	*
Swede	0.26 ±0.10	0.77 ±0.16	2.00 ±0.00	*	*	*	*
Radish	0.34 ±0.11	0.45 ±2.24	2.00 ±0.36	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	2434.40 1097.60	405.70 11.80	34.38	0.001
Brussels Sprout	Among groups Within groups	5 94	4523.80 3642.80	904.80 38.70	32.35	0.001
White Cabbage	Among groups Within groups	4 95	426.37 779.27	106.59 8.20	12.99	0.001
Red Cabbage	Among groups Within groups	4 95	66.93 204.63	16.73 2.15	7.77	0.001
Chinese Cabbage	Among groups Within groups	2 97	57.59 326.57	28.80 3.37	8.55	0.001
Swede	Among groups Within groups	2 97	8.67 86.17	4.34 0.89	4.88	0.01
Radish	Among groups Within groups	2 97	15.47 97.28	77.73 1.00	7.71	0.001

at different aphid densities in the white cabbage, Chinese cabbage, swede and radish crops, although no clear linear relationship was apparent (Table 4.9). However, aphid population size appeared to have no significant influence on batched egg numbers in the red cabbage, cauliflower and Brussels sprout crops. In all crops, except swede and Chinese cabbage, the number of batched eggs per plant declined at the higher aphid densities.

The relationship between aphid population size and the number of egg batches per plant followed a very similar pattern (Table 4.10; Figures C4 a-g, Appendix C) (for batch-laying species, the number of egg batches corresponds to the number of actual ovipositions).

These observations support Chandler's (1968c) findings that oviposition by species laying single eggs is closely related to aphid density whilst oviposition by species laying eggs in batches tends to be fairly independent of aphid population size. In this study, the overall response was mainly due to species laying eggs singly, although oviposition by batch-laying species was important at the lower aphid densities.

Chandler (1968c) and Banks (1953) found that syrphids tended to avoid very high aphid infestations. Large numbers of aphids produce large amounts of honeydew and heavily-infested plants are thus very susceptible to attack by fungal pathogens. In addition, large aphid populations may be easily located by other aphid predators and parasites and also by parasites and predators of the syrphids themselves. Rotheray (1981) showed that female Ichneumonid parasites attacking syrphid eggs and larvae respond to aphid odours to bring them into the vicinity of the aphid colony. Syrphid hosts within the colony are then located by responding to contact chemicals on the larval integument. In this study, the general level of aphid infestation remained relatively low and although, in some crops, the graph of egg numbers versus aphid population size (Figures C1 a,b, Appendix C) levelled off at the higher aphid densities, there was no evidence of a decline in egg numbers at such densities.

Table 4.9: The effect of aphid density on the number of batched eggs laid per plant

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	3.16 ±0.41	0.71 ±0.47	2.73 ±0.57	2.14 ±1.08	2.67 ±1.33	-
Brussels Sprout	*	5.67 ±1.39	4.66 ±0.66	6.50 ±1.33	5.42 ±1.39	3.50 ±0.88	3.18 ±0.89
White Cabbage	-	2.33 ±0.29	5.75 ±0.81	4.33 ±1.18	2.00 ±1.00	*	*
Red Cabbage	0.40 ±0.40	0.46 ±0.13	0.65 ±0.31	-	-	*	*
Chinese Cabbage	0.41 ±0.12	2.81 ±0.68	3.22 ±0.62	*	*	*	*
Swede	0.68 ±0.26	2.42 ±0.38	3.00 ±0.00	*	*	*	*
Radish	0.15 ±0.06	2.00 ±0.65	1.50 ±0.72	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	73.36 866.35	12.23 9.32	1.31	ns
Brussels Sprout	Among groups Within groups	5 94	107.60 1590.60	21.50 16.90	1.27	ns
White Cabbage	Among groups Within groups	4 95	204.01 551.03	51.00 5.80	8.79	0.001
Red Cabbage	Among groups Within groups	4 95	2.34 124.57	0.58 1.31	0.45	ns
Chinese Cabbage	Among groups Within groups	2 97	146.32 411.07	73.16 4.24	17.26	0.001
Swede	Among groups Within groups	2 97	76.88 528.91	38.44 5.45	7.05	0.01
Radish	Among groups Within groups	2 97	40.75 83.77	20.37 0.86	23.59	0.001

Table 4.10: The effect of aphid density on the number of egg batches laid per plant

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	1.00 ±0.13	0.29 ±0.18	1.09 ±0.21	0.71 ±0.36	1.00 ±0.58	-
Brussels Sprout	*	2.00 ±0.48	1.54 ±0.22	2.08 ±0.38	1.58 ±0.45	1.11 ±0.28	1.09 ±0.28
White Cabbage	-	0.90 ±0.11	2.08 ±0.29	1.50 ±0.34	0.67 ±0.33	*	*
Red Cabbage	0.20 ±0.20	0.19 ±0.05	0.17 ±0.08	-	-	*	*
Chinese Cabbage	0.19 ±0.05	1.19 ±0.29	1.33 ±0.24	*	*	*	*
Swede	0.23 ±0.09	1.04 ±0.16	1.00 ±0.00	*	*	*	*
Radish	0.07 ±0.03	0.82 ±0.26	0.67 ±0.33	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	7.23 85.77	1.21 0.92	1.31	ns
Brussels Sprout	Among groups Within groups	5 94	11.63 165.21	2.33 1.76	1.32	ns
White Cabbage	Among groups Within groups	4 95	25.61 77.38	6.40 0.82	7.86	0.001
Red Cabbage	Among groups Within groups	4 95	0.22 13.89	0.06 0.15	0.38	ns
Chinese Cabbage	Among groups Within groups	2 97	24.82 73.82	12.41 0.76	16.30	0.001
Swede	Among groups Within groups	2 97	16.09 86.35	8.05 0.89	9.04	0.001
Radish	Among groups Within groups	2 97	6.85 16.54	3.43 0.17	20.10	0.001

Tables C2 - C13 (Appendix C) summarize the effect of aphid population size on the number of eggs laid per plant by different syrphid species. The twelve species included in this analysis may be conveniently divided into three categories. The first category comprises species whose oviposition responses were closely related to aphid density in most crops and includes *E. balteatus*, *Sph. scripta*, *S. ribesii*, *Metasyrphus luniger*, *M. corollae* and *P. albimanus*. These species laid most of their eggs on aphid-infested plants and rarely laid on uninfested plants. All six species tend to lay eggs singly and conform to Chandler's definition of 'aphidozetic' species. The second group contains three species whose oviposition responses appeared to be mainly independent of aphid population size: *Melanostoma mellinum*, *M. scalare* and *P. clypeatus* all preferred to oviposit on aphid-infested plants, but frequently laid eggs on plants that were aphid-free. All three species lay their eggs predominantly in batches and comply with Chandler's definition of 'phytozetic' species. The third group comprised three *Platycheirus* species whose oviposition responses were significantly influenced by aphid density in some crops, but not in others. *P. manicatus* and *P. scutatus* both tend to lay eggs singly whereas *P. peltatus* frequently lays in batches. These species are probably intermediate between aphidozetic and phytozetic groups.

There was some evidence to suggest that different syrphid species prefer different sizes of aphid population for optimal oviposition. *P. manicatus* oviposited mainly on lightly infested plants (50-100 aphids per plant) and tended to avoid the more heavily infested plants. In contrast, *Metasyrphus corollae*, *M. luniger* and *S. ribesii* oviposited only on the more heavily-infested plants (>100 aphids per plant). Such preferences for aphid populations of a particular size were most marked among the aphidozetic species. Unfortunately, the overall level of aphid infestation in all crops was relatively low and so it was not possible to examine the effect of very high aphid densities on the oviposition patterns of different syrphid species. It might be expected that specific differences in the preferred size of aphid population would be more apparent if a greater range of aphid densities had been available.

Specific differences in the optimum size of aphid population for oviposition have previously been recorded by Chandler (1968c). In addition, he showed that some species show further selection for aphid colonies of a particular size. Thus, once a plant has been selected for oviposition, there may still be selection for individual colonies of a particular size resulting in selection of specific sites for oviposition on the chosen plant. The tendency of different species to select aphid populations of different sizes and distributions can decrease inter-specific competition between larvae.

The effect of aphid population size on egg batch size is examined in Tables C14 - C18 (Appendix C). In general, the results indicated that aphid density had little effect on the number of eggs laid per batch by Melanostoma mellinum, M. scalare, E. balteatus and P. clypeatus. For P. peltatus, however, significant differences were recorded in the size of the egg batches laid at different aphid densities on swede, radish and Brussels sprout plants but no clear density dependent relationship was discernible.

It was quite common to find eggs belonging to several different syrphid species on the same plant. Figures C5 a-g (Appendix C) examines the effect of aphid population size on the number of different species ovipositing per plant. In all crops, a one-way analysis of variance showed that the number of ovipositing species increased significantly with increasing aphid density (Table 4.11). In the cauliflower, Brussels sprout, white cabbage and red cabbage crops, the number of species ovipositing per plant levels off at high aphid densities and may even decline slightly. The pattern of the graph is explained by specific differences in the preferred size of aphid population for optimal oviposition, as described earlier. Thus, at low aphid densities, the oviposition response is due mainly to phytozetic species whereas at high aphid densities, most eggs are laid by aphidozetic species. At intermediate aphid densities, there is an overlap with both phytozetic and aphidozetic species ovipositing together. These results imply that as aphid population size per plant increases, so does the likelihood of inter-specific competition between the larvae.

The results of some previous studies may now be put into context. The absence of any correlation between syrphid oviposition and the level of aphid infestation recorded by van Emden (1963) is doubtless due to the relatively small aphid populations under study. At low aphid densities, the main oviposition response is by phytozetic species whose oviposition behaviour is relatively independednt of aphid density. The findings of Bombosch (1963) that syrphid oviposition and A. fabae infestation on sugar beet were only correlated at high aphid densities suggest that there was a marked response by phytozetic species at the lower densities. In her study on broom, Dixon (1959) reported that most eggs were laid by M. luniger, Syrphus vitripennis, Epistrophe nitidicollis and P. scutatus. All may be considered to be aphidozetic species, laying eggs close to aphid colonies, as recorded. It is inferred from this data that oviposition by phytozetic species was at most low and so the overall response would be density dependent, as recorded. Chandler (1967) found that phytozetic species rarely laid on beans and syrphid oviposition on these plants is due almost entirely to aphidozetic species. It is to be expected, therefore, that studies involving beans as the aphid host-plant would show at all times a density-dependent syrphid oviposition response, and this has been found by Banks (1953).

4.2.2.5 The effect of aphid population size on the number of eggs laid per aphid

The effect of aphid population size on syrphid oviposition was examined in terms of both the effect on egg numbers per plant and the effect on egg numbers per aphid.

Figures C6 a-g (Appendix C) illustrate the effect of aphid population size on total egg numbers laid per aphid. A one-way analysis of variance confirms that in all crops, the ratio of eggs: aphids declined as the aphid population per plant increased. This decline was statistically significant only in the red cabbage, cauliflower and Brussels sprout crops (Table 4.12). The highest egg:aphid ratios were recorded on plants with low aphid densities. A significant proportion of the overall oviposition response at low aphid densities is due to batch-laying species and it has been shown

Table 4.11: The effect of aphid density on the number of syrphid species ovipositing per plant

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	1.71 ±0.16	3.29 ±0.81	4.55 ±0.55	5.00 ±0.79	4.67 ±0.33	4.50 ±0.50
Brussels Sprout	*	3.08 ±0.33	3.57 ±0.32	4.92 ±0.47	5.08 ±0.64	4.28 ±0.25	4.45 ±0.43
White Cabbage	0.44 ±0.18	1.50 ±0.13	2.25 ±0.18	3.83 ±0.60	3.33 ±0.33	*	*
Red Cabbage	0.80 ±0.37	0.77 ±0.09	1.04 ±0.15	1.80 ±0.49	1.50 ±0.50	*	*
Chinese Cabbage	0.56 ±0.12	1.56 ±0.24	2.67 ±0.50	*	*	*	*
Swede	0.43 ±0.11	1.12 ±0.12	2.00 ±0.00	*	*	*	*
Radish	0.31 ±0.08	1.09 ±0.25	1.83 ±0.40	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups	6	171.47	28.58	13.33	0.001
	Within groups	93	199.44	2.14		
Brussels Sprout	Among groups	5	43.70	8.74	3.16	0.05
	Within groups	94	259.66	2.76		
White Cabbage	Among groups	4	55.92	13.98	13.91	0.001
	Within groups	95	95.47	1.00		
Red Cabbage	Among groups	4	6.40	1.60	2.79	0.05
	Within groups	95	54.60	0.58		
Chinese Cabbage	Among groups	2	45.54	22.77	18.65	0.001
	Within groups	97	118.42	1.22		
Swede	Among groups	2	13.20	6.60	9.88	0.001
	Within groups	97	64.80	0.67		
Radish	Among groups	2	17.39	6.70	14.15	0.001
	Within groups	97	59.60	0.61		

Table 4.12: The effect of aphid density on the total number of eggs laid per aphid

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.258 ±0.031	0.101 ±0.029	0.085 ±0.011	0.057 ±0.015	0.033 ±0.001	0.016 ±0.001
Brussels Sprout	0.541 ±0.227	0.140 ±0.013	0.115 ±0.013	0.069 ±0.009	0.038 ±0.001	0.021 ±0.003
White Cabbage	0.470 ±0.074	0.134 ±0.018	0.081 ±0.007	0.046 ±0.006	*	*
Red Cabbage	0.087 ±0.012	0.037 ±0.007	0.021 ±0.007	0.016 ±0.007	*	*
Chinese Cabbage	0.339 ±0.073	0.087 ±0.014	*	*	*	*
Swede	0.475 ±0.123	0.071 ±0.000	*	*	*	*
Radish	0.260 ±0.114	0.049 ±0.030	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.741 4.554	0.148 0.050	2.99	0.05
Brussels Sprout	Among groups Within groups	5 94	2.332 7.071	0.466 0.075	6.20	0.001
White Cabbage	Among groups Within groups	3 87	2.158 26.173	0.719 0.301	2.39	ns
Red Cabbage	Among groups Within groups	3 91	0.061 0.670	0.020 0.007	2.78	0.05
Chinese Cabbage	Among groups Within groups	1 34	0.428 3.722	0.428 0.109	3.91	ns
Swede	Among groups Within groups	1 51	0.159 39.925	0.159 0.783	0.20	ns
Radish	Among groups Within groups	1 15	0.173 1.430	0.173 0.095	1.82	ns

previously that oviposition by such species is largely independent of aphid density. There was also considerable variation in the egg:aphid ratio between individual plants in these low density categories.

Figures C7 a-g (Appendix C) show the effect of aphid population size on the number of single eggs laid per aphid. Again, the ratio of eggs:aphids declined in all crops, but this decrease was statistically significant only in the Brussels sprout crop.

Similarly, both the number of batched eggs per aphid decreased with increasing aphid population size (Figures C8 a-g and C9 a-g, respectively, Appendix C), but these decreases were significant only in the cauliflower and Brussels sprout crops (Tables 4.14 and 4.15).

The effect of aphid population size on the eggs:aphid ratios of different syrphid species is shown in Tables C19 - C30 (Appendix C). The results of a one-way analysis of variance on these data imply that, for most species, the number of aphids present on a plant has no significant effect on the number of eggs laid per aphid. (The two exceptions were Metasyrphus corollae and M. luniger, both of which showed highly significant differences in the number of eggs laid per aphid on plants infested with aphid populations of varying sizes. However, the results for these two species may be explained by the fact that neither species laid any eggs at all on lightly-infested plants).

The interpretation of these results is difficult. A first glance might suggest that individual syrphid species are assessing the number of aphids present on a plant and are laying a more or less fixed number of eggs per aphid, accordingly. This theory provides an attractive explanation for the observed egg-laying patterns of aphidozetic species whose oviposition responses have been shown to be closely related to aphid density. For phytozetic species, however, a fixed egg:aphid ratio is surprising since oviposition by these species has previously been shown to be relatively independent of aphid density. The concept of a fixed egg:aphid ratio also implies that

Table 4.13: The effect of aphid density on the number of single eggs laid per aphid

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.068 ±0.011	0.090 ±0.028	0.065 ±0.010	0.048 ±0.012	0.028 ±0.002	0.016 ±0.001
Brussels Sprout	0.191 ±0.047	0.078 ±0.008	0.073 ±0.008	0.053 ±0.007	0.033 ±0.003	0.018 ±0.003
White Cabbage	0.244 ±0.050	0.134 ±0.018	0.052 ±0.007	0.040 ±0.007	*	*
Red Cabbage	0.064 ±0.011	0.026 ±0.005	0.021 ±0.007	0.016 ±0.007	*	*
Chinese Cabbage	0.207 ±0.067	0.043 ±0.006	*	*	*	*
Swede	0.475 ±0.013	0.029 ±0.000	*	*	*	*
Radish	0.041 ±0.025	0.028 ±0.005	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.016 0.557	0.003 0.006	0.52	ns
Brussels Sprout	Among groups Within groups	5 94	0.235 0.394	0.047 0.004	11.22	0.001
White Cabbage	Among groups Within groups	3 87	0.384 12.183	0.128 0.140	0.91	ns
Red Cabbage	Among groups Within groups	3 91	0.033 0.538	0.011 0.006	1.87	ns
Chinese Cabbage	Among groups Within groups	1 34	0.182 3.109	0.182 0.091	1.99	ns
Swede	Among groups Within groups	1 51	0.195 39.925	0.195 0.783	0.25	ns
Radish	Among groups Within groups	1 15	0.001 0.067	0.001 0.004	0.13	ns

Table 4.14: The effect of aphid density on the number of batched eggs per aphid

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.191 ±0.029	0.012 ±0.008	0.020 ±0.005	0.009 ±0.005	0.005 ±0.003	-
Brussels Sprout	0.350 ±0.199	0.062 ±0.009	0.043 ±0.008	0.016 ±0.004	0.006 ±0.001	0.003 ±0.001
White Cabbage	0.226 ±0.047	0.089 ±0.015	0.028 ±0.007	0.006 ±0.003	*	*
Red Cabbage	0.022 ±0.007	0.011 ±0.005	-	-	*	*
Chinese Cabbage	0.132 ±0.039	0.044 ±0.008	*	*	*	*
Swede	0.348 ±0.092	0.043 ±0.000	*	*	*	*
Radish	0.217 ±0.118	0.015 ±0.008	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.661 3.815	0.132 0.042	3.19	0.01
Brussels Sprout	Among groups Within groups	5 94	1.108 5.319	0.222 0.057	3.92	0.01
White Cabbage	Among groups Within groups	3 87	0.472 10.516	0.157 0.121	1.30	ns
Red Cabbage	Among groups Within groups	3 91	0.005 0.194	0.002 0.002	0.71	ns
Chinese Cabbage	Among groups Within groups	1 34	0.052 1.099	0.052 0.032	1.61	ns
Swede	Among groups Within groups	1 51	0.091 22.245	0.091 0.436	0.21	ns
Radish	Among groups Within groups	1 15	0.159 1.549	0.159 0.103	1.54	ns

Table 4.15: The effect of aphid density on the number of egg batches per aphid

a)

Crop	Mean number of eggs per aphid at each aphid density (SE)					
	2	3	4	5	6	7
Cauliflower	0.065 ±0.010	0.004 ±0.003	0.008 ±0.002	0.003 ±0.002	0.002 ±0.001	-
Brussels Sprout	0.113 ±0.059	0.021 ±0.003	0.014 ±0.002	0.005 ±0.001	0.002 ±0.000	0.001 ±0.000
White Cabbage	0.067 ±0.013	0.032 ±0.005	0.010 ±0.002	0.002 ±0.001	*	*
Red Cabbage	0.009 ±0.003	0.003 ±0.001	-	-	*	*
Chinese Cabbage	0.890 ±0.83	0.020 ±0.003	*	*	*	*
Swede	0.151 ±0.039	0.014 ±0.000	*	*	*	*
Radish	0.100 ±0.059	0.015 ±0.008	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.075 0.472	0.015 0.005	2.91	0.05
Brussels Sprout	Among groups Within groups	5 94	0.115 0.473	0.023 0.005	4.58	0.01
White Cabbage	Among groups Within groups	3 87	0.036 0.783	0.012 0.009	1.35	ns
Red Cabbage	Among groups Within groups	3 91	0.001 0.029	0.00033 0.00032	1.04	ns
Chinese Cabbage	Among groups Within groups	1 34	0.010 0.190	0.010 0.006	0.36	ns
Swede	Among groups Within groups	1 51	0.018 3.992	0.018 0.078	0.23	ns
Radish	Among groups Within groups	1 15	0.028 0.389	0.028 0.026	1.09	ns

syrphids can assess the number of other syrphid eggs already present on the plant and regulate the number of eggs laid accordingly. Evidence from field studies to confirm or deny this hypothesis is scarce. However, Chandler (1968a) found that the oviposition response of E. balteatus females was not affected by the presence of other syrphid eggs, larvae or larval gut contents already on the plant.

Previous work on egg:aphid ratios has concentrated mainly on aphidozetic species: Dixon (1959) showed that the number of eggs laid per aphid by P. scutatus and S. vitripennis on broom infested with Acyrthosiphon spartii (Koch.) increased proportionally with the size of the aphid colony. Ito and Iwao (1977) found that the mean number of eggs per aphid laid by E. balteatus females on cabbage plants infested with Myzus persicae tended to decrease with increasing aphid density per plant. Similar results were obtained by Chandler (1967) for a variety of different species. These results suggest that if syrphids are somehow assessing the size of the aphid population on a plant, then the ability to do so accurately declines at high aphid densities.

4.2.2.6 The effect of crop type on the number of eggs laid per aphid

Table 4.16 compares the number of eggs laid per aphid on different brassica crops (all species considered collectively). There is a very significant difference in the total number of eggs laid per aphid on different crops. The highest ratio of eggs:aphids was recorded on swede plants and the lowest on red cabbage. Similar results were obtained for the number of single eggs per aphid, the number of batched eggs per aphid, and the number of egg batches per aphid.

Differences in the egg:aphid ratio on different crops may be caused by various factors. Firstly, ovipositing syrphid females may respond directly to physical and/or chemical characteristics of the aphid host-plant that may influence its attractiveness as on oviposition site. Oviposition by phytozetic species might be expected to be affected by such plant-associated factors. Secondly, plant structure may indirectly affect the ease with which aphid colonies are located:

Table 4.16: The effect of crop type on the number of eggs laid per aphid (all species considered together)

a)

	Mean number of eggs per aphid ± SE						
	C	BS	WC	RC	CC	S	R
Total number of eggs	0.202 ±0.024	0.145 ±0.031	0.386 ±0.059	0.070 ±0.009	0.276 ±0.058	0.467 ±0.121	0.186 ±0.076
Number of single eggs	0.065 ±0.008	0.073 ±0.008	0.210 ±0.039	0.052 ±0.008	0.167 ±0.051	0.466 ±0.121	0.036 ±0.016
Number of batched eggs	0.136 ±0.022	0.072 ±0.026	0.188 ±0.037	0.018 ±0.005	0.110 ±0.030	0.342 ±0.090	0.145 ±0.079
Number of egg batches	0.046 ±0.008	0.024 ±0.008	0.056 ±0.010	0.007 ±0.002	0.047 ±0.013	0.129 ±0.035	0.070 ±0.039

Key C - cauliflower; BS - Brussels sprout; WC - white cabbage; RC - red cabbage; CC - Chinese cabbage; S - swede; R - radish

b) Anova table

	Source of variation	df	SS	MS	F-ratio	P
Total eggs	Among groups Within groups	6 483	8.53 89.57	1.42 0.19	7.66	0.001
Single eggs	Among groups Within groups	6 483	8.03 57.80	1.34 0.12	11.18	0.001
Batched eggs	Among groups Within groups	6 483	4.25 47.20	0.71 0.10	7.21	0.001
Egg batches	Among groups Within groups	6 483	0.58 5.91	0.10 0.01	7.96	0.001

aphid populations may be more visible on the smaller, less structurally complex plants such as radish and swede than on the larger, more structurally complex crops of cauliflower and Brussels sprout. It might be anticipated that oviposition by aphidozetic species may be influenced by plant structure in this way.

Table 4.17 compares the egg:aphid ratios on different crops for individual syrphid species. Most of the aphidozetic species (ie S. ribesii, Metasyrphus luniger, M. corollae, Sph. scripta and P. scutatus) laid a fixed number of eggs per aphid on all crops. In contrast, the ratio of eggs:aphids often varied considerably between crops for some of the more phytozetic species: P. peltatus and Melanostoma mellinum showed a significant preference for swede, and P. clypeatus for radish. P. albimanus and P. manicatus both laid significantly more eggs per aphid on white cabbage than on any other crop.

These results tend to confirm that plant associated factors may have a considerable influence on the oviposition patterns of phytozetic syrphid species but have relatively little effect on aphidozetic species when an aphid stimulus is present.

It is interesting to note that many species, particularly phytozetic ones, tended to lay fewer eggs per aphid on red cabbage than on the other crops. Prokopy (personal communication) has suggested that the presence of red plant pigments can have an inhibitory effect on insect colonization. It is possible that the red pigments in red cabbage leaves may be exerting a similar inhibitory influence on syrphid oviposition.

Table 4.18 shows the effect of crop type on the size of egg batches laid by different syrphid species. A one-way analysis of variance was applied to this data and confirmed that crop type had a significant influence on egg batch size in Melanostoma mellinum, P. peltatus and P. clypeatus but had no significant effect on the number of eggs laid per batch by M. scalare and E. balteatus.

Chandler (1968a) found that egg batch size in some Platycheirus and Melanostoma species was influenced by the nature of the substrate. He examined oviposition on a range of natural and artificial substrates in the absence of aphids and concluded that stereotactic receptors on the ovipositor were responsible for determining the suitability of the substrate as an oviposition site.

Table 4.17: The effect of crop type on the number of eggs laid per aphid by different syrphid species

Syrphid species	Mean number of eggs per aphid ± SE						
	C	BS	WC	RC	CC	S	R
Episyrphus balteatus	0.014 ±0.004	0.015 ±0.001	0.033 ±0.009	0.021 ±0.004	0.075 ±0.034	0.105 ±0.055	0.024 ±0.012
Sphaerophoria scripta	0.008 ±0.002	0.013 ±0.002	0.020 ±0.011	0.010 ±0.006	0.034 ±0.020	0.019 ±0.007	0.003 ±0.002
Syrphus ribesii	0.007 ±0.003	0.006 ±0.001	0.006 ±0.002	0.001 ±0.001	0.005 ±0.002	0.001 ±0.001	-
Metasyrphus luniger	0.001 ±0.0001	0.001 ±0.0001	0.001 ±0.0002	0.001 ±0.0003	-	-	-
Metasyrphus corollae	0.001 ±0.000	0.0001 ±0.0001	0.0001 ±0.0001	0.0004 ±0.0002	-	-	-
Platycheirus manicatus	0.024 ±0.005	0.013 ±0.002	0.054 ±0.015	0.017 ±0.005	0.051 ±0.028	0.001 ±0.001	0.004 ±0.004
Platycheirus albimanus	0.010 ±0.003	0.012 ±0.006	0.029 ±0.013	0.001 ±0.001	0.004 ±0.002	0.002 ±0.002	0.019 ±0.015
Platycheirus scutatus	0.002 ±0.001	0.003 ±0.001	0.002 ±0.001	-	0.001 ±0.001	0.002 ±0.001	0.004 ±0.004
Platycheirus peltatus	0.069 ±0.015	0.029 ±0.011	0.045 ±0.011	0.007 ±0.003	0.014 ±0.007	0.097 ±0.023	0.043 ±0.022
Platycheirus clypeatus	0.009 ±0.005	0.011 ±0.003	0.037 ±0.017	0.002 ±0.002	0.012 ±0.006	-	0.078 ±0.078
Melanostoma mellinum	0.041 ±0.009	0.015 ±0.004	0.059 ±0.019	0.010 ±0.003	0.059 ±0.020	0.191 ±0.083	0.007 ±0.005
Melanostoma scalare	0.021 ±0.008	0.023 ±0.015	0.009 ±0.006	0.001 ±0.001	0.023 ±0.014	0.053 ±0.038	0.002 ±0.002

Key C - cauliflower; BS - Brussels sprout; WC - white cabbage; RC - red cabbage;
CC - Chinese cabbage; S - swede; R - radish

Table 4.17: continued

Anova table

Syrphid species	Source of variation	df	SS	MS	F-ratio	P
Episyrphus balteatus	Among groups	6	0.420	0.070	3.15	0.01
	Within groups	483	10.743	0.022		
Sphaerophoria scripta	Among groups	6	0.026	0.004	1.01	ns
	Within groups	483	2.044	0.004		
Syrphus ribesii	Among groups	6	0.003	0.00057	1.76	ns
	Within groups	483	0.157	0.00033		
Metasyrphus luniger	Among groups	6	0.00002	0.0000038	1.23	ns
	Within groups	483	0.00148	0.0000031		
Metasyrphus corollae	Among groups	6	0.00001	0.0000015	1.25	ns
	Within groups	483	0.00057	0.0000012		
Platycheirus manicatus	Among groups	6	0.161	0.027	3.76	0.01
	Within groups	483	3.442	0.007		
Platycheirus albimanus	Among groups	6	0.045	0.008	2.12	0.05
	Within groups	483	1.718	0.004		
Platycheirus scutatus	Among groups	6	0.001	0.00010	1.56	ns
	Within groups	483	0.032	0.00007		
Platycheirus peltatus	Among groups	6	0.391	0.065	4.65	0.001
	Within groups	483	6.768	0.014		
Platycheirus clypeatus	Among groups	6	0.150	0.025	2.77	0.05
	Within groups	483	4.345	0.009		
Melanostoma mellinum	Among groups	6	1.374	0.229	4.74	0.001
	Within groups	483	23.334	0.048		
Melanostoma scalare	Among groups	6	0.108	0.018	1.17	ns
	Within groups	483	7.430	0.015		

Table 4.18: <u>The effect of crop type on egg batch size</u>

Syrphid species	Mean egg batch size on different crops ± SE						
	C	BS	WC	RC	CC	S	R
Episyrphus balteatus	2.00 ±0.00	2.68 ±0.14	-	-	2.00 ±0.00	2.00 ±0.00	2.00 ±0.00
Platycheirus peltatus	3.49 ±0.19	3.55 ±0.11	2.82 ±0.12	3.40 ±0.68	2.29 ±0.13	2.64 ±0.13	2.30 ±0.15
Platycheirus clypeatus	5.00 ±0.41	3.26 ±0.18	3.00 ±0.27	4.00 ±0.00	2.50 ±0.27	2.50 ±0.50	2.00 ±0.00
Melanostoma mellinum	2.68 ±0.12	2.92 ±0.11	2.43 ±0.10	2.40 ±0.22	2.30 ±0.19	2.16 ±0.08	2.50 ±0.29
Melanostoma scalare	2.46 ±0.18	2.63 ±0.13	2.50 ±0.29	2.00 ±0.00	2.60 ±0.25	2.29 ±0.19	2.00 ±0.00

<u>Key</u> C - cauliflower; BS - Brussels sprout; WC - white cabbage;
RC - red cabbage; CC - Chinese cabbage; S - swede; R - Radish

Anova table

Syrphid species	Source of variation	df	SS	MS	F-ratio	P
Episyrphus balteatus	Among groups	4	3.20	0.80	2.46	ns
	Within groups	27	8.77	0.33		
Platycheirus peltatus	Among groups	6	39.28	6.55	9.44	0.001
	Within groups	168	116.52	0.69		
Platycheirus clypeatus	Among groups	6	22.01	3.67	3.90	0.01
	Within groups	55	51.69	0.94		
Melanostoma mellinum	Among groups	6	10.81	1.80	4.81	0.001
	Within groups	167	62.54	0.38		
Melanostoma scalare	Among groups	6	1.33	0.22	0.53	ns
	Within groups	51	21.16	0.42		

4.2.2.7 <u>Proximity of oviposition to aphid colonies</u>

During sampling of the Brussels sprout crop, the distance between each syrphid egg and the nearest aphid was recorded for distances up to 25 mm. All eggs laid at a greater distance than this or on uninfested plants were included in a single category (25+ mm). *B. brassicae* aphids, especially the young instars, are relatively immobile and rarely disperse when disturbed by ovipositing syrphid females. It is thus possible to sample several days after the eggs have been laid and still obtain a fairly reliable estimate of the distance between each egg and the nearest aphid at the time of actual oviposition.

The proximity of oviposition to aphids by different syrphid species is shown in Figure 4.2. Some species showed considerable discrimination when selecting an oviposition site, depositing most of their eggs in close proximity to aphids: *E. balteatus*, *S. ribesii*, *Metasyrphus corollae*, and *M. luniger* usually oviposited within 5 mm of the nearest aphid colony. *P. scutatus* and *P. albimanus* laid most of their eggs within 10 mm of the nearest aphid. other species frequently oviposited some considerable distance from aphids: these included *P. manicatus*, *P. peltatus*, *P. clypeatus*, *Melanostoma mellinum* and *M. scalare*.

In general, it seemed that aphidozetic species showed a more marked response to aphid colonies than phytozetic species.

Specific differences in the proximity of eggs to aphids have been recorded previously on Brussels sprouts (Chandler, 1968b) and also on broom (Dixon, 1959). Chandler concluded that the more eggs a given species lays on uninfested plants the greater the mean distance from the nearest aphid of eggs laid on infested plants. In addition, he showed that the mean distance between eggs laid by *Metasyrphus luniger* females and the nearest aphid increased as the females aged. He suggested that this indicated a gradual loss in precision of the oviposition response with age.

Figure 4.2: Proximity of oviposition to the nearest aphid

a) Episyrphus balteatus (n = 373)

b) Sphaerophoria scripta (n = 276)

c) Syrphus ribesii (n = 210)

d) Metasyrphus luniger (n = 28)

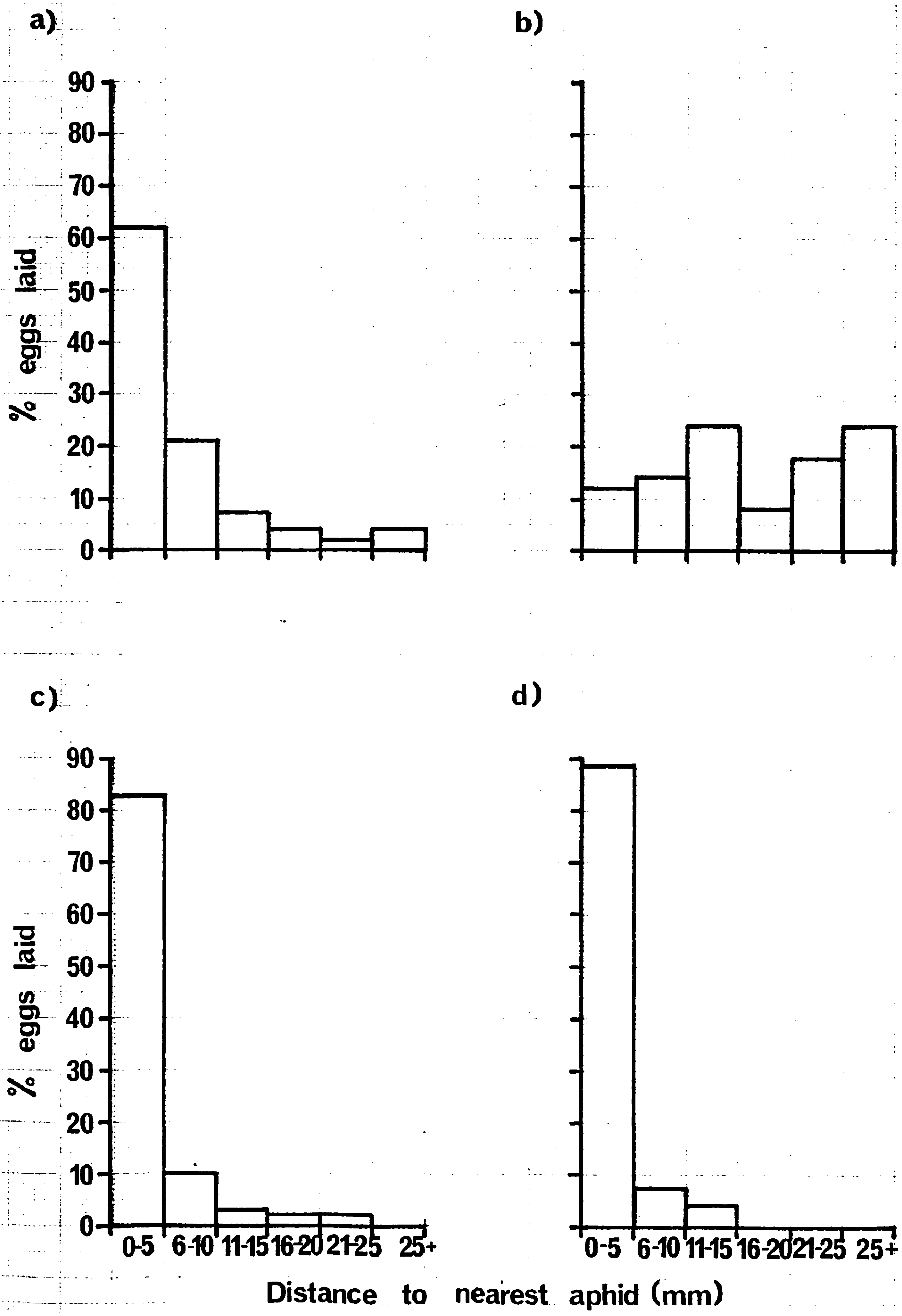

a)
b)
c)
d)
% eggs laid
90
80
70
60
50
40
30
20
10
0
0-5
6-10
11-15
16-20
21-25
25+
Distance to nearest aphid (mm)

Figure 4.2: continued

e) Metasyrphus corollae (n = 10)

f) Platycheirus manicatus (n = 95)

g) Platycheirus albimanus (n = 149)

h) Platycheirus scutatus (n = 47)

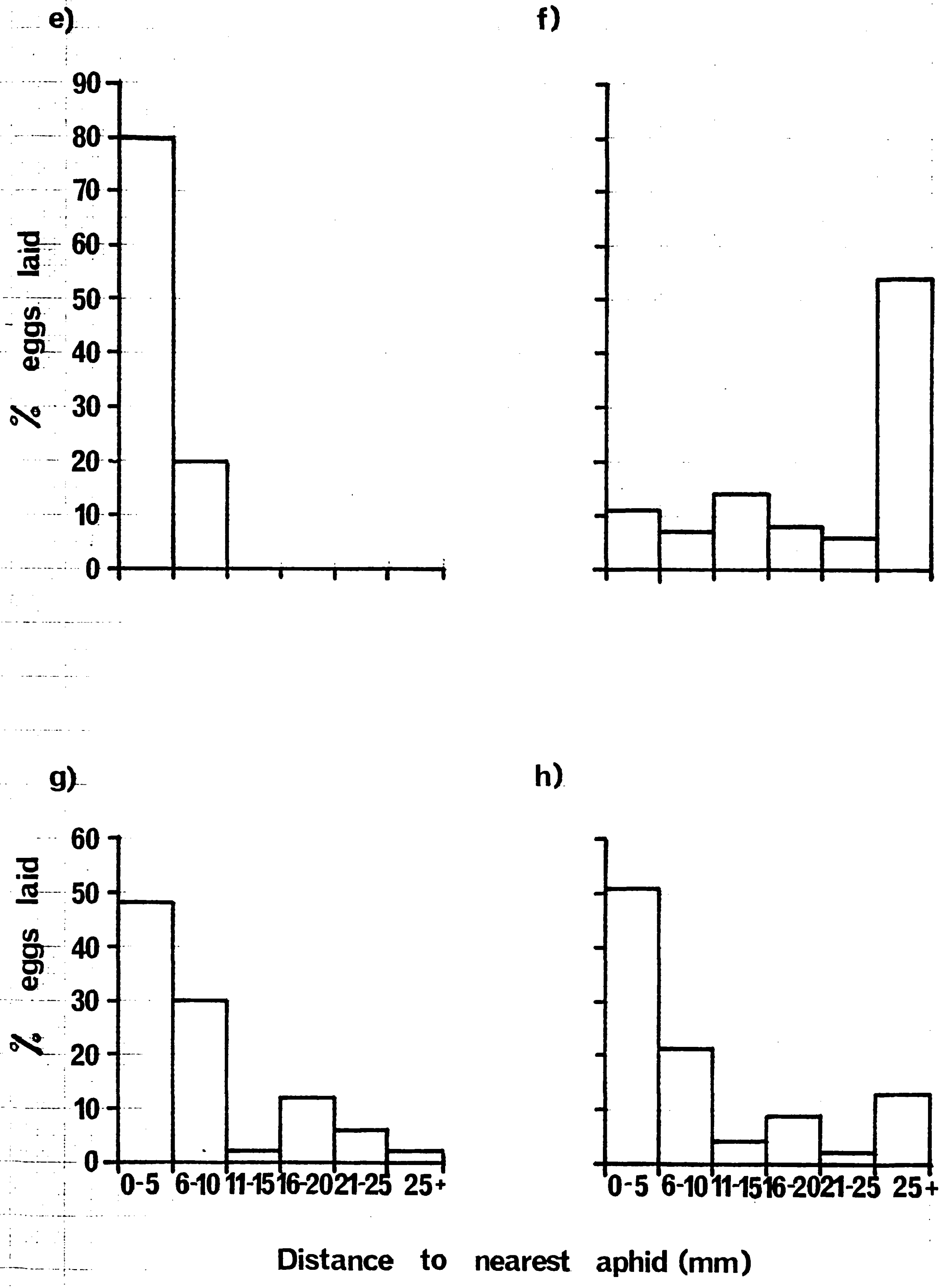

e)
f)
90
80
70
60
50
40
30
20
10
0
% eggs laid
g)
h)
60
50
40
30
20
10
0
% eggs laid
0-5
6-10
11-15
16-20
21-25
25+
0-5
6-10
11-15
16-20
21-25
25+
Distance to nearest aphid (mm)

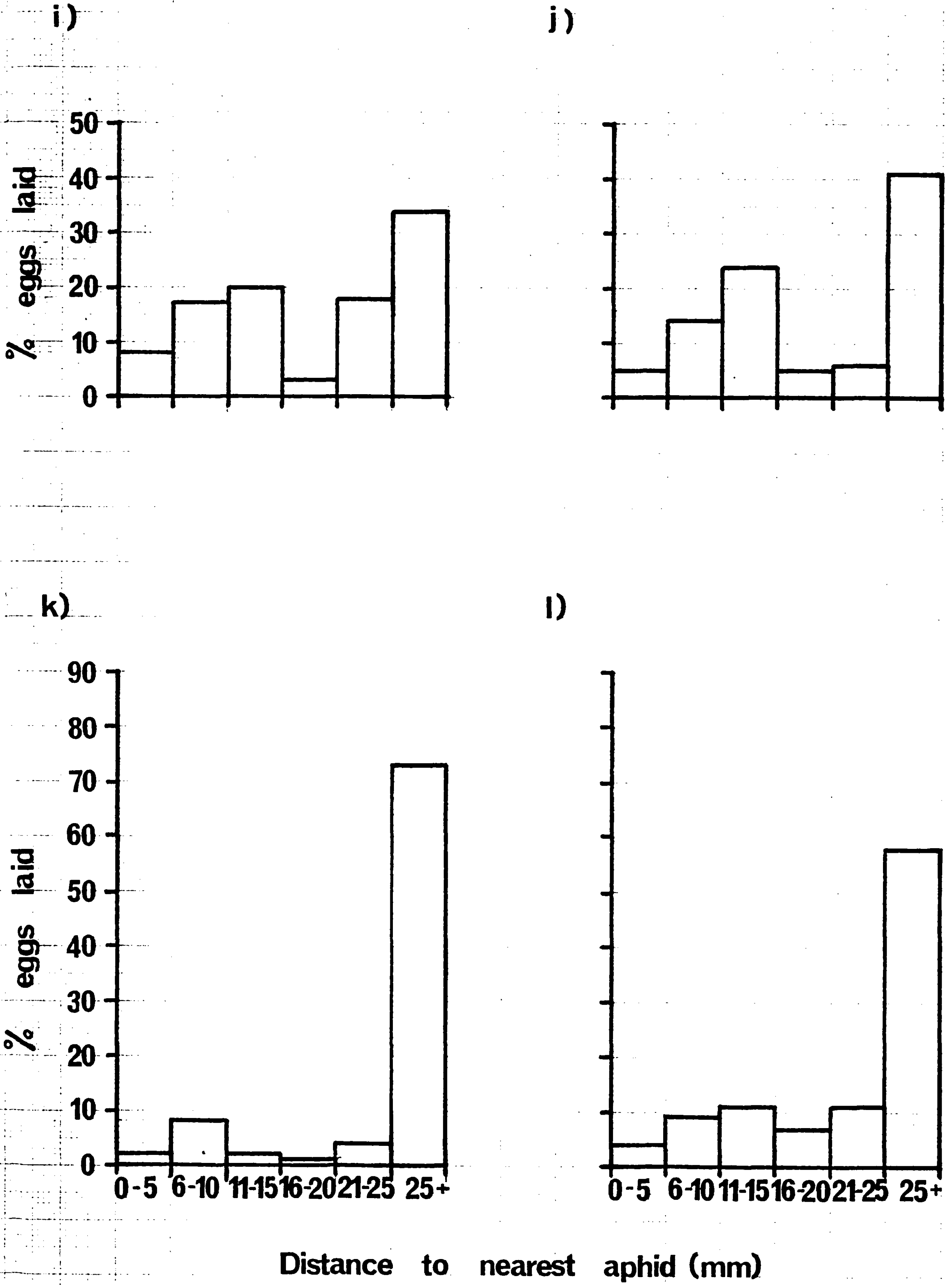
Figure 4.2: continued

i) <u>Platycheirus peltatus</u> (n = 184)

j) <u>Platycheirus clypeatus</u> (n = 88)

k) <u>Melanostoma mellinum</u> (n = 125)

l) <u>Melanostoma scalare</u> (n = 73)


i)
j)
% eggs laid
50
40
30
20
10
0
k)
l)
90
80
70
60
0-5
6-10
11-15
16-20
21-25
25+
Distance to nearest aphid (mm)

4.3 THE EFFECT OF PLANT BACKGROUND ON SYRPHID OVIPOSITION

This section examines the effect of plant background on syrphid oviposition when aphid density and crop type are kept constant.

4.3.1 MATERIALS AND METHODS

Thirty 19-week old Brussels sprout plants (cv Winter Harvest) in 4" diameter pots were used in the experiment. The heart leaves of each plant were removed at the beginning of the experiment to facilitate sampling and all plants were infested with approximately 200 B. brassicae aphids. Ten plants were placed in each of the three habitats:

1) Within a Brussels sprout crop (43 m x 40 m),
2) At the centre of an area of fallow ground (40 m x 42 m)

and 3) In a weedy grass verge bordering both the Brussels sprout crop and fallow ground.

The plants were examined at daily intervals and the number of syrphid eggs recorded. All eggs were removed from the plants and transferred to the laboratory for identification. The aphid infestations on the plants were checked at two-day intervals and it was ensured that the aphid population per plant remained approximately constant throughout the experiment. The experiment was carried out on nine successive days during late August and early September 1980 (25, 26, 27, 28 August; 4, 5, 6, 7, 8 September).

Adult syrphid activity in each of the three habitats was also monitored throughout the experiment using Malaise traps sited immediately adjacent to the potted Brussels sprout plants. The traps were sampled daily at 2100 h and all adult syrphids captured were identified.

4.3.2 RESULTS AND DISCUSSION

A list of the syrphid species caught in the Malaise traps in each site is given in Table 4.19. Thirty-four species were recorded overall and, of these, twenty-three have an aphidophagous larval stage. More syrphids were caught in the Malaise trap sited in the grassy verge than in the other two traps ($\chi^2 = 21.59$, 2df, $p < 0.001$). More females were caught overall than males ($\chi^2 = 102.26$, 1 df, $p < 0.001$). This phenomenon was discussed in Chapter 2 where it was suggested that the Malaise trap may be biassed towards catching females as a result of ecological or behavioural differences between the sexes. There was a highly signficant difference in the ratio of males:females in different sites: the ratio was highest in the grassy verge (1:3) and lowest within the brassica crop (1:14) ($\chi^2 = 13.48$, 2 df, $p < 0.001$). These results may indicate that males visit the grass verge to feed on flowers but are not so active in the vicinity of oviposition sites alone.

The seven most abundant species recorded were all species with an aphidophagous larval stage and included Sphaerophoria scripta, Platycheirus albimanus, P. peltatus, P. angustatus, Melanostoma mellinum, M. scalare and Syrphus ribesii. Some of these species were more active in certain sites than in others: Sph. scripta was most active within the brassica crop ($\chi^2 = 7.81$, 2 df, $p < 0.05$); S. ribesii ($\chi^2 = 16.34$, 2 df, $p < 0.001$), P. angustatus ($\chi^2 = 10.80$, 2 df, $p < 0.01$), and M. scalare ($\chi^2 = 32.84$, 2 df, $p < 0.001$) were all most active in the grassy verge, and P. albimanus was most active over the bare soil ($\chi^2 = 12.26$, 2 df, $p < 0.01$). Other species, eg P. peltatus and M. mellinum were equally active in all three sites.

Table 4.20 shows the number of eggs laid on the ten potted Brussels sprout plants placed in each site. Eggs belonging to ten different syrphid species were collected from these plants during the experiment. All were species with an aphidophagous larval stage. The two most abundant species recorded were P. peltatus and Sph. scripta. Again, there were specific differences in the preferred oviposition site: Sph. scripta laid significantly more eggs on the Brussels sprout

Table 4.19: Adult syrphid activity in different habitats

Species	Number of syrphids caught in different sites											
	Crop			Verge			Bare Soil			Total		
	♂♂	♀♀	T	♂♂	♀♀	T	♂♂	♀♀	T	♂♂	♀♀	T
Chrysotoxum bicinctum	-	-	-	-	2	2	-	2	2	-	4	4
Dasysyrphus albostriatus	-	1	1	-	1	1	-	-	-	-	2	2
Dasysyrphus tricinctus	-	-	-	-	1	1	-	-	-	-	1	1
Didea fasciata	-	-	-	-	-	-	-	1	1	-	1	1
Epistrophe grossulariae	-	-	-	-	-	-	-	1	1	-	1	1
Episyrphus balteatus	-	1	1	-	-	-	2	-	2	2	1	3
Meligramma cincta	-	1	1	-	-	-	-	1	1	-	2	2
Meliscaeva cinctella	-	-	-	-	1	1	-	4	4	-	5	5
Metasyrphus latifasciatus	-	-	-	-	-	-	-	1	1	-	1	1
Metasyrphus luniger	-	1	1	-	1	1	-	-	-	-	2	2
Sphaerophoria scripta	2	16	18	4	6	10	1	4	5	7	26	33
Syrphus ribesii	-	1	1	-	14	14	-	3	3	-	18	18
Baccha obscuripennis	-	-	-	-	1	1	-	1	1	-	2	2
Melanostoma mellinum	-	3	3	3	6	9	2	6	8	5	15	20
Melanostoma scalare	-	1	1	5	15	20	-	1	1	5	17	22
Platycheirus albimanus	-	7	7	3	6	9	-	13	13	3	26	29
Platycheirus angustatus	-	2	2	1	10	11	-	2	2	1	14	15
Platycheirus clypeatus	-	1	1	1	2	3	-	1	1	1	4	5
Platycheirus fulviventris	-	1	1	-	1	1	-	-	-	-	2	2
Platycheirus peltatus	2	15	17	2	10	12	1	12	13	5	37	42
Platycheirus scambus	-	-	-	-	1	1	-	-	-	-	1	1
Platycheirus scutatus	-	1	1	-	-	-	-	-	-	-	1	1
Pyrophaena granditarsa	-	1	1	1	-	1	-	-	-	1	1	2

Cont/. . .

Table 4.19: continued

Species	Number of syrphids caught in different sites											
	Crop			Verge			Bare Soil			Total		
	♂♂	♀♀	T	♂♂	♀♀	TT	♂♂	♀♀	T	♂♂	♀♀	T
Cheilosia bergenstammi	-	1	1	-	-	-	-	-	-	-	1	1
Cheilosia illustrata	-	1	1	-	-	-	-	-	-	-	1	1
Cheilosia variabilis	-	-	-	-	-	-	-	1	1	-	1	1
Rhingia campestris	-	-	-	-	-	-	-	3	3	-	3	3
Neoascia podagrica	-	-	-	-	1	1	-	1	1	-	2	2
Eristalis arbustorum	-	-	-	1	-	1	-	-	-	1	-	1
Eristalis nemorum	-	-	-	1	1	2	-	-	-	1	1	2
Helophilus pendulus	-	-	-	1	1	2	-	-	-	1	1	2
Pipiza sp	-	1	1	-	-	-	-	-	-	-	1	1
Syritta pipiens	-	2	2	7	2	9	-	-	-	7	4	11
Xylota sylvarum	-	-	--	-	-	-	1	-	1	1	-	1
Total number of individuals	4	56	60	30	83	113	7	58	65	41	197	238
Number of species		17			22			20			34	

plants within the brassica crop than on the plants in the other two sites ($\chi^2 = 40.09$, 2 df, $p < 0.001$). S. ribesii oviposited preferentially on the Brussels sprout plants in the grassy verge ($\chi^2 = 6.40$, 2 df, $p < 0.05$), as did both M. mellinum ($\chi^2 = 11.56$, 2 df, $p < 0.01$) and M. scalare ($\chi^2 = 37.29$, 2 df, $p < 0.001$). P. albimanus laid most eggs on the Brussels sprout plants sited at the centre of the bare soil area ($\chi^2 = 45.45$, 2 df, $p < 0.001$). P. peltatus laid significantly fewer eggs on the plants in the grassy verge than on the plants in the other sites ($\chi^2 = 45.35$, 2 df, $p < 0.001$). The number of eggs laid by other species was too low to be analysed statistically.

Table 4.20: Number of eggs laid by different syrphid species on potted Brussels sprouts in different habitats

Species	Number of eggs laid in each site			
	Crop	Verge	Bare soil	Total
Episyrphus balteatus	3	-	2	5
Metasyrphus luniger	1	-	-	1
Sphaerophoria scripta	51	4	17	72
Syrphus ribesii	4	12	4	20
Melanostoma mellinum	6	12	2	20
Melanostoma scalare	-	25	4	29
Platycheirus albimanus	10	3	41	54
Platycheirus angustatus	-	5	-	5
Platycheirus clypeatus	8	-	4	12
Platycheirus peltatus	53	8	68	129
Total number of eggs laid	136	69	142	347
Number of species ovipositing	8	7	8	10

Figure 4.3 compares the activity and oviposition patterns of different syrphid species in each site. The results are expressed in

terms of the percentage of all individuals/eggs recorded in each site represented by different syrphid species. In general, the egg-laying patterns in a particular site correlated well with adult female activity in that site. This implies that the Malaise trap catches could be considered to be reliable indicators of syrphid oviposition activity.

Specific differences in the effect of plant background on syrphid oviposition patterns have also been reported by Bombosch (1963), Pollard (1971) and Smith (1976). Smith found that plant background greatly influenced the egg-laying patterns of Melanostoma spp and some Platycheirus spp but had little effect on the oviposition behaviour of Syrphus spp. Oviposition by the latter species were more influenced by the distribution of aphids.

It is interesting that the highest numbers of adults were captured in the grassy verge site although the lowest egg numbers were recorded here. It may be postulated that the comparatively low egg numbers recorded on sprout plants surrounded by weeds are due to syrphid females distributing their eggs between weeds and sprout plants. However, casual inspection of the weeds immediately adjacent to the sprout plants indicated that this was not necessarily the case. Most of the species listed in Table 4.20 laid very few eggs on the weeds. The only exceptions were the two Melanostoma spp whose eggs were found in large numbers on weed plants, particularly Raphanus raphanistrum and Sinapis arvensis. An alternative explanation is that many of the adults captured in the grassy verge were feeding on flowers and not ovipositing.

The results of this study confirm that syrphid oviposition may be influenced by plant background. The presence of weeds in a crop can affect syrphid oviposition both directly by providing alternative oviposition sites and/or indirectly by subtly altering the optical attractiveness of the crop (in terms of plant height, density, contrast or colour of the background) to ovipositing syrphids. Phytozetic species appear to be more influenced by the presence of weeds than aphidozetic species.

Figure 4.3: The relationship between adult syrphid activity and oviposition on potted Brussels sprout plants in different habitats

a) Crop

b) Weedy verge

The number of adult females of each species is expressed as a percentage of all the females caught in a particular site. In addition, the number of eggs laid by each syrphid species in a particular site is expressed as a percentage of all eggs laid in that site.

Key

1	Episyrphus balteatus
2	Metasyrphus luniger
3	Sphaerophoria scripta
4	Syrphus ribesii
5	Melanostoma mellinum
6	Melanostoma scalare
7	Platycheirus albimanus
8	Platycheirus angustatus
9	Platycheirus clypeatus
10	Platycheirus peltatus
░	Adult females
□	Eggs

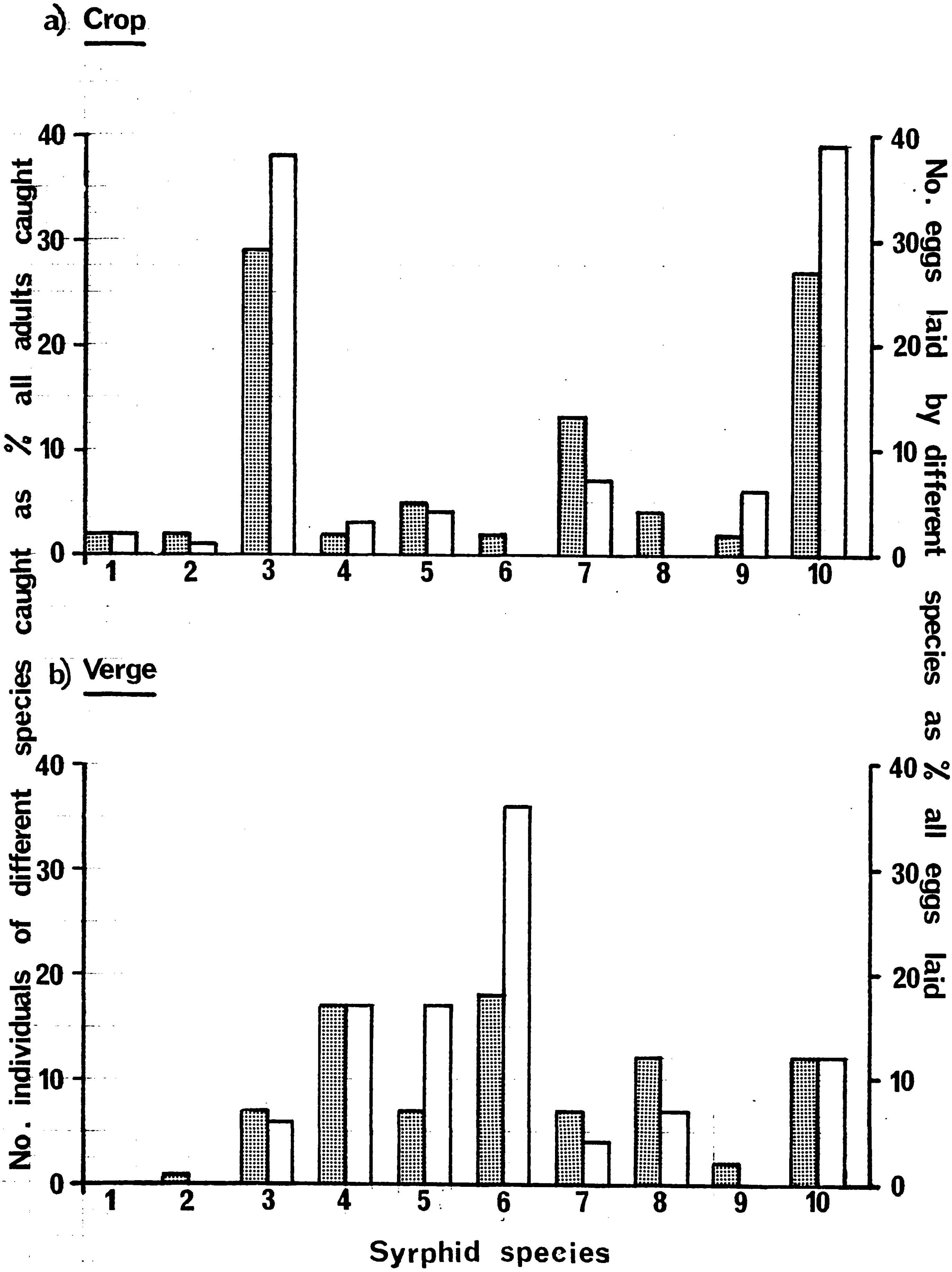

a) Crop
b) Verge
No. individuals of different species caught as % all adults caught
No. eggs laid by different species as % all eggs laid
0
10
20
30
40
1
2
3
4
5
6
7
8
9
10
Syrphid species

Figure 4.3: continued

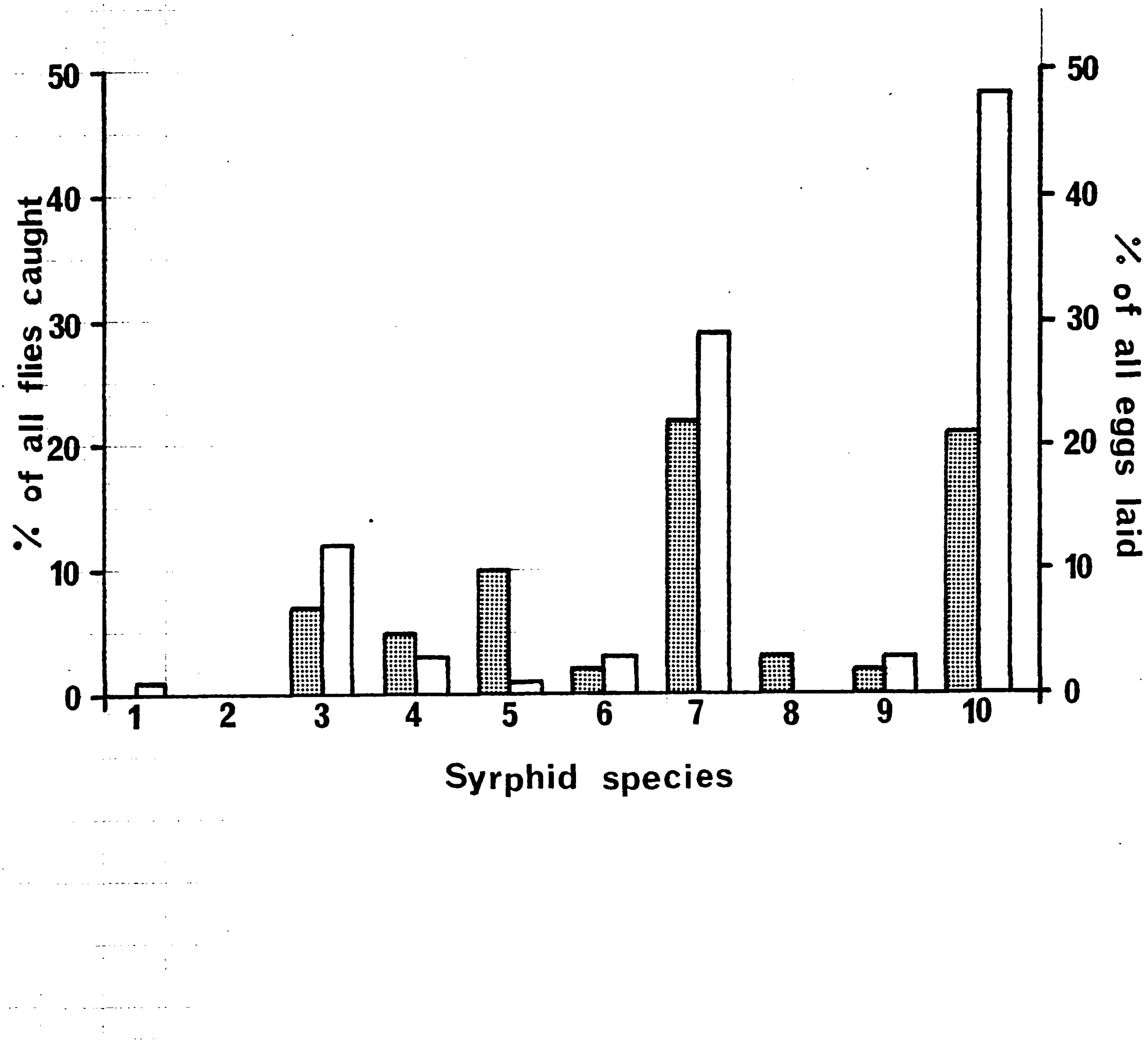
c) Bare soil

The number of adult females of each species is expressed as a percentage of all the females caught in a particular site. In addition, the number of eggs laid by each syrphid species in a particular site is expressed as a percentage of all eggs laid in that site.

<u>Key</u>

1	Episyrphus balteatus
2	Metasyrphus luniger
3	Sphaerophoria scripta
4	Syrphus ribesii
5	Melanostoma mellinum
6	Melanostoma scalare
7	Platycheirus albimanus
8	Platycheirus angustatus
9	Platycheirus clypeatus
10	Platycheirus peltatus
░	Adult females
□	Eggs

c) **Bare soil**


50
40
30
20
10
0
% of all flies caught
50
40
30
20
10
0
% of all eggs laid
1
2
3
4
5
6
7
8
9
10
Syrphid species

4.4 GENERAL DISCUSSION AND CONCLUSIONS

The oviposition patterns of the adult syrphid reflect the nutritional requirements of the larvae. The oviposition strategies of aphidophagous syrphids can be conveniently divided into two main groups (aphidozetic and phytozetic) on the basis of the stimuli required to elicit oviposition. The larvae of aphidozetic species are usually obligate aphidophages and often require large numbers of aphids to complete development. Oviposition by aphidozetic adults occurs mainly in response to aphid-associated stimuli and eggs are usually laid singly, close to well-established aphid colonies. In contrast, the larvae of phytozetic species are believed to be only facultative aphidophages which can complete development on a diet of a few aphids only, supplemented if necessary by non-aphid food. Oviposition site selection by phytozetic adults is much less dependent on the presence of aphids and eggs are often laid in small batches on uninfested plants. The batch-laying habit is thought to be a mechanism that ensures survival of at least one member of the batch: if aphids are scarce, then the first-emerged larvae may cannibalise the remainder, thus sustaining itself during the search for food elsewhere.

Of the species encountered in the present study, Episyrphus, Syrphus and Metasyrphus spp could be classified as aphidozetic species whereas Melanostoma and some Platycheirus spp adopted the phytozetic strategy. It is generally accepted that the phytozetic strategy is the longer-established of the two and that the aphidozetic strategy developed with the evolution of obligate aphidophages.

Chapter 4 examined the egg-laying patterns of aphidophagous syrphids attacking the cabbage aphid, B. brassicae, in brassica crops. The results presented here show how competition between the larvae of different species may be reduced or even avoided by the oviposition strategies of the adult female. One of the most effective mechanisms that reduces inter-specific larval competition is the temporal separation of the peak egg-laying periods of different syrphid species. In the study described in Section 4.2, a complex of syrphids attacked the aphid throughout the study period with the most abundant species occurring at different times. Such a situation has valuable implications in relation to the continuous effective biological control of the aphid.

Spatial separation of the larvae of different species may occur by differential responses to aphid and/or aphid host-plant factors. The oviposition patterns of aphidozetic species are influenced by the number of aphids present on a plant: different aphidozetic species prefer different sizes of aphid population for optimal oviposition. In addition, once a plant has been selected for oviposition there may still be further selection for aphid colonies of a particular size. The oviposition patterns of phytozetic species are influenced mainly by the size, shape and general appearance of the aphid host-plant and different species prefer different plant species for oviposition. The presence of weeds in a crop was also shown to affect the oviposition behaviour of phytozetic species: weeds influence oviposition either directly (by providing alternative oviposition sites) or indirectly (by altering the optical attractiveness of the crop).

However, despite specific differences in the egg-laying patterns of adult females, eggs and larvae belonging to different species were frequently found together on the same plant and it seems inevitable that some element of competition does occur. Competition between larvae can radically influence the bionomics of the species (Hagvar, 1972, 1973). Rotheray (unpubl) has shown that an obligate aphidophage (Syrphus ribesii) has a higher attack rate, lower handling time and a greater speed of movement at every larval instar, and for every aphid instar, than a facultative aphidophage (Melanostoma mellinum). In Section 4.2.2.3 it was noted that the abundance of certain aphidozetic syrphid species, relative to the abundance of other species, increased successively from the egg through to the pupal stage, whereas the relative abundance of some phytozetic species showed a corresponding decline. There are several possible explanations. There have been no studies to date that have compared the mortality factors acting on the immature stages of different syrphid species. It seems possible that if food resources are scarce, cannibalism among larval members of the same egg batch may be a significant factor influencing the survival of phytozetic larvae. Secondly starved larvae are very active and may rapidly move off plants if no aphids are found. Thus larval migration from low density plants may well be higher than from high density plants and this might account for the apparent reduction in relative abundance of P. peltatus from egg to the pupal stage. Thirdly, the competitiveness of different larval species has been shown to vary considerably (Rotheray, unpubl) and interactions between different species on the same aphid host plant may have significant effects on the bionomics of these species. More studies on intra- and interspecific competition in syrphid larvae are necessary before we can hope to evaluate the true significance of the adult oviposition patterns and also the usefulness of different syrphid species as potential biocontrol agents of aphids.

CHAPTER 5

GENERAL ASPECTS OF THE BIOLOGY AND BEHAVIOUR OF EPISYRPHUS BALTEATUS FLIES IN THE LABORATORY

5.1 INTRODUCTION

Previous chapters have examined the foraging patterns of ovipositing syrphid flies in relation to exogenous factors such as climate and the distribution of adult and larval food resources. However, these patterns are also influenced by endogenous factors (eg nutritional status, ovipositional drive, innate activity rhythms), and a good understanding of the insect's biology and behaviour is essential if a complete picture of oviposition strategy is to be achieved.

The reproductive potential of an insect is determined by its fecundity and longevity. Fecundity is influenced by various factors. The nutrients for egg production come from either of two sources: adult feeding or reserves carried over from the larval stage. Studies on Heliconiine butterflies have demonstrated that a third source of of nutrients may involve substances transferred from the male to the females during mating (Boggs and Gilbert, 1979; Boggs, 1981). Several authors have noted that little or no oviposition occurs without adult feeding: pollen appears to be essential for ovarial maturation (Schneider, 1948; Doucette and Eide, 1955; Adashkevich and Karelin, 1972; Maier, 1978). The nutritional value of different pollens may vary: Kurir (1963) found that *Narcissus* pollen was inadequate for ovarial development for both *Pipiza festiva* Meig. and *Heringia heringia* Zett., while Tanke (1976) reported that *Episyrphus balteatus* rejected coniferous pellen. Kurir (1963) suggested that more than one type of pollen was needed for optimal development of the reproductive system.

Larval nutrition has also been shown to affect adult fecundity. Periods of prolonged starvation during the larval stage may result in the production of 'dwarf' adults (Scott, 1939; Wilkening, 1961; Růžička and Cairo, 1976) which, in the case of females, have lowered fecundity and may even be sterile (Cornelius and Barlow, 1980).

Egg production is also influenced by environmental factors: in *Drosophila*, retentions and resorptions of mature eggs are rare in mated, well-fed females when environmental conditions are favourable (Cohet and David, 1978; Kambysellis *et al*, 1980), but adverse conditions of temperature and relative humidity can drastically reduce egg production. Field-caught *D. melanogaster* contain only one-third as many mature eggs as laboratory-reared females (Roff, 1981). Flight can cause a reduction in Dipteran egg production (Roff, 1977). The fecundity of *Sphaerophoria scutellaris* has been shown to be strongly affected by temperature and relative humidity (Lal and Haque, 1955).

Another important factor influencing reproductive output is the availability of suitable ovipositional stimuli: egg retention (*Metasyrphus corollae*: Dixon, 1959) or resorption (*Merodon equestris*: Lyon, 1965, 1968) has been shown to occur in the absence of such stimuli. Studies on the cabbage root fly (*Delia radicum*) have demonstrated that egg retention occurs when females are denied a mate or a suitable oviposition site whereas egg resorption takes place when the flies are deprived of an adequate diet. Moreover, the age at which a females becomes mated also seems to affect total egg output (Finch, 1974).

Longevity is influenced by nutritional and environmental factors. Doucette and Eide (1955) and Lal and Haque (1955) demonstrated that different sugars vary considerably in their effect on longevity. Temperature and relative humidity also have an important effect: high temperature combined with low humidity adversely affected both the longevity and fecundity of laboratory reared *Sphaerophoria scutellaris* whereas high humidity had a beneficial effect (Lal and Haque, 1955).

Little published data is available on the longevity of wild syrphids. However, evidence from a study by Gilbert (1981a) suggests that in the field, females rarely live long enough to lay more than one complete batch of eggs: predation is thought to be an important mortality factor acting on the adult stage.

It was demonstrated in an earlier chapter (Chapter 3) that many syrphids exhibit diel patterns of flight activity in the field. The periodicity of insect activity is influenced by both exogenous and endogenous factors. The exogenous components are mainly climatic and their effect on the diel patterns of syrphid flight have already been described in Chapter 3. The most important endogenous factors are rhythms: periodically-repeated fluctuations controlled by an innate time-measuring sense or biological clock (Corbet, 1966). The phase of the rhythm is usually set by external time cues and normally follows a diel periodicity. Examples of such rhythms are the timing of emergence, flight and oviposition. The phase and expression of the rhythm may be modified by various physiological factors such as hunger (Green, 1964), age (Corbet, 1960) and the stage in the gonotrophic cycle (Davies, 1961; Fredeen, 1963).

Observations on an insect's biology and behaviour are best carried out under closely-controlled conditions in the laboratory. Unfortunately, many species of aphidophagous syrphid are difficult to rear in captivity because of their exacting dietary and behavioural requirements: the adults need carbohydrate and protein to mature their eggs and the larvae require large numbers of live aphids. Many species copulate exclusively in flight and demand exacting conditions with respect to space, temperature, humidity and illumination to mate in captivity. Metasyrphus corollae is the most easily-cultured species: adults will copulate in preserving jars even after amputation of the wings (Bombosch, 1957; Barlow, 1961). Consequently, most of the laboratory studies on syrphid biology have used this species. Other syrphid species that have been reared in captivity include Metasyrphus luniger (Dixon, 1959; Tokmakoglu, 1965), Episyrphus balteatus (Bombosch, 1957; Tanke, 1976), Syrphus ribesii and S. vitripennis (Bombosch, 1957). In the present study, a rearing technique was developed for Episyrphus balteatus which successfully bred twenty-two successive generations of this species in the laboratory.

The following chapter comprises a collection of observations on the biology and behaviour of Episyrphus balteatus flies in the laboratory. This species is very common in Britain where it is ubiquitous in its distribution. It was selected for study mainly on account of the relative ease with which it may be reared in the laboratory.

The system used for rearing Episyrphus balteatus flies in the laboratory is described in the first section of the chapter. The following section examines the fecundity, fertility and longevity of laboratory-reared flies. The third section describes the characteristic sequence of behaviours exhibited by ovipositing Episyrphus balteatus females. The fourth section of this chapter considers the diel patterns of feeding, oviposition and flight activity of Episyrphus balteatus flies under closely-controlled laboratory conditions. The activity budgets of male and female flies are compared and the effect of age on these activity patterns is considered.

The final section discusses the relevance of laboratory studies on biology and behaviour to the field situation.

5.2 REARING TECHNIQUES FOR EPISYRPHUS BALTEATUS FLIES

5.2.1 Syrphid cultures

The syrphid culture was initiated using gravid females collected from the field.

Adult flies were maintained in a large wooden-framed glass cage (150 x 114 x 105 cm) at 20 ± 0.5 °C, 65 ± 5% RH and a 16 h photoperiod. The flies were provided with a diet of 10% sucrose solution, water and pollen. The sucrose solution and water were presented in glass bottles containing blotting-paper wicks, flies could alight on the wicks and feed without risk of drowning in the food. The pollen was a commercially-obtained mixture of several different pollens, collected from bees. Pollen grains were moistened slightly with sucrose solution and presented to the flies in plastic petri dishes. The food was placed on wooden platforms at a height of approximately 0.3 m above the cage floor. These platforms are an essential feature of the cage: adult flies seldom visit the cage floor and will not feed if the food is placed at floor-level. Fresh food was provided at 2-day intervals. A diagram of the adult cage is shown in Figure 5.1.

The flies were provided with potted Brussels sprout plants (cv Winter Harvest) infested with the cabbage aphid, Brevicoryne brassicae, four times each week. Females were allowed to oviposit for approximately 5 hours and then the plants were removed from the cage. Large numbers of eggs were obtained in this way.

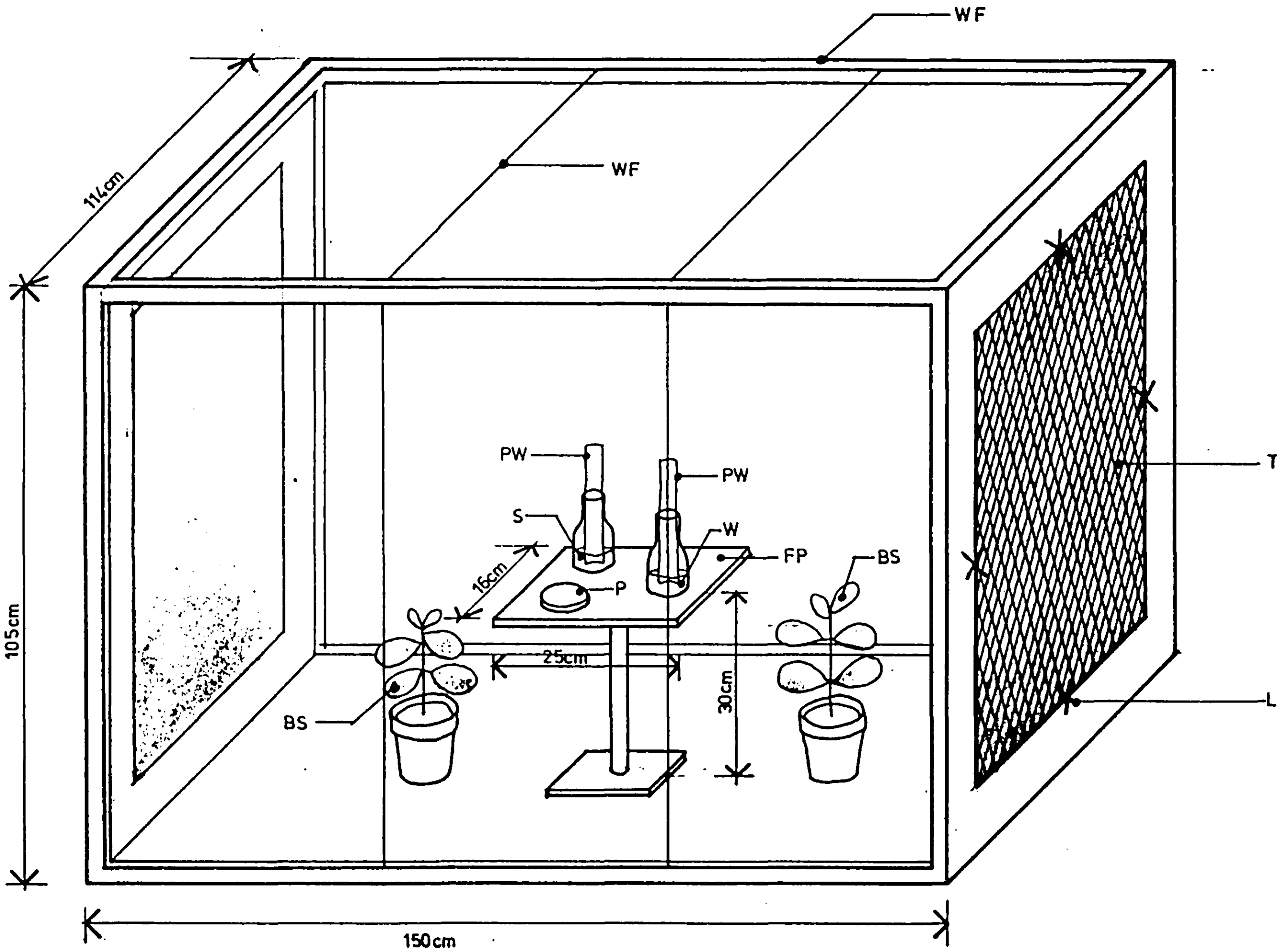
The eggs were transferred on the sprout plants to a second rearing room maintained at 20 ± 0.5 °C, 70 ± 5% RH and 16 h photoperiod. Eggs normally hatched within two days and the young larvae were allowed to remain on the plants for a further one or two days. They were then transferred to plastic trays (30 x 45 x 3 cm) containing newly-detached Brussels sprout leaves infested with B. brassicae. A separate tray was used for each batch of larvae. Fresh aphid-infested leaves were supplied daily so that the larvae were assured of an abundant food-supply. This is important as syrphid larvae are highly cannibalistic and will readily feed on syrphid eggs and other larvae in the absence of aphid food. This problem may be further reduced by keeping different larval instars on different trays. The larvae usually pupated within 10 days of hatching from the egg. Pupae were collected from the trays and placed in a wooden-framed emergence cage with terylene net sides and top, together with sucrose solution, water and pollen. The adults emerged approximately 8 days later and were transferred to the adult culture cage.

E. balteatus larvae were also reared successfully on Myzus persicae Sulz. on Brussels sprouts and on Acyrthosiphon pisum on beans (Vicia faba cv Ticminer).

Figure 5.1: Diagram of the cage used for rearing adult Episyrphus balteatus

Key

T - Terylene net door
L - Latch (allowing removal of door)
S - Sucrose solution
P - Pollen
W - Water
BS - Aphid-infested Brussels sprout plant
FP - Feeding platform
PW - Paper wick
WF - Wooden frame of cage


WF
WF
114cm
105cm
PW
PW
S
W
FP
BS
P
16cm
25cm
30cm
BS
T
L
150cm

5.2.2 Aphid cultures

A large culture of B. brassicae was maintained on potted Brussels sprout plants (cv Winter Harvest) in 50 x 50 x 60 cm wooden-framed cages with a wooden floor and a glass top and sides. The cages were kept in a rearing room maintained at 20 ± 0.5 °C, 65 ± 5% RH and a 16 h photoperiod. New plants were provided when necessary. The cultures were checked regularly for aphid parasites.

5.3 STUDIES ON THE BIOLOGY OF EPISYRPHUS BALTEATUS FLIES IN THE LABORATORY

5.3.1 MATERIALS AND METHODS

All experiments were carried out in a room illuminated for 16 h and maintained at 20 ± 1 °C and 65% RH.

Ten newly-emerged flies of each sex were placed in pairs (one male and one female) in standardized 50 x 45 x 70 cm wooden-framed cages. The flies were provided with 10% sucrose solution, pollen and water. Fresh food was supplied daily. Each cage also contained a single potted Brussels sprout plant (cv Winter Harvest) infested with a standard number (approximatley 300) of Brevicoryne brassicae aphids. These plants were infested by confining small numbers of aphids in clip cages on the ventral surfaces of three leaves. The same leaves were selected for infestation on all plants. This method ensured that the distribution of aphids on all plants was approximately similar. Females were allowed to oviposit for a period of ten hours each day and then the plants were removed. The daily number of eggs laid by each female was recorded, together with the percentage of eggs hatching. The distribution of eggs on the plant in relation to aphids was also determined by measuring the distance between each syrphid egg and the nearest aphid.

The experiment continued until all the flies were dead. After death, the ovaries of female flies were dissected out in Ringer's solution and the number of ovarioles recorded.

5.3.2 RESULTS AND DISCUSSION

5.3.2.1 Copulation

Copulation was first observed in 3-day old flies. Both sexes mated frequently during the first fifteen days after emergence but much less frequently thereafter. Copulation occurred exclusively in flight and lasted for a few seconds only.

5.3.2.2 Longevity

The life-span curves for male and female flies are shown in Figure 5.2. During the first 22 days following emergence, the survival rates of males and females were similar. After day 22, however, the proportion of surviving males became progressively higher than that of females. The average longevity of males was 44 ± 12 days and of females was 30 ± 9 days.

5.3.2.3 Fecundity and fertility

Ovarial dissections of ten female flies showed that each ovary consisted of a number of polytrophic egg-tubes or ovarioles containing oocytes at varying stages of development. The number of ovarioles per ovary ranged from 35-55 with an average of 42.3 ± 5.8. Assuming that each ovariole produces one egg during a single ovarian cycle, each female is capable of laying approximately 84 eggs per cycle.

Table 5.1 summarizes data on the fecundity and fertility of the ten female flies used in these experiments. The results for individual females are given in Table D1 (Appendix D). The total number of eggs laid by a single female during her life-time ranged from 137 to 1521 with an average of 862 ± 395 eggs per female. These results imply that each female undergoes several gonotrophic cycles during her lifetime.

The average fertility of these eggs (in terms of the percentage of eggs hatching) was 63 ± 10%. The pre-oviposition period averaged 8.8 ± 3.0 days whilst the oviposition period was 19.0 ± 7.0 days. The post-oviposition period averaged 0.9 ± 1.5 days with most females laying eggs almost to the day they died.

Table 5.1: Fecundity and fertility of ten laboratory-reared *Episyrphus balteatus* flies

Average number of eggs/♀♀ (± SD)	862 ± 395
Average length of pre-oviposition period (days) (± SD)	8.8 ± 3.0
Average length of oviposition period (days) (± SD)	19.0 ± 7.0
Average length of post-oviposition period (days) (± SD)	0.9 ± 1.5
Average % of eggs hatching (± SD)	63 ± 10

Figures 5.3 a and b illustrate the daily oviposition patterns for two different females. The figure indicates an oscillating pattern of egg production with a series of peaks representing days when large numbers of eggs were laid, separated by intervals of 1-2 days when egg production was low. The figure also shows the percentage of eggs laid each day that hatched. Again, there was considerable variation with daily hatching percentages sometimes varying from 0 to 100% for the same female. There appeared to be no clear relationship between the number of eggs laid per day and the percentage of eggs that hatched. Variation in the daily fertility of laboratory-reared *Metasyrphus corollae* females has been reported by Barlow (1961) and Benestad (1970a). Barlow suggested that fertility depends, at least in part, on sensory stimuli perceived by the ovipositing female. Day-to-day variation in the strength of such stimuli may influence the release of sperm from the spermathecae.

Figure 5.2: Life-span curves for male and female *Episyrphus balteatus* flies in the laboratory

a) Males

b) Females

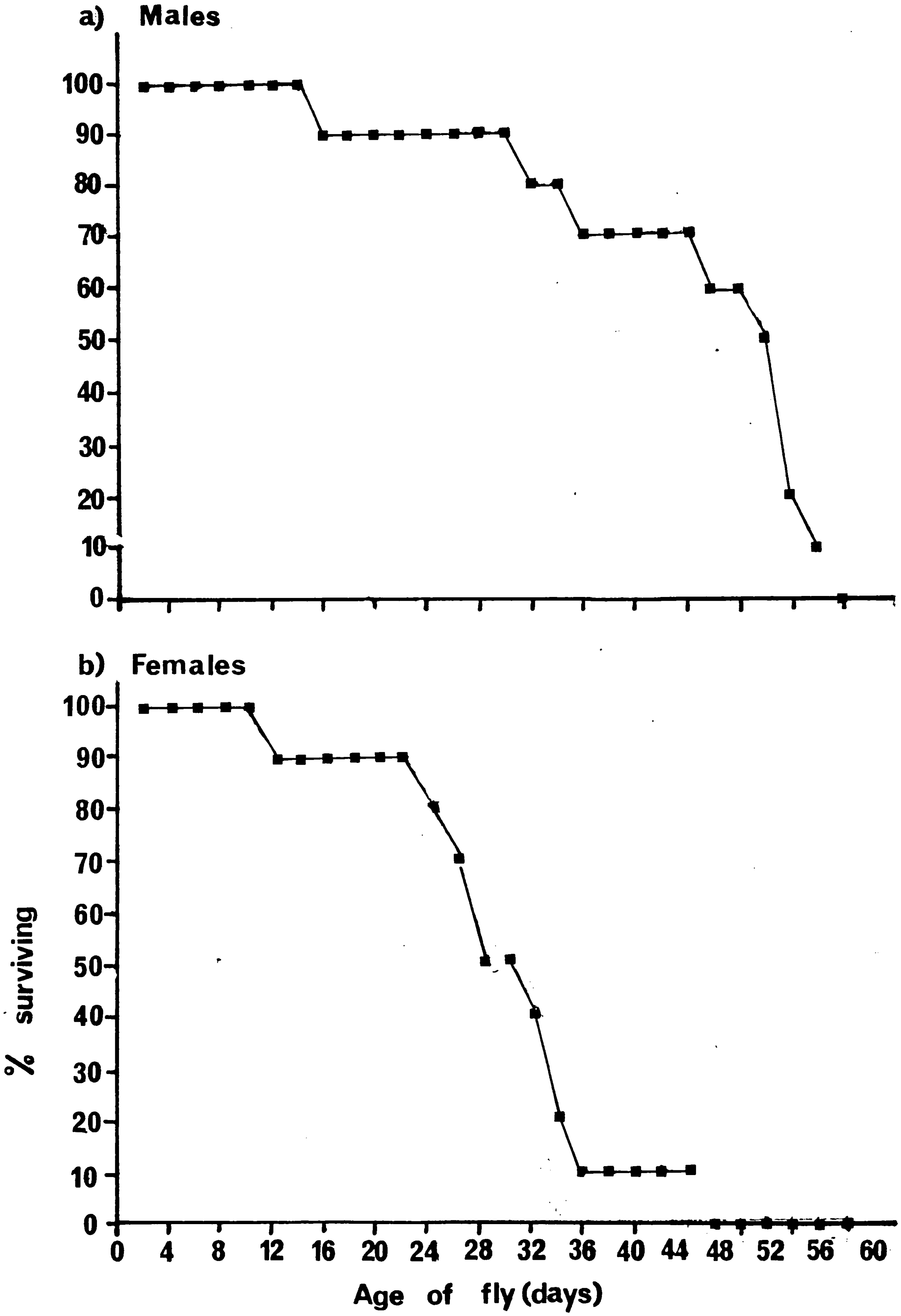

a) Males
b) Females
% surviving
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
Age of fly (days)

Figure 5.3: Daily egg-laying patterns of two *Episyrphus balteatus* females

●——● Number of eggs laid

○——○ Percentage of eggs hatching

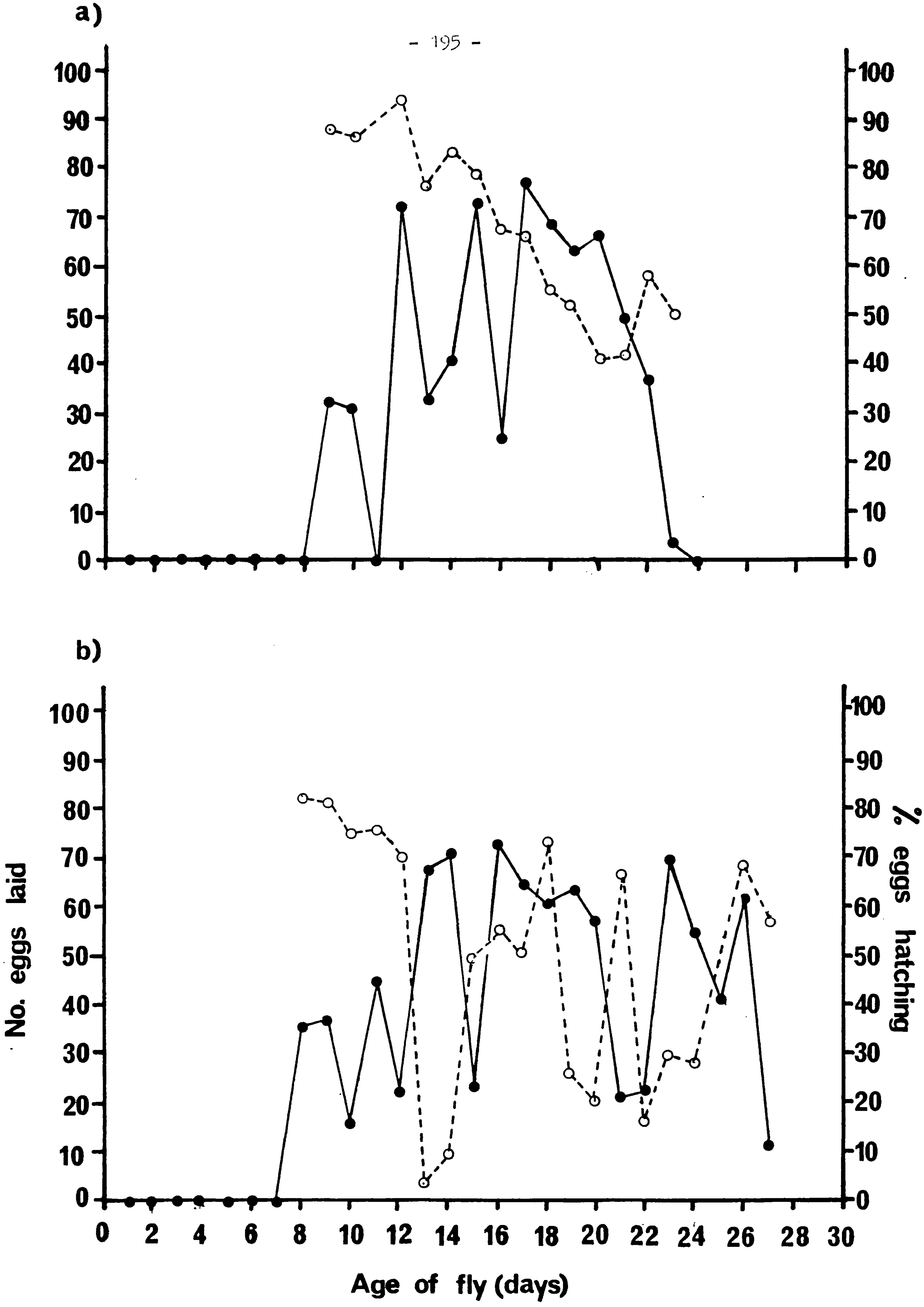
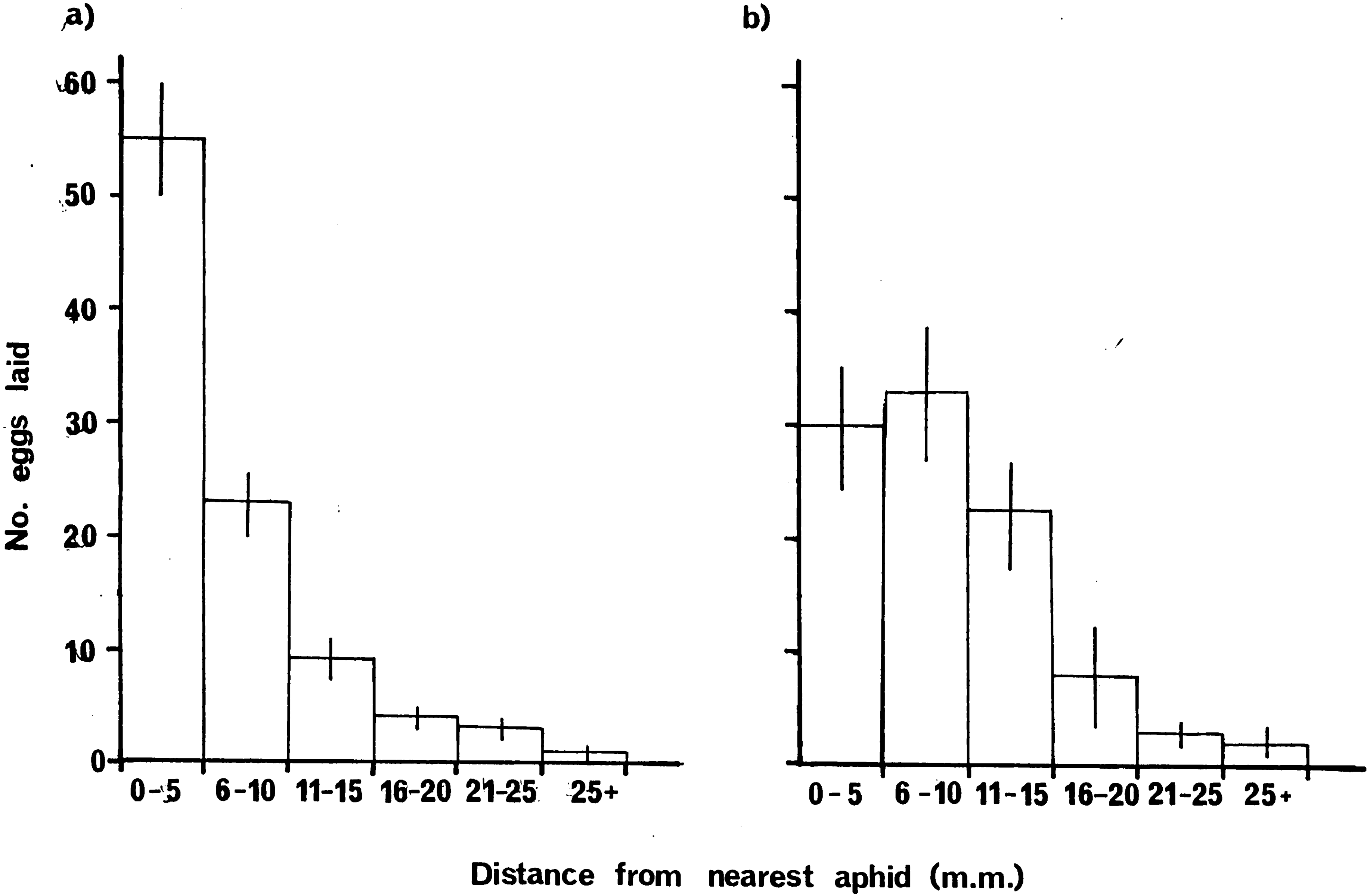

a)
b)
No. eggs laid
% eggs hatching
Age of fly (days)
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Figure 5.4: Average distance of the first and last hundred eggs laid by ten *Episyrphus balteatus* females from the nearest aphid (with standard error bars)

a) First hundred eggs
b) Last hundred eggs


a)
b)
60
50
40
30
20
10
0
No. eggs laid
0-5
6-10
11-15
16-20
21-25
25+
0 - 5
6 - 10
11-15
16-20
21-25
25+
Distance from nearest aphid (m.m.)

5.3.2.4 Distribution of eggs in relation to aphid colonies

The discrimination shown by females in selecting oviposition sites was determined by measuring the distance between each syrphid egg laid on the plant and the nearest aphid. The results are illustrated in Figures 5.4 a and b for the first and last hundred eggs laid by the ten experimental females. Young gravid E. balteatus females showed considerable discrimination in selecting an oviposition site, preferring to lay their eggs at a distance of between 0 and 5 mm from the nearest aphid. As the females aged however, there was a gradual increase in the mean distance between an egg and the nearest aphid and many eggs were laid both on the plant pot and on the cage floor. It was noted that the amount of wing damage was often quite severe in older flies and it seems likely that the loss of discrimination in the precise site of oviposition was due mainly to a decreased ability to manoeuvre accurately. A second explanation is that older flies are less sensitive to tactile stimuli from the substrate surface.

5.4 OBSERVATIONS ON THE BEHAVIOUR OF OVIPOSITING EPISYRPHUS BALTEATUS FEMALES

The following section describes the characteristic sequence of behaviours normally observed when a gravid Episyrphus balteatus female encounters an aphid-infested plant.

The fly approaches the plant and hovers up and down the stem and around individual leaves (Figure 5.5). Occasionally, she may brush the plant surface with her tarsi (Figure 5.6). On encountering an aphid colony, she normally alights on the plant with her ovipositor extended. She may then walk across the plant surface extending and withdrawing both the proboscis and the ovipositor alternately. At the same time, the antennae are held in a vertical plane and the wings are extended. This behaviour has been termed ovipositor and proboscis 'probing' (Figure 5.7).

Eventually, the fly may bend her ovipositor ventrally and drag it across the substrate (Figure 5.8). This behaviour has been termed 'cocking'. Cocking frequently, but not invariably, results in the deposition of an egg.

Grooming of the head, legs and ovipositor may frequently occur throughout this sequence of events (Figure 5.9).

The initial attraction to the plant is believed to be primarily in response to visual stimuli associated with the plant shape and colour. Visual stimuli from the aphids (ie aphid form and movement of aphid appendages) may also be important.

The characteristic hovering behaviour has previously been photographed by Brantjes (1980) for Episyrphus balteatus flies feeding at flowers. It seems likely that its purpose is to make some initial visual assessment of the plant's suitability as a feeding/oviposition site before making the decision to land or not. The brushing of the plant surface with the tarsi (also observed by Brantjes) may be a means of gathering chemical cues: studies on other Diptera have shown that the tarsi are well-equipped with chemoreceptors (eg Stomoxys - Adams, 1961; Adams et al, 1965; Calliphora - Stürckow, 1962, 1970, 1971; Stürckow et al, 1967, 1973; Peters and Richter, 1965; Phormia - Grabowski and Dethier, 1954; Larsen, 1962; Rees, 1968; Stürckow, 1962, 1970, 1971; Stürckow et al, 1973).

'Probing' behaviour (involving the alternate extension and withdrawal of the proboscis and ovipositor) characteristically occurs in the presence of oviposition stimuli (eg aphids or aphid honeydew). This response has also been observed in gravid onion fly females (Delia antiqua) responding to the volatile chemicals (isothiocyanates, thiocyanates and nitriles) produced by their cruciferous host-plants (Matsumoto and Thorsteinson, 1968). The labellar lobes are also well-equipped with sensory hairs and it seems likely that probing with both the proboscis and ovipositor provides the fly with chemical cues relating to the quality of the oviposition stimulus. It is not clear whether the fly actually feeds on the honeydew whilst she is sampling it. Proboscis extension is the first act in the feeding sequence of insect possessing retractable mouthparts. However, proboscis extension may be associated with several different aspects of behaviour and

Figure 5.5: Hovering behaviour of *Episyrphus balteatus*

The fly is hovering around an aphid-infested Brussels sprout plant.

Note the extended ovipositor

Figure 5.6: Hovering behaviour of *Episyrphus balteatus*

The fly is hovering above an aphid-infested leaf. The fore-tarsi are extended and are brushing the plant surface.

Figure 5.7: Probing behaviour of Episyrphus balteatus

The fly is walking across the leaf with her wings outstretched, alternately extending and contracting both the ovipositor and proboscis.

Figure 5.8: Cocking behaviour of Episyrphus balteatus

The ovipositor is bent ventrally and dragged across the plant surface resulting in the deposition of an egg.

Figure 5.9: Grooming behaviour of Episyrphus balteatus

cannot be interpreted solely in terms of feeding (Dethier, 1976). For example, Phormia extends its proboscis in response to several compounds (eg oil of caraway) that do not occur in its normal feeding environment (Saxena, 1958). Ingestion of sugar does not increase in the presence of these vapours (which are, incidentally, toxic to the fly). and the character of the proboscis extension resembles cleaning behaviour (Evans, 1961).

'Cocking' usually resulted in the deposition of an egg. Occasionally, however, no egg was laid. The reasons for this were not clear. Abortive cocking was usually observed on days when egg production was low. It seems possible that the intra-abdominal pressure from the accumulation of mature eggs decreases as some of the eggs are laid and so it may become increasingly difficult to lay the last few eggs of each batch.

5.5 STUDIES ON THE ACTIVITY PATTERNS OF EPISYRPHUS BALTEATUS FLIES IN THE LABORATORY

5.5.1 MATERIALS AND METHODS

The experimental design was as described in Section 5.3.1. Ten newly-emerged flies of each sex were placed in pairs (one male and one female) in standardized 50 x 45 x 70 cm wooden-framed cages. The flies were provided with 10% sucrose solution, pollen and water; fresh food was supplied daily. The flies were also provided with a potted Brussels sprout plant (cv Winter Harvest) infested with approximately 300 B. brassicae aphids. The plant remained in the cage for a period of ten hours each day and was then removed. A new plant was provided daily.

The activity patterns of the flies were monitored at 2-day intervals over a period of 28 days. On each occasion, flies were observed continuously over a period of 10 hours (0900-1900 hours) and their behaviour recorded at 10-minute intervals throughout. Seven categories of behaviour were determined: 1) flying, 2) resting,

3) feeding, 4) walking, 5) grooming, 6) probing, and 7) cocking. In addition, the location of the fly was recorded for each observation as: 1) cage, 2) plant, or 3) food (sucrose, pollen or water).

These data may be used to estimate the time budgets of syrphid flies. It was assumed that the number of occasions on which a fly was observed feeding, flying etc was a measure of the amount of time that the animal allocated to each particular activity.

5.5.2 RESULTS AND DISCUSSION

5.5.2.1 Time budgets of male and female flies

Figures 5.10 - 5.15 illustrate the effect of age on the amount of time spent engaged in different behavioural activities by male and female flies. The number of observations of each activity is expressed as a percentage of the total number of observations.

Figure 5.10 shows that both sexes spent a very large proportion of their time resting; this was especially true of very young and very old flies. During the first four days following emergence, both males and females were mainly inactive. After four days, however, females activity increased markedly and for the next eighteen days, females were consistently more active than males. After day 22, female activity declined and old flies of both sexes spent most of their time resting.

In general, females spent more time flying than males, although young and old flies of both sexes spent approximately the same amount of time on the wing (Figure 5.11). Wing wear increased considerably with age and was particularly severe in old females. Flies with damaged wings were unable to fly properly and rarely survived for very long.

Walking accounted for a very small proportion of the time budgets of both male and female flies (Figure 5.12). The increased walking activity shown by older females was probably a direct result of their impaired flight capabilities.

In general, females spent more time feeding than males (Figure 5.13). Females showed two main peaks of feeding activity on days 6 and 16, respectively. The second peak was considerably larger than the first. After day 16, feeding activity by females declined steadily for the remainder of the experiment. In contrast, males showed three main peaks of feeding on days 4, 16 and 24, respectively Each peak was progressively smaller than the previous one. The pattern of visits to the three different food sites will be considered in greater detail in Section 5.5.2.2.

Very few observations of cocking behaviour were made throughout the entire duration of the experiment. For this reason, probing and cocking have been considered together as oviposition-associated activities. These two behaviours were first observed in 6-day old females. Figure 5.14 shows that the amount of time spent probing and cocking fluctuated considerably during the twenty-eight days of the experiment. with peaks of activity on days 8, 12 and 18-24. These fluctuations may be due to differences in the egg-production cycles of individual females. As more flies started to lay eggs, so the fluctuations became ironed out. Figure 5.14 also shows the average number of eggs laid on different days of the experiment: the number of eggs per female gradually increased as more flies started to oviposit. There was, however, no clear relationship between the amount of time spent probing and cocking and the number of eggs laid per female.

Figure 5.15 shows the amount of time spent on the plant by male and female flies of different ages. Flies of both sexes used the plant as a resting site. In addition, females used it as an oviposition site. Females first visited the plant on day 6: this was the earliest age at which eggs were laid. After day 18, female activity on the plant declined rapidly. This was associated with a decrease in flight activity in older flies due to wing damage. Older females were less able to fly on to the plant to oviposit and large numbers of eggs were found scattered on the cage floor at the base of the plant pot. Male flies first visited the plant on day 2. After day 10, male activity on the plant declined rapidly although, unlike the females, this did not appear to be associated with an impaired flight capability. In general, females spent considerably more time on the plant than males.

Figure 5.10: The average amount of time spent resting by male and female flies of different ages

The figure shows the average number of observations of resting behaviour expressed as a percentage of the total number of observations (with standard error bars)

•——• Females

•- - -• Males

Figure 5.11: The average amount of time spent flying by male and female flies of different ages

The figure shows the average number of observations of flying behaviour expressed as a percentage of the total number of observations (with standard error bars)

•——• Females

•- - -• Males

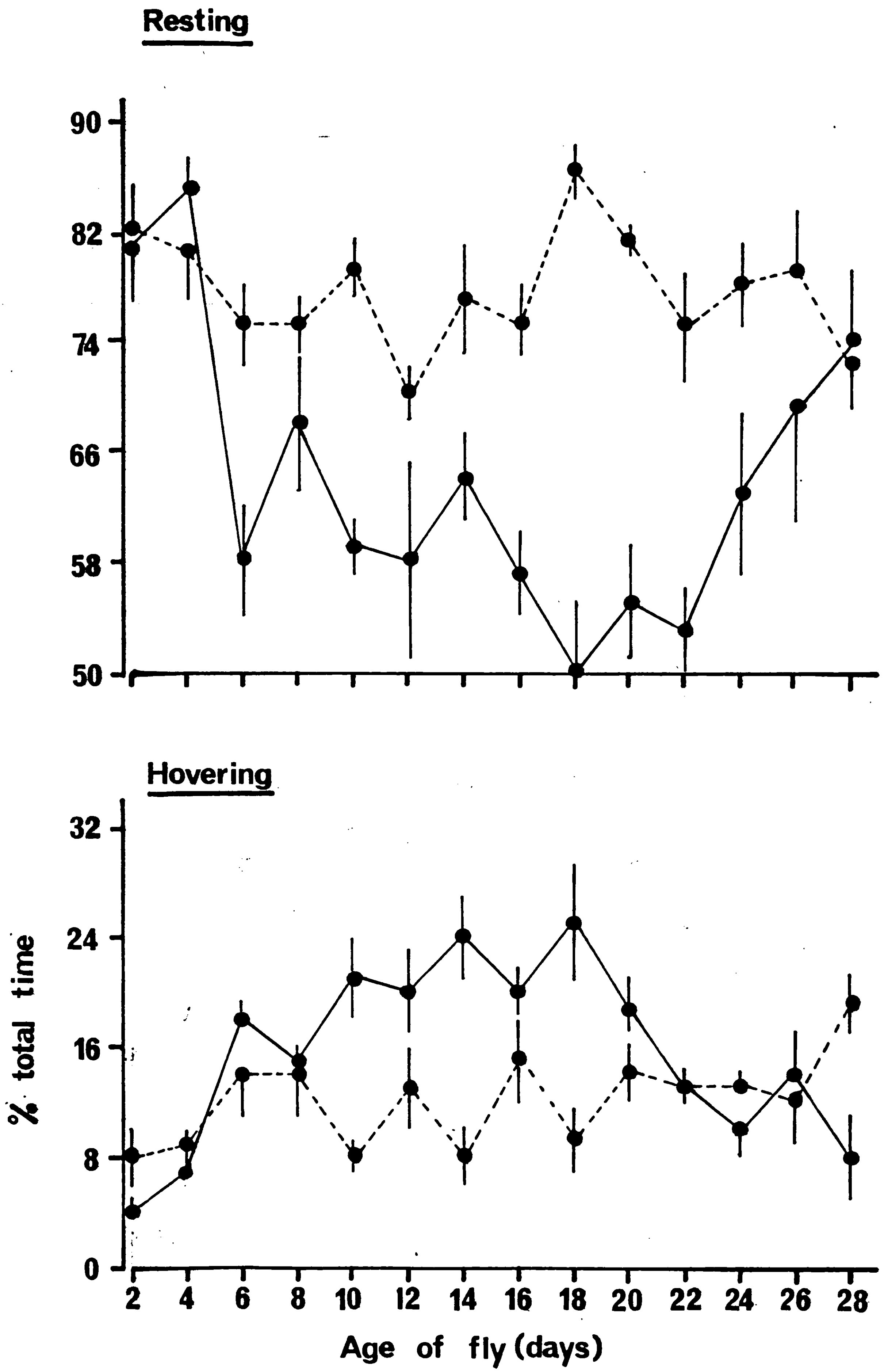

Resting
90
82
74
66
58
50
Hovering
32
24
16
8
0
% total time
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Age of fly (days)

Figure 5.12: The average amount of time spent walking by male and female flies of different ages

The figure shows the number of observations of walking behaviour expressed as a percentage of the total number of observations (with standard error bars)

•——• Females

•----• Males

Figure 5.13: The average amount of time spent feeding by male and female flies of different ages

The figure shows the number of observations of feeding behaviour expressed as a percentage of the total number of observations (with standard error bars)

•——• Females

•----• Males

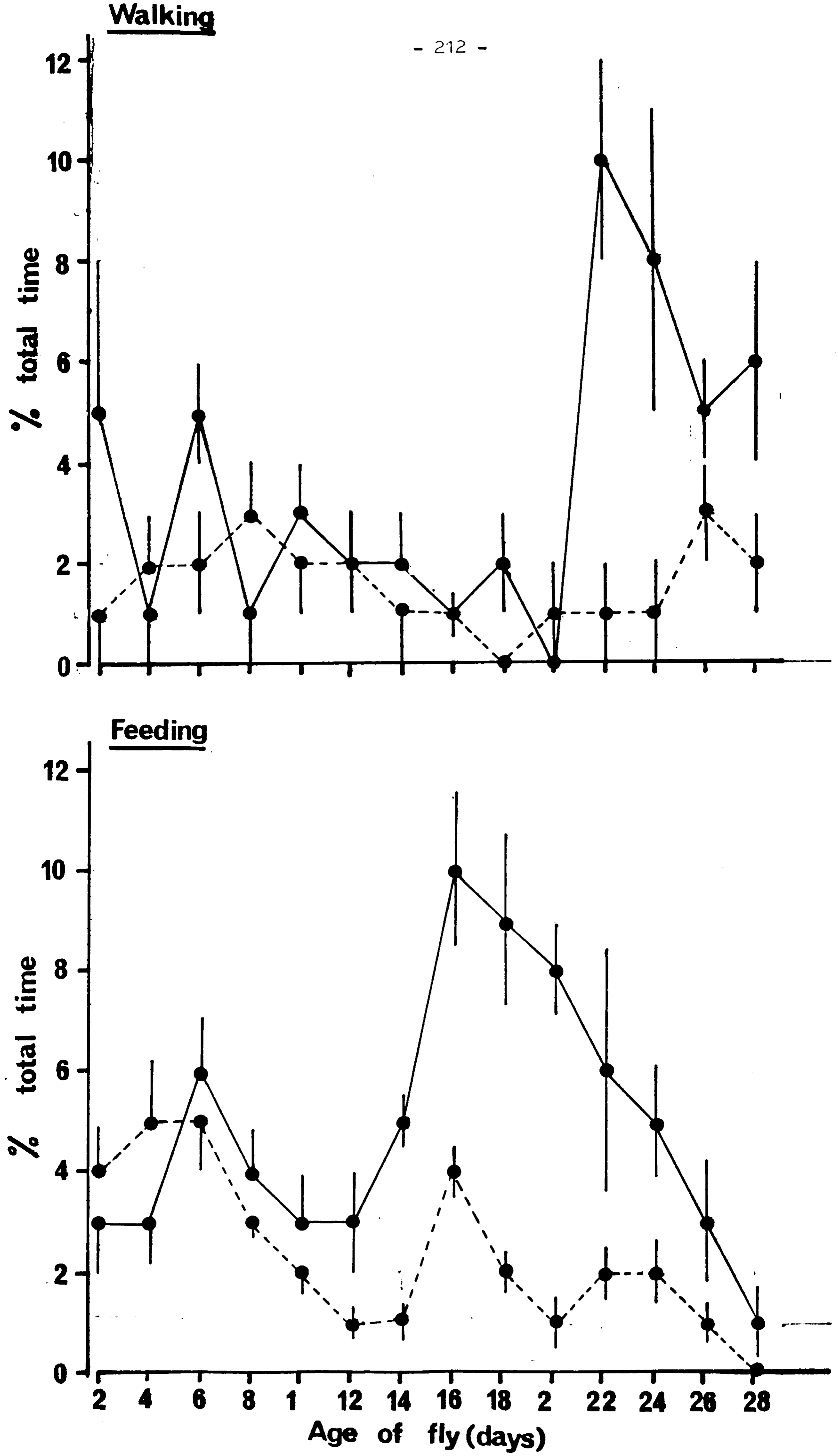

Walking
12
10
8
6
4
2
0
% total time
Feeding
12
10
8
6
4
2
0
% total time
2
4
6
8
1
12
14
16
18
2
22
24
26
28
Age of fly (days)

Figure 5.14: The average amount of time spent probing and cocking by female flies of different ages, together with the average number of eggs laid

The figure shows the number of observations of probing and cocking behaviour expressed as a percentage of the total number of observations (with standard error bars)

•——• % of total time spent probing and cocking

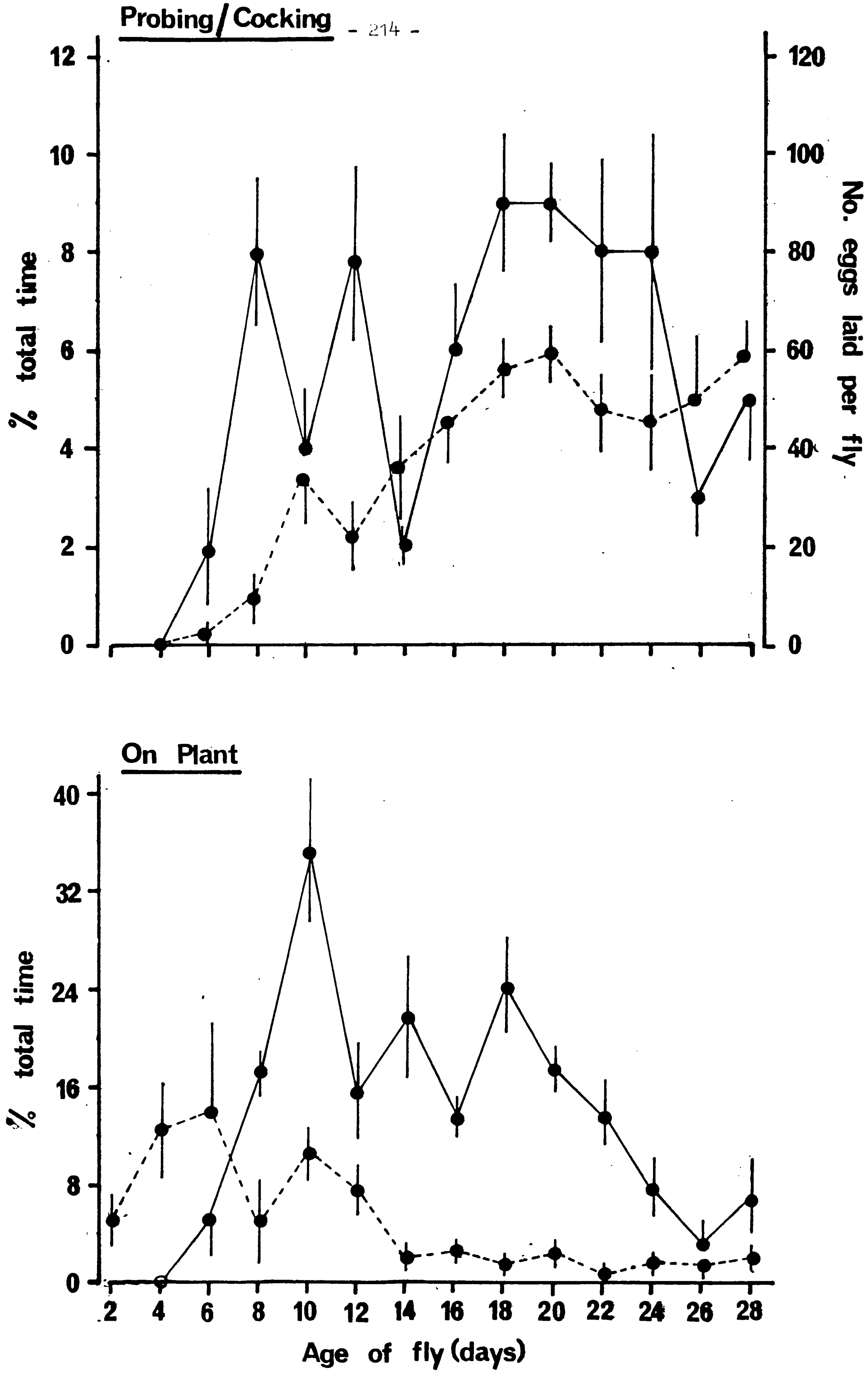
•----• Average number of eggs laid per fly

Figure 5.15: The average amount of time spent on the plant by male and female flies of different ages

The figure shows the number of observations of 'on plant' activity expressed as a percentage of the total number of observations (with standard error bars)

•——• Females

•----• Males


Probing/Cocking
12
10
8
6
4
2
0
% total time
120
100
80
60
40
20
0
No. eggs laid per fly
On Plant
40
32
24
16
8
0
% total time
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Age of fly (days)

5.2.2.2 Feeding patterns of male and female flies

The number and proportions of observations of flies feeding on sucrose, pollen and water may be used to estimate the amount of time spent feeding upon each type of food and also the importance of each food in the diet.

Figure 5.16 a and b illustrates the pattern of visits to the sucrose, pollen and water sites by female and male flies during the first 28 days of the experiment. Both sexes appeared to have two main periods of sucrose ingestion, although these were less clearly defined for the males. The first peak of sucrose feeding occurred on day 8 for the males and on day 10 for the females. The second peak occurred on day 18 for both sexes and, thereafter, sucrose ingestion gradually declined. One-way analysis of variance showed that males and females spent approximately the same amount of time feeding on sucrose on all occasions (Table D2, Appendix D).

Female flies showed two main periods of pollen-feeding with peaks occurring on days 6 and 16. The second peak was much larger than the first with females visiting the site most frequently between days 16 and 20. In contrast, males showed three main peaks of pollen-feeding with peaks occurring on days 4, 16 and 22. Each peak was progressively smaller than the previous one with maximum pollen ingestion by male flies occurring on days 2-4 following emergence. One-way analysis of variance showed that both sexes spent approximately the same amount of time feeding on pollen during the first 12 days after emergence (Table D3, Appendix D). After day 12, however, females made significantly more visits to the pollen site than males on all occasions except days 22 and 28.

Both sexes rarely visited the water site throughout the 28 days of the experiment.

Pollen feeding has been shown to be essential for ovarial maturation and females accordingly take more pollen than males: this is a common pattern among the Diptera (Dethier, 1976; Belzer, 1978a, b;

Webster et al, 1979). The relationship between pollen ingestion and egg maturation has been studied by Haslett (1981). He showed that periods of increased pollen feeding were associated with the expansion of yolk deposits.

A period of pollen-feeding may also be important in male flies as well as in females. Kevan (1970) has suggested that newly-emerged males of Carposcalis carinata Curran may require pollen to mature the testes and initiate sperm production. Belzer (1978a) found that male Phormia regina Meig. ingested moderate amounts of protein on the first day or two after emergence but little or none thereafter. Gilbert (1981a) noted that newly-emerged males of Syrphus ribesii invariably contained pollen grains in their crops and/or guts but pollen was rarely found in the digestive tract of older males. Mature males were, however, frequently observed feeding on aphid honeydew. Gilbert concluded that the males of S. ribesii emerge in an immature state and need to feed on pollen to mature their reproductive system. Once mature, they can satisfy their nutritional requirements by taking honeydew. Wilkening (1961) claims that male Metasyrphus corollae were capable of fertilizing eggs immediately after emergence, but it is not known if this occurs in wild flies.

No data was available on the relative efficiencies with which Episyrphus balteatus flies can ingest sucrose and pollen. It is not therefore possible to directly compare the number of observations of sucrose feeding with those of pollen feeding. However, it was clear that the flies spent considerably more time feeding on pollen than on sucrose. The relative proportions of pollen and nectar taken in the diel has been shown to vary considerably in different syrphid species (Gilbert, 1981b): Episyrphus balteatus is believed to feed mainly on pollen (Gilbert, 1981b; Haslett, 1981). Holloway (1976) demonstrated that pollen feeding by certain syrphid species is accomplished mainly by combing the grains from body hairs which in some cases appear to be specialized for this purpose. If this is the case for Episyrphus balteatus, the number of observations of flies feeding on pollen underestimates the importance of this food in the diet, since time spent grooming should also be included.

Figure 5.16: Feeding patterns of male and females flies

The figure shows the average number of observations of feeding on sucrose, pollen and water by

a) female and

b) male

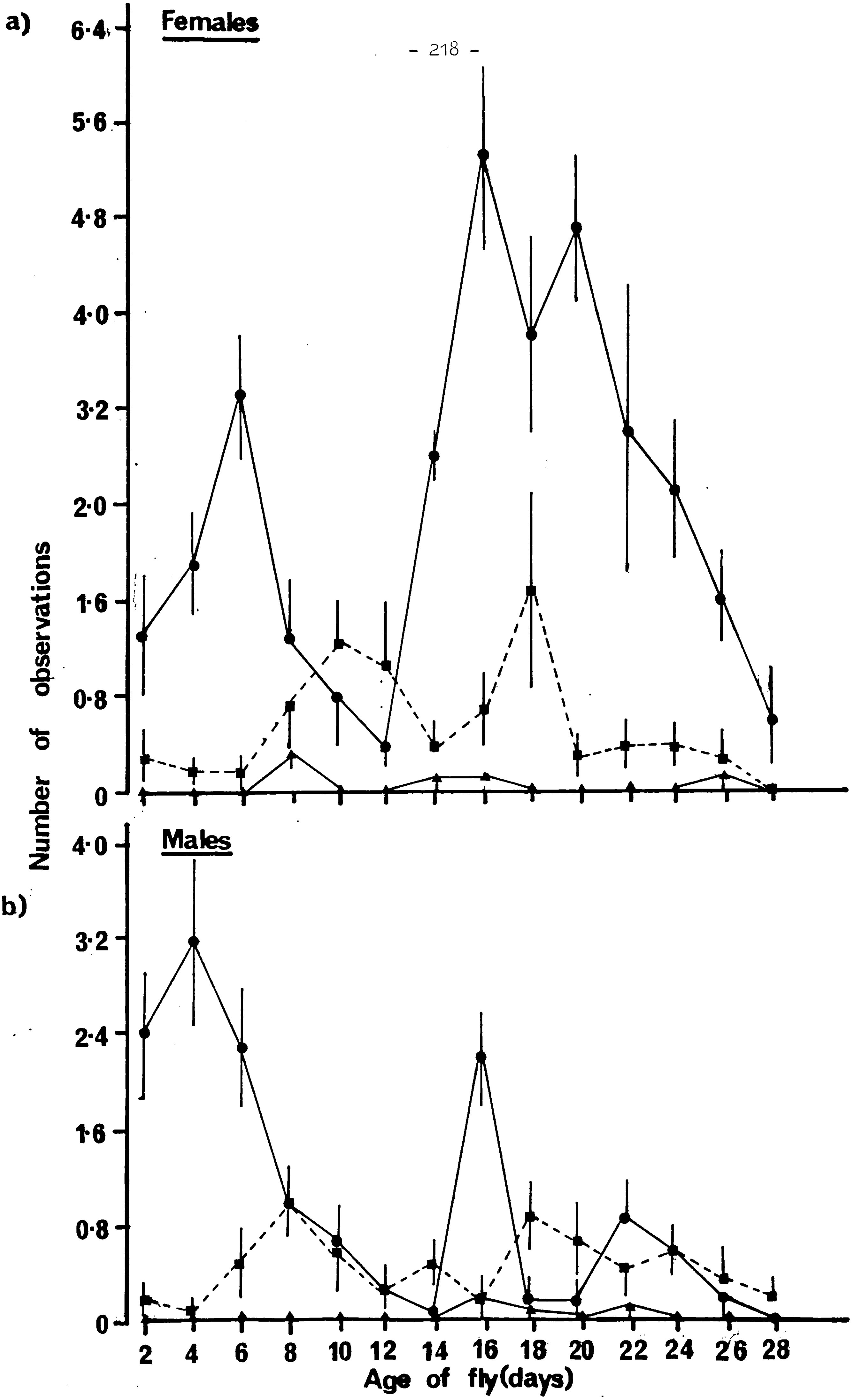
flies of different ages (with standard error bars)

Key

●——● Sucrose

■——■ Pollen

▲——▲ Water


a)
Females
6·4
5·6
4·8
4·0
3·2
2·0
1·6
0·8
0
Number of observations
b)
Males
4·0
3·2
2·4
1·6
0·8
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Age of fly(days)

5.5.2.3 Diel patterns of activity in 12-day old flies

Figures 5.17 - 5.21 illustrate the diel patterns of different behavioural activities in 12-day old male and female flies. The results are expressed in terms of the mean number of observations of each activity that were made during each hour of the experiment. The results for individual flies are given in Tables D4 - D8 (Appendix D).

Figure 5.17 shows the diel pattern of resting activity in male and female flies. The patterns for both sexes were similar with resting activity gradually decreasing during the morning and then increasing again during the late afternoon. A two-way analysis of variance (Table 5.2) confirmed that there was a significant difference in the number of observations of resting activity at different times of the day ($F = 3.39$; $p < 0.001$). Males spent significantly more time resting than females ($F = 16.41$; $p < 0.001$).

Table 5.2: A two-way analysis of variance on the number of observations of resting activity in male and female flies recorded during each hour of the experiment

Source of variation	df	SS	MS	F-ratio	p
Time of day	9	65.52	7.28	3.39	< 0.001
Sex	1	35.28	35.28	16.41	< 0.001
Interaction	9	30.12	3.35	1.56	ns
Error	180	386.20	2.15		
Total	199	517.12			

The diel patterns of flight activity in male and female flies are illustrated in Figure 5.18. Female flight activity gradually increased during the day to reach a peak in the late afternoon. In contrast, males flew mainly during the morning and were much less flight-active during the afternoon. A two-way analysis of variance (Table 5.3)

Table 5.3: A two-way analysis of variance on the number of observations of flight activity in male and female flies recorded during each hour of the experiment

Source of variation	df	SS	MS	F-ratio	p
Time of day	9	34.88	3.88	2.90	< 0.01
Sex	1	10.58	10.58	7.90	< 0.01
Interaction	9	35.52	3.95	2.95	< 0.01
Error	180	241.00	1.34		
Total	199	321.98			

showed that both time of day (F = 2.90; $p < 0.01$) and sex (F = 7.90; $p < 0.01$) had a significant effect on flight activity. However, there was also a significant interactive effect (F = 2.95; $p < 0.01$) which indicated that females were significantly more flight-active than males only at certain times of the day.

Figure 5.19 compares the diel patterns of feeding activity in male and female flies. The number of observations of feeding activity by both sexes was low. The graph shows that female flies fed mainly in the morning while males were only observed to feed during the afternoon. A two-way analysis of variance (Table 5.4) showed that time of day had no significant effect on the feeding patterns of the flies (F = 1.95; ns). Females fed significantly more frequently than males (F = 4.31; $p < 0.05$), but only at certain times of day.

Table 5.4: A two-way analysis of variance on the number of observations of feeding activity in male and female flies recorded during each hour of the experiment

Source of variation	df	SS	MS	F-ratio	p
Time of day	9	1.64	0.18	1.95	ns
Sex	1	0.41	0.41	4.31	< 0.05
Interaction	9	1.85	0.21	2.18	< 0.05
Error	180	16.90	0.09		
Total	199	20.80			

The diel pattern of visits to the plant by male and female flies is illustrated in Figure 5.20. The pattern of female visits showed three distinct peaks: in the early morning, early afternoon and late afternoon. The pattern of male visits was similar but each peak occurred slightly later in the day. A two-way analysis of variance (Table 5.5) confirmed a significant difference in the number of visits to the plant at different times of day ($F = 2.55$; $p < 0.01$). Females visited the plant significantly more often than males ($F = 3.95$; $p < 0.05$).

Table 5.5: A two-way analysis of variance on the number of visits to the plant by male and female flies recorded during each hour of the experiment

Source of variation	df	SS	MS	F-ratio	p
Time of day	9	35.64	3.96	2.55	< 0.01
Sex	1	6.12	6.12	3.95	< 0.05
Interaction	9	16.12	1.79	1.15	ns
Error	180	279.50	1.55		
Total	199	337.39			

Figure 5.17: Diel patterns of resting activity in 12-day old flies

The figure shows the average number of observations of resting activity for male and female flies at different times of day (with standard error bars)

■——■ Females

■----■ Males

Figure 5.18: Diel patterns of flight activity in 12-day old flies

The figure shows the average number of observations of flight activity for male and female flies at different times of day (with standard error bars)

■——■ Females

■----■ Males

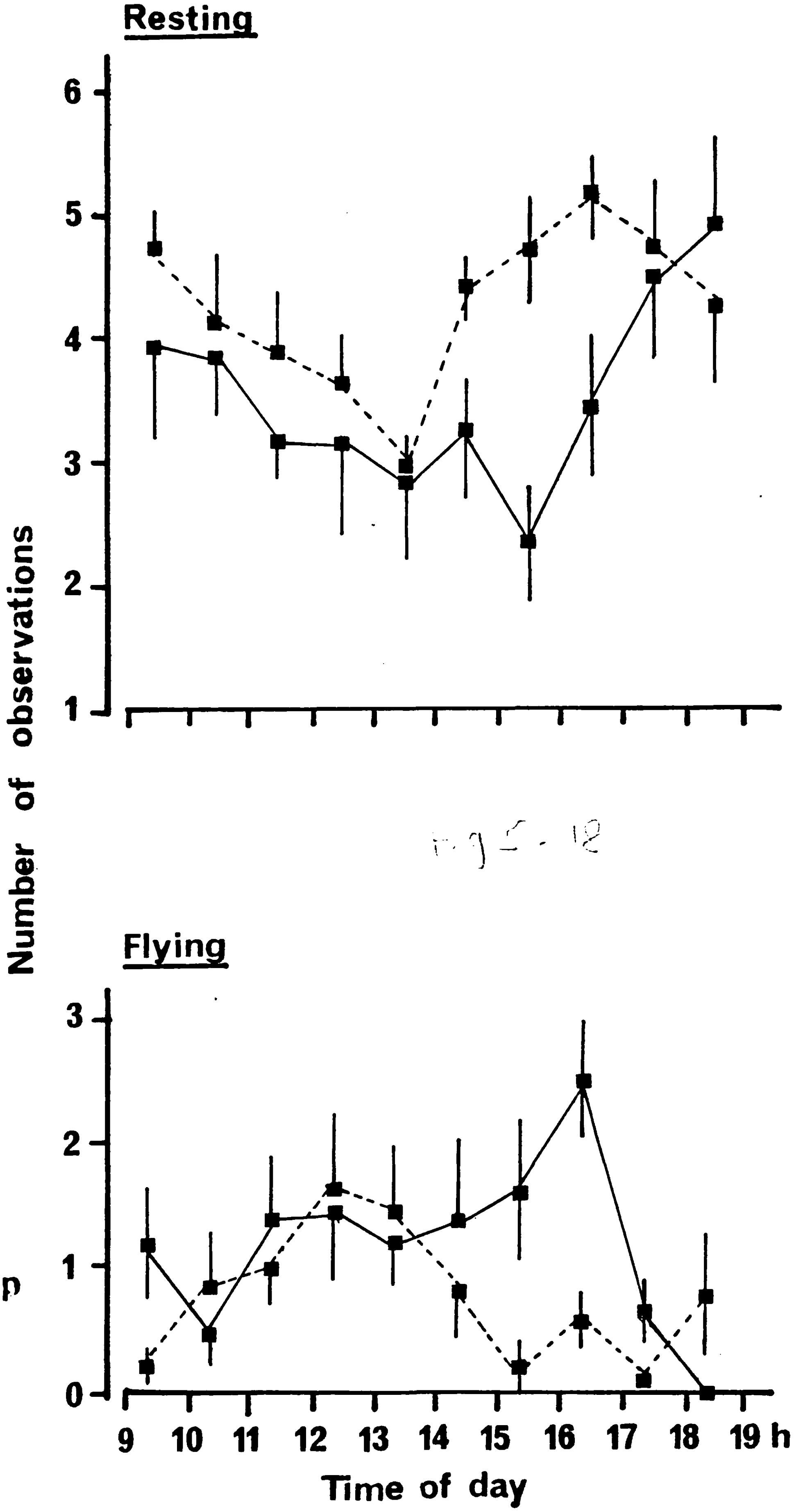

Resting
6
5
4
3
2
1
Number of observations
Flying
3
2
1
0
p
9
10
11
12
13
14
15
16
17
18
19 h
Time of day

Fig 5.18

Figure 5.19: Diel patterns of feeding activity in 12-day old flies

The figure shows the average number of observations of feeding activity for male and female flies at different times of day (with standard error bars)

•———• Females

•- - - -• Males

Figure 5.20: Diel patterns of on-plant activity in 12-day old flies

The figure shows the average number of observations of on-plant activity for male and female flies at different times of day (with standard error bars)

•———• Females

•- - - -• Males

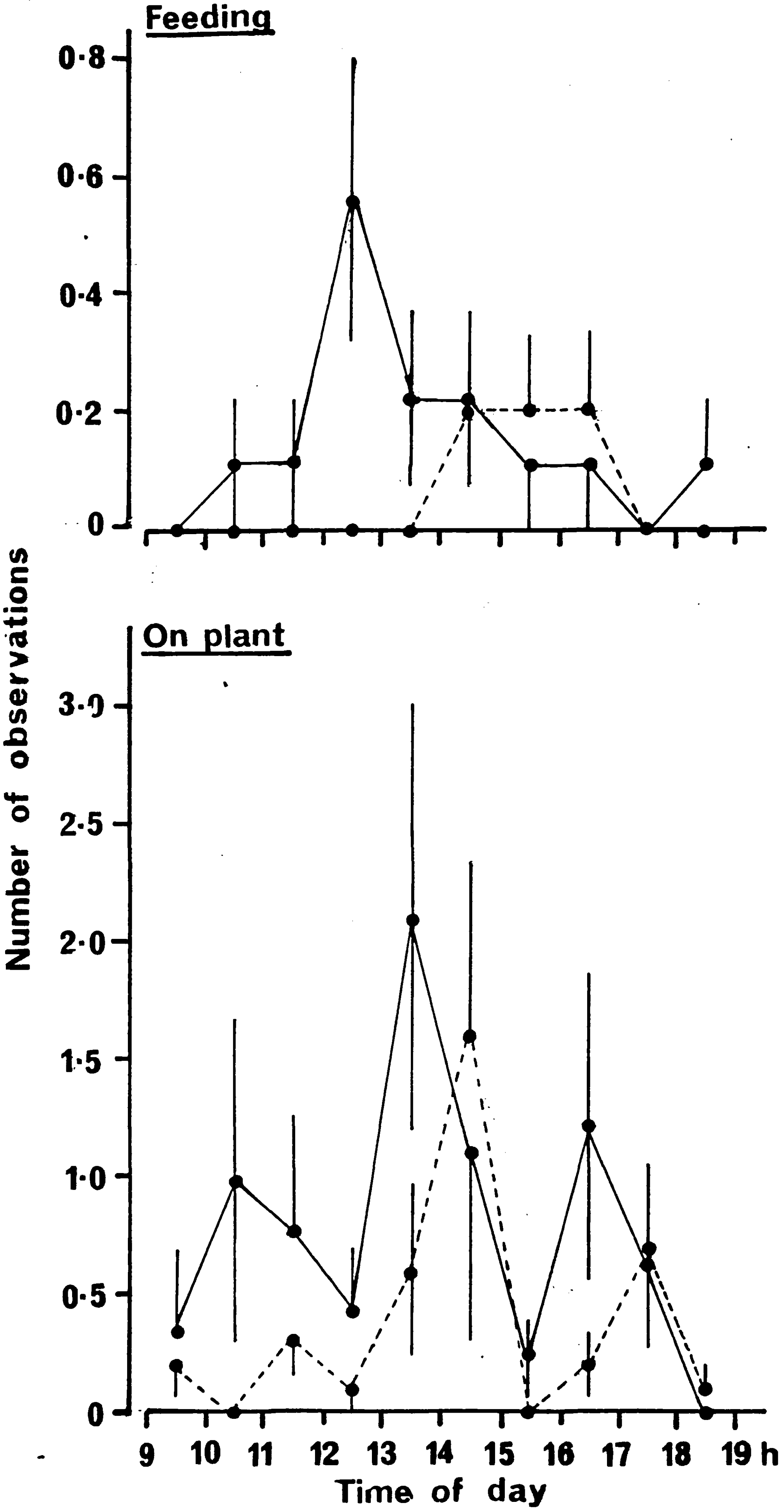

Feeding
0·8
0·6
0·4
0·2
0
Number of observations
On plant
3·0
2·5
2·0
1·5
1·0
0·5
0
9
10
11
12
13
14
15
16
17
18
19 h
Time of day

Figure 5.21 illustrates the diel pattern of probing and cocking activity of female flies. These two behaviours are considered together as oviposition-associated activites. Three main peaks of probing/cocking activity occurred: in the early morning, early afternoon and late afternoon. These three periods of oviposition-associated activity were correlated with the diel pattern of visits to the oviposition site (ie the plant). A one-way analysis of variance (Table 5.6) confirmed that there was a significant difference in the number of observations of probing/cocking behaviour at different times of the day ($F = 2.64$; $p < 0.01$).

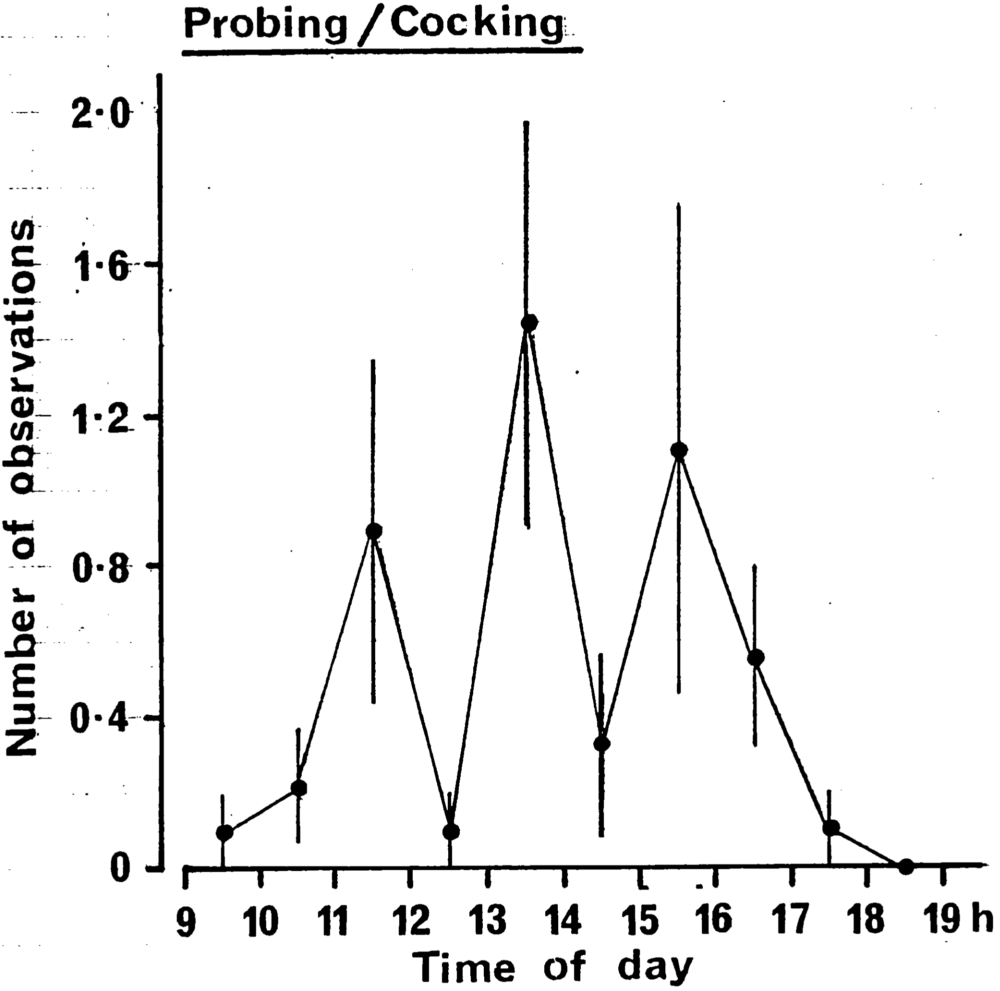
Table 5.6: A one-way analysis of variance on the number of observations of probing and cocking activity recorded during each hour of the experiment

Source of variation	df	SS	MS	F-ratio	p
Time of day	9	21.04	2.34	2.64	< 0.01
Error	90	79.80	0.89		
Total	99	100.84			

These results may be compared to the activity patterns of flies in the field. In Chapter 3, Malaise traps were used to monitor the diurnal flight patterns of wild syrphid populations. In the field, Episyrphus balteatus flies first became flight-active around 0900 h. Activity gradually increased during the day and then declined again in the late afternoon/early evening. This basic response was modified by the prevailing climatic conditions. Thus, there was a broad agreement between the diel patterns of flight activity observed in the field and in the laboratory.

Figure 5.21: Diel patterns of probing and cocking activity in 12-day old flies

The figure shows the average number of observations of probing and cocking activity for female flies at different times of day (with standard error bars)


Probing / Cocking
Number of observations
2·0
1·6
1·2
0·8
0·4
0
9
10
11
12
13
14
15
16
17
18
19 h
Time of day

5.6 GENERAL DISCUSSION AND CONCLUSIONS

This chapter has examined aspects of the biology of *Episyrphus balteatus* flies under closely-controlled laboratory conditions. Such studies are of value in that they provide some indication of an animal's potential fitness under 'optimal' conditions (ie adequate diet and stable environmental conditions). Fitness is a function of fecundity and longevity (Mitchell, 1981).

Fecundity is a function of the number of ovarioles, the rate of egg-production by the ovarioles, the frequency of resorption and the frequency of retention of mature oocytes (Cohet and David, 1978). Egg production in laboratory-reared *Episyrphus balteatus* flies appeared to be more or less continuous with each female undergoing several ovarian cycles during her life-time. Ovarial dissections showed no evidence of any egg resorption.

In the field, however, fecundity may be strongly influenced by nutritional and environmental factors. Population studies on field-caught *Drosophila mimica* indicated that only 50% of the ovarioles contained mature eggs at any one time during the year (Kambysellis *et al*, 1980). Atresic or degenerating follicles were a common feature of the ovarioles. Low relative humidity was the most important factor responsible for terminating the growth of oocytes at the stage of RNA yolk synthesis. Adverse conditions of temperature can affect the rate of egg production. Protein shortages may result in little or no oviposition. Lack of suitable oviposition sites prolongs the time required to complete each ovarian cycle and also results in the retention of mature eggs.

In the field, many individuals may die before they have realized even a small proportion of their reproductive potential. Predation is probably one of the most important factors acting to reduce the longevity of wild syrphids.

In the present study, *Episyrphus balteatus* flies mated frequently during the first few days after emergence. Wilkening (1961) has shown that a single copulation is necessary for females of

Metasyrphus corollae to fertilize all or a large proportion of their eggs. Benestad (1970a) reports that M. corollae females could lay fertilized eggs for at least 25 days after a copulation.

The day-to-day fertility of laboratory-reared Episyrphus balteatus females often varied considerably: this may be due to daily variation in the strength of the sensory stimuli perceived by the ovipositing fly which bring about the release of sperm from the spermathecae. There is little published data on the fertility of wild syrphids. However, Wilkening (1961) showed that the fertility of field-caught Metasyrphus corollae changed according to the season being about 40-60% in the spring and 80-90% in the summer.

Studies on the feeding patterns of laboratory-reared Episyrphus balteatus flies indicated that patterns of pollen and sucrose ingestion change during the fly's life-time. Both sexes spent approximately the same amount of time feeding on sucrose but females took more pollen than males. An initial period of pollen-feeding appears to be a pre-requisite for sexual maturation in both sexes.

Patterns of carbohydrate and pollen ingestion may be related to different physiological and behavioural events that occur during a fly's life-time. In Rhingia campestris, two peaks of carbohydrate ingestion are separated by a peak of pollen-feeding (Haslett, 1981). The pattern of pollen infestion is closely related to the egg maturation cycle: peak pollen-intake coincides with the deposition of yolk reserves. The first carbohydrate peak occurs shortly after emergence when the fly requires extra energy to seek mates. The second carbohydrate peak is probably associated with the energetic requirements of oviposition and the need to locate oviposition sites.

The diel activity patterns of Episyrphus balteatus flies were examined under closely-controlled laboratory conditions and were related to patterns of flight activity in the field. Flies of both sexes spent a very large proportion of their time resting. This has important implications in relation to optimal foraging theory. Most optimal foraging models take little account of time-budgets, assuming that foraging is the sole activity. Studies on time-allocation have been reviewed by Herbers (1981) who notes that most time is spent either resting or foraging. A simple Markov model of activity predicts that large proportions of time should be spent being inactive: the primary assumption of the model is that the animal's main aim is to remain alive. 'Laziness' may thus be a direct consequence of the foraging strategy of animals. Some models of foraging strategy incorporate this assumption (eg Caraco, 1980; Stephens, 1981) and generate more realistic results than the simple deterministic models of optimal foraging.

CHAPTER 6

BEHAVIOURAL ASPECTS OF OVIPOSITION IN EPISYRPHUS BALTEATUS DEGEER

6.1 INTRODUCTION

It was shown in Chapter 4 that some syrphid species can discriminate between plants infested with aphid populations of different sizes. The number of eggs laid by these species was closely related to the number of aphids present on a plant and increasing numbers of eggs were laid in response to increasing aphid density. The following chapter aims to examine the behavioural mechanism of this response.

The way in which a foraging animal exploits resources (eg food, shelter etc) that are patchily-distributed in its environment is a question that is currently of considerable interest to behavioural ecologists. Several models have been developed to explain and predict how animals might behave if they were to forage efficiently or optimally (MacArthur and Pianka, 1966; Hassell and May, 1974; Murdoch and Oaten, 1975; Charnov, 1976; Cook and Hubbard, 1977; Oaten, 1977; Waage, 1979). The aim of an optimal foraging strategy is generally assumed to be the maximization of the animal's fitness (usually expressed in terms of net energy intake). The precise behaviour of the forager, how it apportions its time between different resource patches, is considered to be the mechanism by which the optimal strategy is approached.

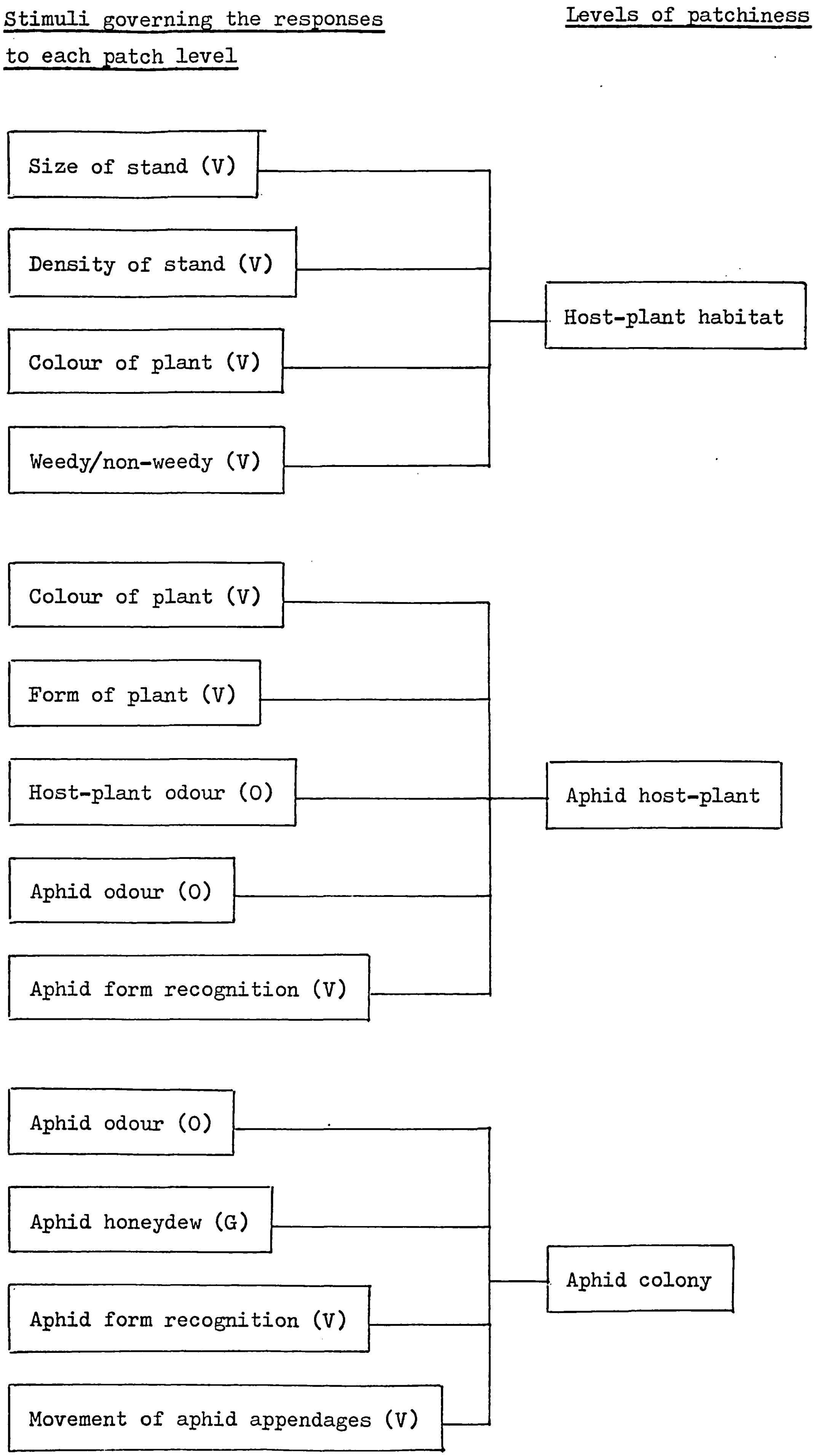
The study of foraging behaviour is usually concerned with how a forager allocates its time between a set of resource patches of varying profitability. To study the allocation of time between patches, it is first necessary to define the term 'patch'; various interpretations have been put forward (Wiens, 1976). It is important to know what the forager perceives as a patch, and here we should consider the forager's behaviour: specific changes in behaviour as the animal forages may be associated with the recognition of patch and non-patch areas. Waage (1978) proposed that a patch may be defined as an area containing a stimulus or stimuli that at the proper intensity elicits a characteristic foraging activity in a responsive forager. These patch-characterizing 'arrestant' stimuli may or may not be distinct from the 'attractant' stimuli which mediate orientation to patches from non-patch areas. This definition avoids attributing more patches to the environment of a responsive forager than to an unresponsive one.

There is evidence that foraging animals may respond to several different levels of patchiness. For example, the ichneumonid parasitoid, Diadromus pulchellus Wesm., which attacks pupae of the leek moth Acrolepia assectella (Zell.), shows a behavioural response to three levels of patchiness: the host's food plant, the part of the plant occupied by the host, and to the host itself (Noyes, 1974). The identification of these different levels must involve the indentification of stimuli governing the responses to each level and characterization of these responses.

Figure 6.1 is a schematic diagram showing the hypothetical levels of patchiness encountered by Episyrphus balteatus females foraging for oviposition sites in agricultural crops. The stimuli governing the responses to each patch level are also shown. Three levels of patchiness may be distinguished: the habitat (in this case, the crop), the individual aphid host-plant within the crop, and the individual aphid colony on the host-plant. Habitat selection usually occurs on the basis of plant-associated stimuli (eg the size and density of the plant stand, the size, colour and general appearance of the crop plants; presence of weeds within the crop). It was shown in Chapter 4 that the oviposition response (in terms of the number of eggs laid per aphid) of E. balteatus flies varied significantly in different brassica crops. The response to crop type was shown to be independent of aphid stimuli.

Figure 6.1: Hypothetical levels of patchiness encountered by an ovipositing *Episyrphus balteatus* female

Key
O - Olfactory stimulus
V - Visual stimulus
G - Gustatory stimulus


Stimuli governing the responses to each patch level
Levels of patchiness
Size of stand (V)
Density of stand (V)
Colour of plant (V)
Weedy/non-weedy (V)
Host-plant habitat
Colour of plant (V)
Form of plant (V)
Host-plant odour (O)
Aphid odour (O)
Aphid form recognition (V)
Aphid host-plant
Aphid odour (O)
Aphid honeydew (G)
Aphid form recognition (V)
Movement of aphid appendages (V)
Aphid colony

Once a particular crop has been selected for oviposition, further selection for a particular aphid host-plant occurs. In the case of E. balteatus, host-plant selection probably occurs mainly in response to aphid-associated stimuli: results presented in Chapter 4 and in this chapter show that host-plant selection is closely related to the overall size of the aphid population present on a plant. Plant factors may also play a role in host-plant selection by E. balteatus, especially in the case of older females (Chandler, 1968b).

The third and final level of patchiness constitutes the individual aphid colony on a plant. Many aphidozetic syrphids, including E. balteatus, oviposit in close proximity to aphid colonies. Some species have been shown to seek out colonies of a particular size: E. balteatus prefers to oviposit next to small colonies rather than larger ones

Such a classification of the environmental levels perceived by a forager is important if we are to consider the components of foraging and place them within a general framework. It is also important to the testing of current foraging theories, such as the Marginal Value Theorem (Charnov, 1976) which assumes that the forager perceives as discrete units both habitats and the patches that comprise them. Each level within the hierarchy should be unambiguously characterized by specific stimuli and associated with specific responses in the forager's behaviour.

The allocation of foraging time between patches involves two decisions on the part of the forager: which patches to visit, and how long to spend in each patch (Krebs et al, 1974). Waage (1979) lists four different behavioural mechanisms that may determine the duration of a patch visit:

1. Fixed number mechanisms: the forager leaves a patch after a fixed number of food items have been captured. This is the 'hunting by expectation' hypothesis of Gibb (1962).
2. Fixed time mechanisms: the forager leaves after a fixed amount of time has been spent in a patch. This is the 'hunting by time expectation' hypothesis of Krebs (1973)

3. Fixed searching time mechanisms: the forager leaves after a constant searching time per patch.
4. Fixed rate mechanisms: the forager leaves when the capture of food items falls below a fixed threshold rate.

The fixed rate mechanism is at the heart of most optimal foraging models. In the population models of Hassell and May (1974) and Murdoch and Oaten (1975), the threshold capture rate is assumed to be constant. In contrast, optimal foraging models such as that of Charnov (1976) assume that the 'giving-up' threshold depends upon the average prey density in a particular habitat. The forager should therefore tend to reduce all patches to the same 'marginal' value which is the forager's expected rate of intake for that particular habitat.

A more complex behavioural model has been proposed by Waage (1978) for the foraging behaviour of the ichneumonid Nemeritis canescens parasitizing flour moth caterpillars within circular dishes serving as patches. Here, patch time is mainly determined by two factors together. The amount of patch odour (due to hosts) sets a level of responsiveness which then decays with time on the patch. Any oviposition serves to increase this responsiveness by a set amount and so prolongs time on the patch. The parasitoid finally leaves the patch when this responsiveness decays below a threshold level. This model could be further refined: for example, the level of responsiveness set by host odour, the extent of the increment in responsiveness after each oviposition and the threshold level are all likely to be influenced by the parasitoid's ovipositional drive, which is set predominantly by the number of eggs in the oviduct.

The graphical optimal foraging model of Royama (1971) is concerned more with patch selection than patch time. Given a set of patches of different profitabilities and a certain amount of foraging time, the forager spends most time in the most profitable patches (those with the highest capture rates). This model proposes no specific patch-time mechanism, but implies that a new patch is entered when the profitability of patches currently being exploited falls to the level of this patch. So, the forager again is assumed to base its decision on a measurement of the rate of prey capture. A similar mathematical model has been developed by Cook and Hubbard (1977) which also predicts an optimal set of patches to be visited and postulates that the rate of prey capture on these patches will be equal at the end of the foraging period.

Optimal foraging models suggest testable hypotheses as to the way in which foragers exploit a patchy environment. However, allocation of searching time may also be influenced by factors other than those maximising food intake. Several mathematical models have recently been developed which consider the influence of risks during foraging (eg Caracao, 1980).

Many of the optimal foraging models so far discussed relate specifically to predator-prey or parasitoid-prey systems. The case of syrphid females foraging for oviposition sites is slightly different. First-instar syrphid larvae are not very mobile and tend to have poorly developed sensory systems for locating aphid prey. The survival of the larvae therefore depends largely on where the adult female lays her eggs. As larvae and adults feed on different foods, oviposition is based on cues that correlate with larval survival. In this respect, the foraging strategies of ovipositing syrphids can be considered to be analogous to the oviposition behaviour of butterflies. As with syrphids, butterflies use visual and chemical cues to locate larval host-plants. Once a suitable host has been selected, chemical stimuli, often supplemented by perceptions of surface texture and moisture determine oviposition. Secondary plant compounds are often used to recognise specific host-plants (Ma and Schoonhoven, 1973; Calvert, 1974; Reese, 1979). The dispersal of butterfly eggs has been shown to be influenced by factors such as plant size (Latheef and Irwin, 1979), phenology (Singer, 1971), or site (Cates and Rhoades, 1977), in addition to chemical cues (Gilbert and Singer, 1975). Some species deposit their eggs singly whilst others lay in batches (Gilbert, 1975; Gilbert and Singer, 1975; Stamp, 1980).

The oviposition responses of free-ranging butterflies cannot be reduced to a set of stimuli and responses. An elegant comparative study of oviposition by Pieris rapae in Australia and Canada revealed that local populations of this butterfly differed in their oviposition patterns (Jones, 1977). The movement patterns of adult butterflies searching for oviposition sites were incorporated into a stochastic simulation model which may be used to predict and explain egg distributions. Some of the parameters of the model (those concerned with probabilities of landing and ovipositing) depend on host plant quality and particularly on the age and species of host plant. Other parameters, and notably the degree of attraction towards hosts, depend on the egg-load of the butterfly.

Jaenike (1978) has developed a model that predicts whether an insect should oviposit on a potential larval host plant when it is encountered. Optimal behaviour depends on the suitability of the plant for larval development and on the probability of finding a more suitable host in the available time. The model assumes that:

1. An individual produces eggs at a constant rate and that only a limited number of them can be carried at one time, and
2. The insect searches for host plants in a random manner.

The following chapter considers behavioural aspects of oviposition in the aphidophagous syrphid, Episyrphus balteatus. Results presented in Chapter 4 demonstrated that oviposition by this species in the field was closely related to aphid density. The aim of the following chapter is to examine the behavioural mechanism of this density-dependent oviposition response.

6.2 PRELIMINARY EXPERIMENT TO EXAMINE THE EFFECT OF APHID DENSITY ON THE EGG DISTRIBUTION RESPONSE OF EPISYRPHUS BALTEATUS

6.2.1 MATERIALS AND METHODS

Experiments were carried out in a room maintained at 20 ± 1 °C, 65 ± 5% RH and 16 h photoperiod.

The experimental apparatus is illustrated in Figure 6.2. The experimental cage was wooden-framed with glass sides and top. The cage contained seven twelve-week old Brussels sprout plants (cv Winter Harvest) in 5" diameter plastic pots. The structural complexity of each plant was reduced to a single leaf and this was artificially infested with a variable number of the cabbage aphid, Brevicoryne brassicae L..

Aphid infestations were established several days before the experiment commenced by confining aphid nymphs within clip cages on the ventral surface of the leaf. A range of seven different levels of aphid infestation were used in these experiments: 0, 10, 50, 100, 200, 400 and 800 aphids per plant. The larger infestations were established using several clip cages per leaf. Care was taken to try and maintain the plants in a healthy condition but this often proved difficult with the more heavily-infested plants.

Female E. balteatus flies used in the experiment were standardized in the following way. Newly-emerged females were released into a 150 x 114 x 105 cm wooden-framed glass cage with the equivalent numbers of males. The flies were provided daily with sucrose, water and pollen, as described in Section 5.2. Aphid-infested potted Brussels sprout plants were also provided for 2 hours daily to serve as oviposition sites. When the females were fourteen days old they were used in the experiment.

Groups of five standardized females were introduced into the experimental cage and allowed to oviposit on the plants for a period of four hours. At the end of this period, the flies were removed from the cage and the number of eggs on each plant was recorded.

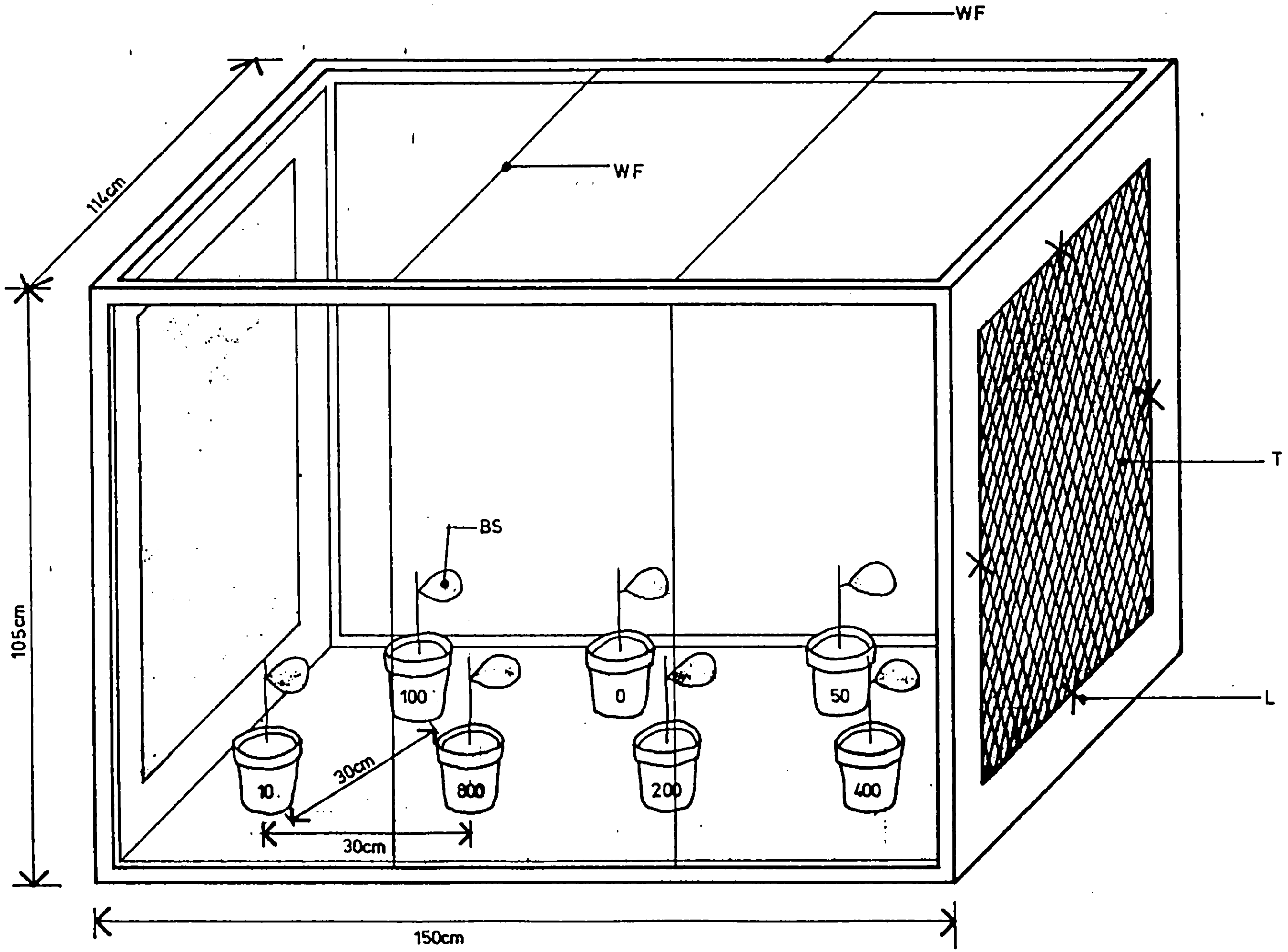
The experiment was replicated five times.

Figure 6.2: Experimental apparatus for examining the effect of aphid density on the egg distribution response of Episyrphus balteatus flies

The cage contains seven single-leaved Brussels sprout plants infested with varying numbers of aphids: 0, 10, 50, 100, 200, 400, 800

Key

L - Latch (allowing removal of door)
T - Terylene net door
BS - Aphid-infested Brussels sprout plant
WF - Wooden frame of cage


WF
WF
114cm
105cm
BS
T
L
100
0
50
10
800
200
400
30cm
30cm
150cm

6.2.2 RESULTS AND DISCUSSION

Figure 6.3 shows the mean number of eggs laid by five females on plants infested with different numbers of aphids. The graph indicates that increasing numbers of eggs were laid in response to increasing aphid density up to an optimum (of approximately 200 aphids per plant) beyond which egg numbers decreased. A one-way analysis of variance confirmed that there were highly significant differences in the number of eggs laid at different aphid densities (Table 6.1).

Table 6.1: The number of eggs laid per plant by five E. balteatus flies on plants infested with different aphid densities

Aphid Density	Mean number of eggs per plant ± SE
0	3.8 ± 0.85
10	6.6 ± 1.30
50	13.6 ± 1.09
100	17.8 ± 1.62
200	23.4 ± 1.34
400	21.0 ± 2.08
800	13.8 ± 1.47

Anova table

Source of variation	df	SS	MS	F-ratio	P
Among densities	6	3706.6	617.8	19.93	< 0.001
Within densities	28	868.0	31.0		
Total	34	4574.6			

The decline in egg numbers at high aphid densities is interesting. This phenomenon has also been reported to occur in the field on heavily-infested Brussels sprouts (Chandler, 1968b) and beans (Banks, 1953). Section 4.2 describes a study in which syrphid oviposition patterns on different brassica crops were monitored over a five-week period. The number of syrphid eggs laid per plant increased with increasing aphid density. In some crops, egg numbers levelled off at the higher aphid densities but there was no evidence of an actual decline in egg numbers at such densities. (See Figures C1 a and b, Appendix C). However, the general level of aphid infestation in all crops was relatively low.

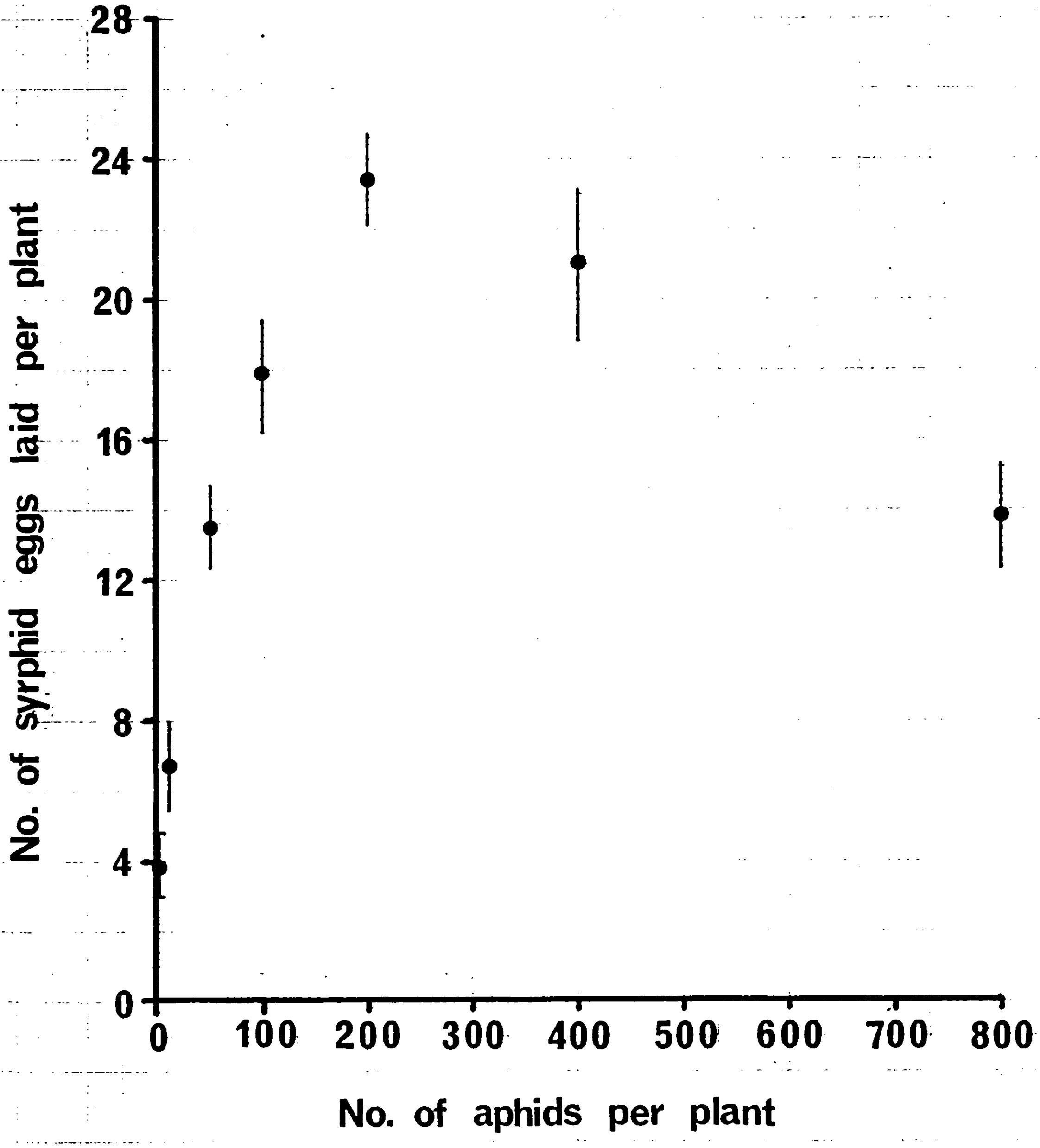
Large aphid infestations may be avoided for a number of reasons:

1. The growth and general condition of heavily-infested plants is usually poor;
2. Large concentrations of aphids may be more readily located and exploited by other aphid parasites and predators; and
3. Some syrphid parasites (eg diplazontin Ichneumonids) locate their hosts by responding to aphid-associated stimuli (eg aphid odour, honeydew) (Rotheray, 1981).

Thus, syrphid females may prefer to oviposit on less heavily-infested plants in order to reduce the likelihood of detection by their own natural enemies.

Figure 6.3: The relationship between aphid density and the number of eggs laid per plant by five *Episyrphus balteatus* females

The figure shows the average number of eggs laid on plants infested with different densities of aphids (with standard error bars)


No. of syrphid eggs laid per plant
0
4
8
12
16
20
24
28
No. of aphids per plant
0
100
200
300
400
500
600
700
800

6.3 EXPERIMENT TO EXAMINE THE BEHAVIOURAL MECHANISM DETERMINING THE EGG DISTRIBUTION RESPONSE OF EPISYRPHUS BALTEATUS TO PATCHES OF DIFFERENT APHID DENSITIES

6.3.1 INTRODUCTION

The previous section established that when E. balteatus females are presented with a set of plants infested with different numbers of aphids, the number of eggs laid per plant depends on the number of aphids present. What is the behavioural mechanism controlling this oviposition response? How does a female decide which plants to visit and how many eggs to lay on each plant?

The characteristic behaviour patterns shown by gravid E. balteatus females on encountering aphid-infested plants have already been described in Section 5.4. Briefly, the initial attraction to the plant is believed to be in response to visual stimuli associated with the plant colour and shape. Once in the immediate vicinity of the plant the fly hovers up and down the stem and around individual leaves. Occasionally, she may brush the plant surface with her tarsi. The fly may or may not land on the plant. If a landing does occur, the fly walks across the plant surface with her antennae held in a vertical plane. As soon as she encounters aphids or aphid honeydew, she exhibits a characteristic 'probing' behaviour. This involves walking across the plant surface probing with an extended proboscis and ovipositor alternately. Eventually, she may bend her ovipositor ventrally and drag it across the substrate. This behaviour has been termed 'cocking'. Cocking frequently, but not invariably results in the deposition of an egg.

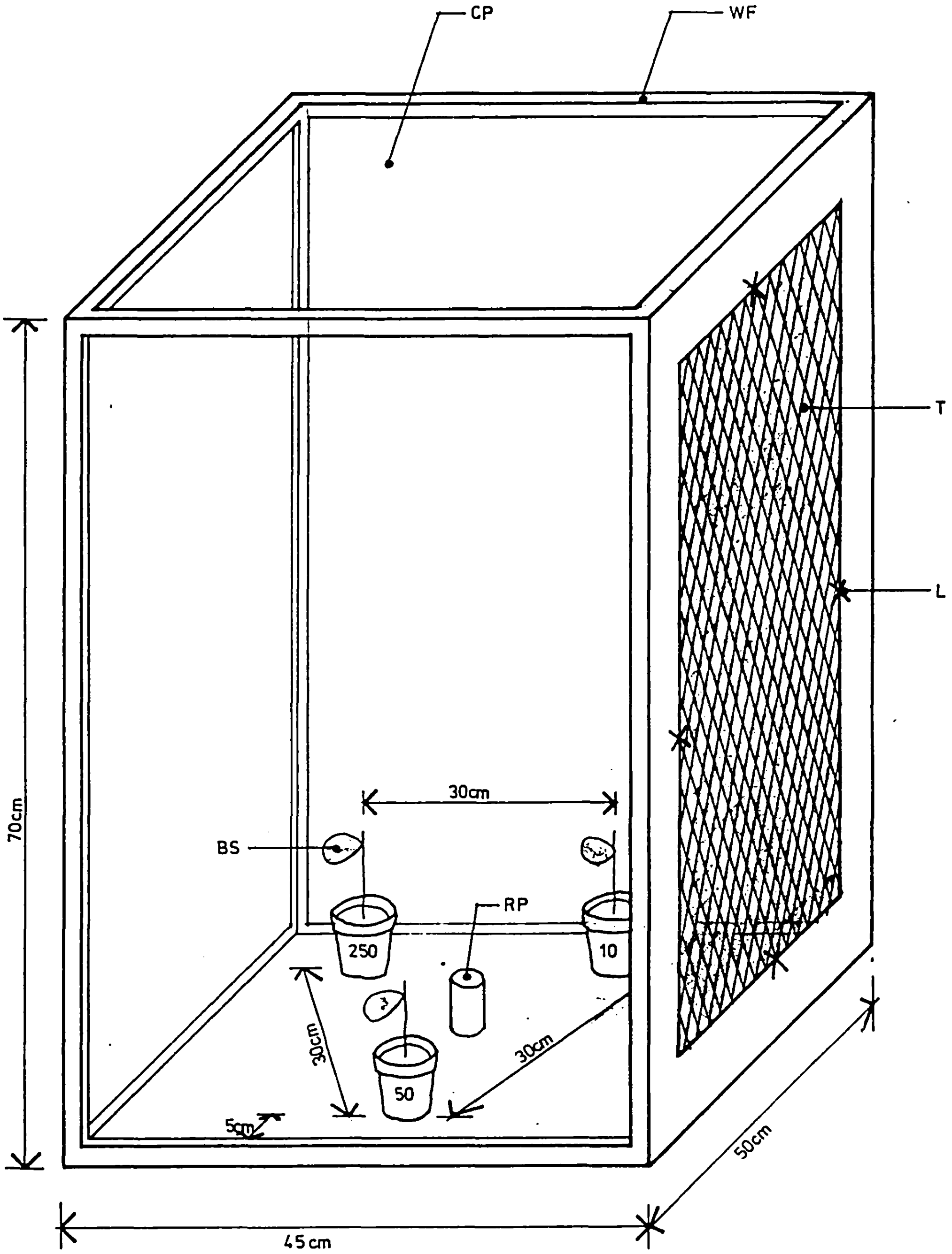
The following section examines the behavioural responses of gravid E. balteatus females to a set of three plants infested with different numbers of aphids. Each plant may be considered to be a 'patch' in the sense defined in Section 6.1 as the behaviour of flying syrphid females is arrested by the presence of the plant with its associated aphid stimulus.

Figure 6.4: Experimental apparatus for examining the egg distribution responses of Episyrphus balteatus flies to a set of three patches of different aphid densities

The cage contains three single-leaved potted Brussels sprout plants arranged in a triangular array. The plants are infested with 10, 50 and 250 aphids, respectively

Key

L - Latch (enabling removal of cage door)
T - Terylene net door
BS - Aphid-infested Brussels sprout plant
CP - Clear plastic top of cage
RP - Release point for experimental flies
WF - Wooden frame of cage


CP
WF
T
L
30cm
BS
RP
250
10
3
50
30cm
30cm
5cm
70cm
45cm
50cm

6.3.2 MATERIALS AND METHODS

The experiments were carried out in a room maintained at 20 ± 1 °C, 65 ± 5% RH and 16 h photoperiod.

The experimental apparatus comprised of a 50 x 45 x 70 cm wooden-framed cage with clear plastic sides and top containing three potted Brussels sprout plants (cv Winter Harvest) arranged in a triangular array, as shown in Figure 6.4. Each plant was reduced to a single leaf so as to simplify the spatial complexity of the experimental system. Each plant was artificially infested with a known number of aphids (B. brassicae), as described in Section 6.2.1. The range of aphid infestations used in these experiments were 10, 50 and 250 aphids per plant. These particular levels of infestation were selected on the basis of the results obtained in the preliminary experiments (6.2).

All flies used in these experiments were standardized in the following way. Newly-emerged females were placed in a 150 x 114 x 105 cm wooden-framed glass cage with an equivalent number of males. The flies were provided daily with 10% sucrose solution, pollen and water, as described in Section 5.2. Potted Brussels sprout plants infested with B. brassicae were introduced into the cages daily for a period of two hours to serve as oviposition sites. When the females were 12 days old, they were transferred to individual 50 x 45 x 70 cm wooden-framed cages for three days. On the first two days, both food and oviposition sites were provided as before, but on the third day, food only was given. On the fourth day, ie when the flies were aged 15 days, the females were used in experiments. Only females known to have laid eggs previously were used in these experiments.

A single standardized female was introduced into the experimental cage in a 2.5 cm diameter glass tube. This tube was placed open-end upwards at the centre of the trangular array of plants and the female was allowed to emerge at will. Occasionally, flies remained inactive in the tube or on the sides of the cage for long periods. A criterion was therefore established that a fly must locate a plant within 20 minutes of being introduced into the cage. Any fly which did not find a plant within this period was removed and a new standardized fly was introduced into the cage.

As soon as the fly located a plant, the experiment was commenced. The behaviour of the insect was observed for one hour and the duration of the following activities was recorded on a 15-channel event recorder†: presence on the patch, presence off the patch, flying, resting, grooming, probing and cocking. The location of each activity was also recorded as being inside or outside the patch. Flying was classified as occurring within the patch if the fly was facing the plant when hovering around it, and outside the patch if she was facing away from the plant whilst hovering. All other activities were classified as occurring inside the patch if the fly was present on the plant and outside the patch if they occurred elsewhere in the cage. The number of eggs on each plant was recorded at the end of the experiment.

The one-hour observation period was determined on the basis of a previous observation that the average duration of a foraging bout by an individual fly was approximately one hour.

6.3.3 RESULTS AND DISCUSSION

Table 6.2 shows the number of visits to patches of different aphid densities. All visits are included in this analysis, regardless of whether or not the fly landed on the plant. A one-way analysis of variance confirmed that there was no significant difference in the number of approaches made to each patch.

Table 6.2: <u>The number of visits to patches of different aphid densities</u> (All visits considered)

Aphid Density	Mean number of visits (± SE)
10	8.40 ± 2.51
50	7.50 ± 2.40
250	7.00 ± 2.01

---

† Designed and built by Tony Eastley, Dept of Electrical Engineering, Imperial College, London

Table 6.2: continued

Anova Table

Source of variation	df	SS	MS	F-ratio	P
Among densities	2	10.1	5.0	0.09	ns
Within densities	27	1442.9	53.4		
Total	29	1453.0			

Table 6.3 shows the average proportion of visits in which the fly landed on the plant. A one-way analysis of variance showed that the proportion of visits in which a landing occurred increased significantly with increasing aphid density.

Table 6.3: <u>The proportion of visits to patches of different aphid densities in which the fly landed on the plant</u>

Aphid Density	Average proportion of visits when fly landed on plant (± SE)
10	0.42 ± 0.07
50	0.58 ± 0.08
250	0.92 ± 0.05

Anova Table

Source of variation	df	SS	MS	F-ratio	P
Among densities	2	1.3045	0.6522	13.51	< 0.001
Within densities	27	1.3037	0.0483		
Total	29	2.6081			

Table 6.4 shows the order in which different patches were discovered by each of the ten replicates. Selection of the first and subsequent patches appears to be random and no significant bias occurs.

Table 6.4: The order in which patches of different aphid densities were discovered

Rep No	Patch discovered		
	1st	2nd	3rd
1	10	50	250
2	50	250	10
3	250	10	-
4	10	250	50
5	50	10	250
6	50	10	250
7	10	250	50
8	50	250	10
9	250	10	50
10	10	50	250

Table 6.5 shows the mean number of eggs laid on plants of different aphid densities. The number of eggs laid per plant increased signficiantly with increasing aphid density ($\chi^2 = 6.42$, 2 df, $p < 0.05$).

There was considerable variation in the number of eggs laid by different flies. The minimum number laid by a single female was 6 and the maximum was 76. Table E1 (Appendix E) summarizes the total number of eggs laid by individual flies.

Table 6.5: The number of eggs laid per plant on patches of different aphid densities

Aphid Density	Mean number of eggs per plant (± SE)
10	5.9 ± 2.62
50	7.6 ± 2.47
250	9.4 ± 2.41

Table 6.6 shows the average number of eggs laid per patch visit. These figures were calculated by dividing the total number of eggs laid on a particular patch by the total number of landings on that patch. A one-way analysis of variance showed that there was no significant difference in the number of eggs laid per patch visit on patches of different aphid densities. These results suggested that the flies laid a more or less fixed number of eggs per visit, regardless of the number of aphids present. Since more landings were made on higher density patches, so more eggs were ultimately laid on the higher density plants.

Table 6.6: The number of eggs laid per patch visit on patches of different aphid densities

Aphid Density	Mean number of eggs/visit (± SE)
10	1.72 ± 0.22
50	1.68 ± 0.34
250	1.73 ± 0.17

Table 6.6: continued

Anova Table

Source of variation	df	SS	MS	F-ratio	P
Among densities	2	0.011	0.006	0.01	ns
Within densities	27	17.248	0.639		
Total	29	17.259			

Table 6.7 shows the average duration of each visit to patches of different aphid densities. These figures were calculated by dividing the total time spent on each patch by the number of visits in which a landing occurred. A one-way analysis of variance confirmed that there was no significant difference in the duration of visits to patches of different densities.

Table 6.7: The average duration of visits to patches of different aphid densities

Aphid Density	Average duration of patch visit (seconds) (± SE)
10	5.9 ± 2.62
50	7.6 ± 2.47
250	11.8 ± 4.15

Anova Table

Source of variation	df	SS	MS	F-ratio	P
Among densities	2	184	92	0.92	ns
Within densities	27	2715	101		
Total	29	2899			

These results imply that the fly spends a more or less fixed amount of time in a patch during each visit, regardless of the number of aphids present. There was considerable variation in the total amount of time spent by individual flies visiting patches during the one hour period; the results for 10 replicates are presented in Table E2 (Appendix E).

Table 6.8 summarizes the apportioning of time to different activities in patches of different aphid densities. A one-way analysis of variance showed that there were no significant differences in the average amount of time spent flying, grooming or cocking per visit on patches of different aphid density. However, the amount of time spent resting showed a significant decrease with increasing aphid density indicating that flies were more active on the higher density patches.

Table 6.8: <u>The time spent engaged in different activites on patches of different aphid densities</u>

Activity	Average amount of time per patch visit (seconds) (± SE)		
	10	50	250
Flying	37.5 ± 11.30	50.9 ± 18.29	50.6 ± 14.68
Resting	90.2 ± 30.98	33.5 ± 15.92	18.6 ± 6.52
Grooming	36.3 ± 16.57	25.0 ± 12.55	17.0 ± 6.17
Probing	10.4 ± 3.35	28.3 ± 7.63	47.5 ± 10.35
Cocking	13.0 ± 4.21	34.5 ± 13.10	17.5 ± 5.22

Table 6.8: continued

Anova Table

Activity	Source of variation	df	SS	MS	F-ratio	p
Flying	Among densities Within densities	2 27	1168 60970	584 2258	0.26	ns
Resting	Among densities Within densities	2 27	28551 112976	14276 4184	3.41	< 0.05
Grooming	Among densities Within densities	2 27	1826 42305	913 1567	0.58	ns
Probing	Among densities Within densities	2 27	6899 15864	3449 588	5.87	< 0.01
Cocking	Among densities Within densities	2 27	2571 19468	1286 721	1.78	ns

The amount of time spent probing per visit increased significantly with increasing aphid density. The precise role of probing behaviour in the oviposition response is unclear. Aphid honeydew elicits both feeding and oviposition responses in E. balteatus flies but the extent to which these two responses are physiologically interrelated is unknown. Proboscis extension occurs mainly in response to stimuli received from chemoreceptors on the tarsi and labellum. The fact that increased probing activity did not result in more eggs being laid on higher density plants per visit suggested that probing may be more directly concerned with feeding than with oviposition. However, it seems likely that sensory information received from the probing process plays some part in the oviposition response.

Table 6.9 shows the oviposition rate (in terms of number of eggs laid per unit time spent cocking) on plants of different aphid densities.

Table 6.9: Oviposition rates on patches of different aphid densities

Aphid Density	Oviposition rate (eggs/second) (± SE)
10	0.12 ± 0.05
50	0.06 ± 0.02
250	0.12 ± 0.05

Anova Table

Source of variation	df	SS	MS	F-ratio	p
Among densities	2	0.0235	0.0117	0.71	ns
Within densities	27	0.4450	0.0165		
Total	29	0.4685			

A one-way analysis of variance showed that there was no significant difference in the oviposition rate on plants of different aphid densities. This might imply that the rate at which eggs can be laid may be limiting the number of eggs deposited on the higher density plants during each visit. However, casual observations on ovipositing females confined within glass tubes with aphid-infested leaves showed that the flies were capable of laying eggs at the rate of one egg/second. The rates of oviposition observed in the above experiments were much lower than this, suggesting that mechanical constraints were not responsible for insignificant differences in oviposition rates on patches of different aphid densities.

6.4 GENERAL DISCUSSION AND CONCLUSIONS

A very simple mechanism has been presented to explain how E. balteatus females forage in a set of patches of different aphid densities. The initial approach to a patch appears to be random and independent of the number of aphids present. The fly initially hovers up and down the stem and around individual leaves. This initial visual assessment of the plant appears to determine whether or not the fly will land on the plant. The probability of landing is closely related to aphid density: more landings are made on higher density plants. A fixed number of eggs are laid per patch visit, regardless of the number of aphids present. The average duration of eachpatch visit also appears to be similarly fixed. Flies were more active on higher density patches and spent more time probing although the significance of this activity in relation to the oviposition response was not clear.

This mechanism explains the aggregative response observed in the field (see Chapter 4) whereby more eggs are laid on higher density plants: flies are more likely to land on the higher density plants and so, eventually, more eggs will be laid there.

The mechanism for oviposition-site selection described above implies that increasing numbers of eggs are laid in response to increasing aphid densities. However, this may be too simplistic. It was shown in Section 6.2.2 that the number of syrphid eggs laid per plant declines at high aphid densities. This phenomenon has also been observed in the field (Banks, 1953; Chandler, 1968b). Reasons for avoidance of heavy aphid infestations have already been discussed (Section 6.2.2) and may be related to larval survival. Most optimal foraging models assume that the goal of an ovipositing syrphid female should be to maximise her own fitness through her offspring. This may be achieved by maximising the number of eggs laid and/or by maximising the survival prospects of the eggs and larvae. Thus, the model for oviposition-site selection should perhaps also include a component that relates to the survival of the eggs/larvae on plants of different aphid densities.

A final criticism of the model is that it takes no account of the effect of previous patch experience or the role of learning in influencing the oviposition response.

CHAPTER 7

THE MANIPULATION OF SYRPHID OVIPOSITION BEHAVIOUR USING FOOD SPRAYS

7.1 INTRODUCTION

The purpose of this chapter is to evaluate the potential role of syrphids as biocontrol agents of aphids and to consider ways in which their effectiveness may be improved.

7.1.1 Effectiveness of syrphids as biocontrol agents of aphids

The effectiveness of aphidophagous insects in controlling aphid populations is determined by three factors:

1) voracity (a function of appetite, activity and abundance;
2) the multiplication rate of the aphid;
3) synchronisation with the aphid population (van Emden, 1966).

Syrphids show considerable potential as biocontrol agents of aphids. The adults are highly mobile and can search widely for aphid colonies. Many species oviposit in close proximity to aphids so that newly-hatched larvae are assured of a readily-available food supply. The destructive capacity of the larvae is high: laboratory studies on *Metasyrphus corollae* have shown that each larva may consume several hundred aphids during the course of its development (Bombosch, 1963; Yakhontov, 1966; Benestad, 1970b; Tawfik *et al*, 1974a; Ruzicka, 1975; Barlow, 1979; Cornelius and Barlow, 1980; Polak, 1980). The larvae of some species can survive for long periods without food, especially during the second and third instars; starved syrphid larvae are very active (Bänsch, 1964, 1966).

Polyvoltine predatory species tend to have very short life-cycles with no obligatory diapause (Schneider, 1948; Bombosch, 1957; Láska, 1959; Hamrum, 1966) so aphid infestations may be heavily and repeatedly attacked during a single season. In addition, such species usually have relatively high rates of increase: Barlow (1961) calculated that the rate of increase of Metasyrphus corollae was 2.44 individuals per female per week.

The effectiveness of syrphids in controlling aphid populations is often limited by poor synchronisation. Although gravid females may search crop fields before aphids immigrate (Dunn, 1949; Bombosch, 1963; 1967), oviposition usually only occurs when the aphid population is firmly established. (Dunn, 1949; Banks, 1953; Dixon, 1959; van Emden, 1963). Although massive aphid destruction may occur and population growth be curbed (Way and Banks, 1962), the restraint may still be overcome by aphid multiplication (eg van Emden, 1963, 1966; Dunn and Kempton, 1971; Grigorov, 1982). In such cases the check may even benefit the aphids if the predator thereby retards pest build-up until the host plant has increased in size and can support a larger aphid population (Way, 1966).

If syrphid oviposition could be better synchronised with aphid immigration into crops, their control potential would be greatly enhanced.

7.1.2 The use of food sprays to enhance the effectiveness of natural enemies in the field

In recent years, considerable attention has been focussed on the use of behavioural chemicals for augumenting natural enemy populations in the field.

The adults of many entomophagous species, including syrphids, feed on aphid honeydew (Zoebelein, 1956). Honeydew has also been shown to stimulate oviposition in Metasyrphus corollae (Volk, 1964).

Several studies have shown that the application of artifical honeydews increases the effectiveness of entomophagous insects in the field. Hagen et al (1971, 1976) applied a 'food spray' based on protein hydrolysate and Feed-Wheast^{R*} to alfalfa and cotton crops. There was a significant increase in the number of adult Chrysopa carnea (Steph.) and egg production in this species was also enhanced. As a result, populations of the spotted alfalfa aphid (Therioaphis trifolii (Monell)) and lapidopteran larvae were significantly reduced. The treated plots also showed higher numbers of coccinellids (Hippodamia spp).

Ben Saad and Bishop (1972, 1976) showed that treatments with artificial honeydews combined with honey and molasses significantly increased numbers of chrysopids, coccinellids, syrphids and nabids when applied to potato plots. In addition, the fecundity of Chrysopa carnea was significantly increased by the treatments. In consequence, populations of Myzus persicae (Sulz.), Lygus hesperus (Knight), Leptinotarsa decemlineata (Say) and Autographa californica (Speyer) were significantly reduced in treated areas. These food sprays were, however, only effective when a low level of aphid infestation also occurred: neither artificial honeydew nor aphid extract stimulated syrphid oviposition on aphid-free plants.

Fructose solutions applied to corn increased the numbers of coccinellids (Hippodamia spp) and reduced numbers of the European corn borer, Ostrinia nubialis (Hbn) (Ewart and Chiang, 1966; Carlson and Chiang, 1973). Schiefelbein and Chiang (1966) found that the application of sucrose sprays to corn significantly increased the numbers of coccinellid and chrysopid adults and this led to a decrease in populations of the aphid Rhopalosiphum maidis (Fitch). The aggregative effect of the sugar spray was, however, reduced in the presence of high aphid populations.

The aim of the following chapter is to examine the effect of food sprays on syrphid oviposition in brassica crops and to evaluate the potential of this technique as a means of enhancing the effectiveness of syrphids as aphid predators.

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* Feed-Wheast^{R} is a commercially obtained yeast (Saccharomyces fragilis) plus its whey substrate.

7.2 MATERIALS AND METHODS

Three field trials were carried out in Brussels sprout, red cabbage and cauliflower crops during 1980, 1981 and 1982, respectively. The experimental design for each trial is described separately.

7.2.1 Field Trial 1

7.2.1.1 Experimental design

The experiment was carried out in an area of bare soil ($40 \times 40\ m^2$) during July and August 1980.

The experimental design comprised nine plots of 12-week old potted Brussels sprout plants (cv Winter Harvest) arranged in a 3 x 3 Latin square design (see Figure 7.1). Each plot contained 64 plants arranged in an 8 x 8 grid.

The plant pots were buried below the soil surface such that the pot rim was set level to the soil surface.

All plants were artificially infested in the laboratory with low numbers (approximately 50 aphids/plant) of the cabbage aphid *Brevicoryne brassicae*. The aphid populations on these plants were checked regularly throughout the experiment and supplemented if necessary using aphids from a laboratory culture.

7.2.1.2 Food spray treatment

Three treatments were applied:-

1. Sucrose solution
   10 g sucrose per 100 ml distilled water
2. Sucrose + 'Yeastrel'*
   10 g sucrose + 2 g 'Yeastrel' per 100 ml distilled water
3. Distilled water

Each treatment was replicated three times (see Figure 7.1).

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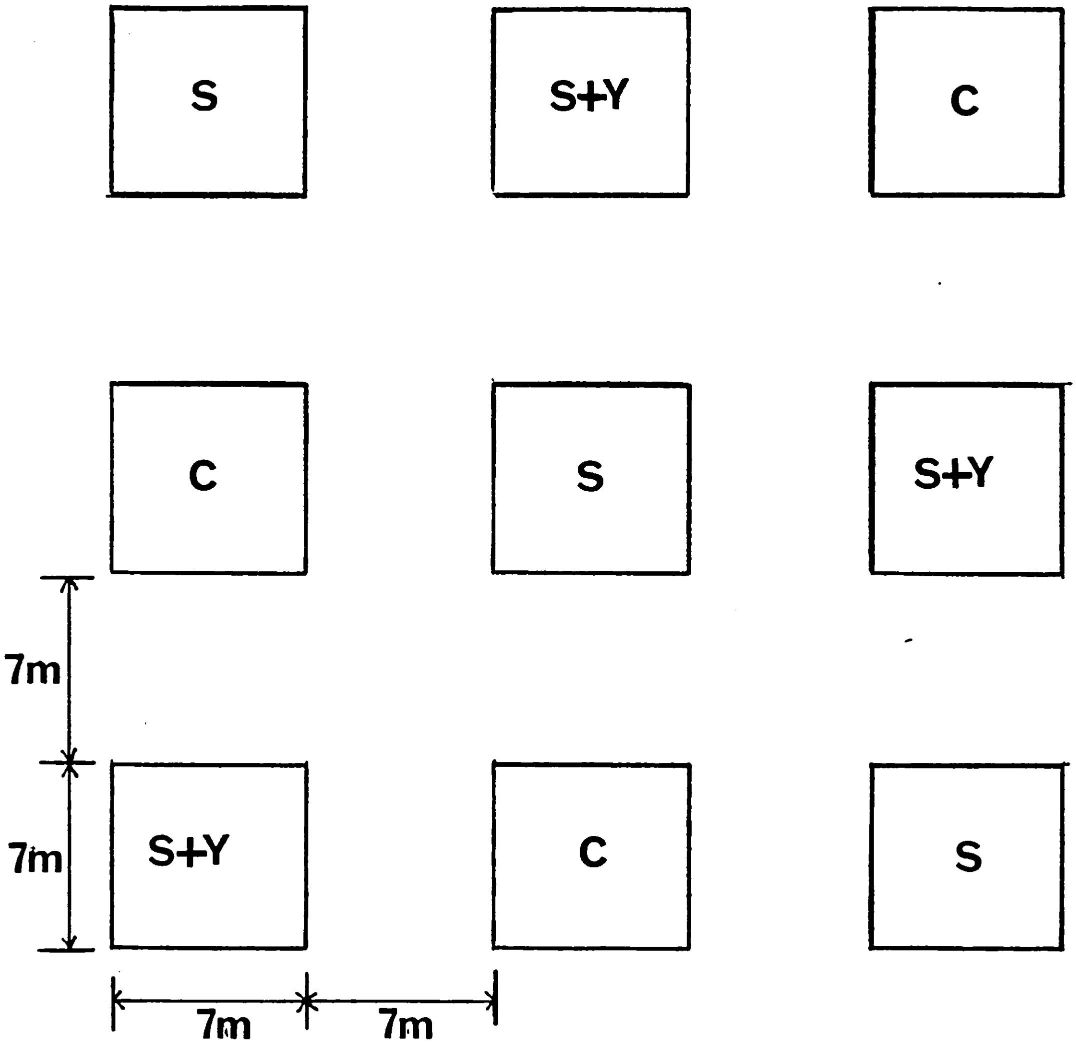
* 'Yeastrel' is a commercially-obtained protein hydrolysate of yeast.

Figure 7.1: <u>Experimental design for Field Trial 1</u>

<u>Key</u>

C - Control
S - Sucrose
S+Y - Sucrose + 'Yeastrel'


S
S+Y
C
C
S
S+Y
S+Y
C
S
7m
7m
7m
7m

7.2.1.3 Application of food sprays

All treatments were applied as sprays using a 'Herbi' ultra-low volume spinning disc sprayer.

Three successive sprays were applied: the spray dates together with the weather conditions at the time of spraying are given in Table F1 (Appendix F). All sprays were applied at 1900 h. The rate of application was 20 l/ha.

7.2.1.4 Sampling of plants

The dates for each sample occasion are given in Table F2 (Appendix F). Two pre-spray samples and three post-spray samples were carried out. The post-spray samples were made two days after the application of each spray. The weather conditions for the period between the date of spray application and the sample date are also shown in Table F2 (Appendix F).

Ten plants in each plot were selected at random and labelled. These plants were inspected on each sample date and the following information was recorded:

1. Number of syrphid eggs per plant. Only unhatched eggs were recorded.
2. Number of syrphid larvae per plant.
3. Number of syrphid pupae per plant.

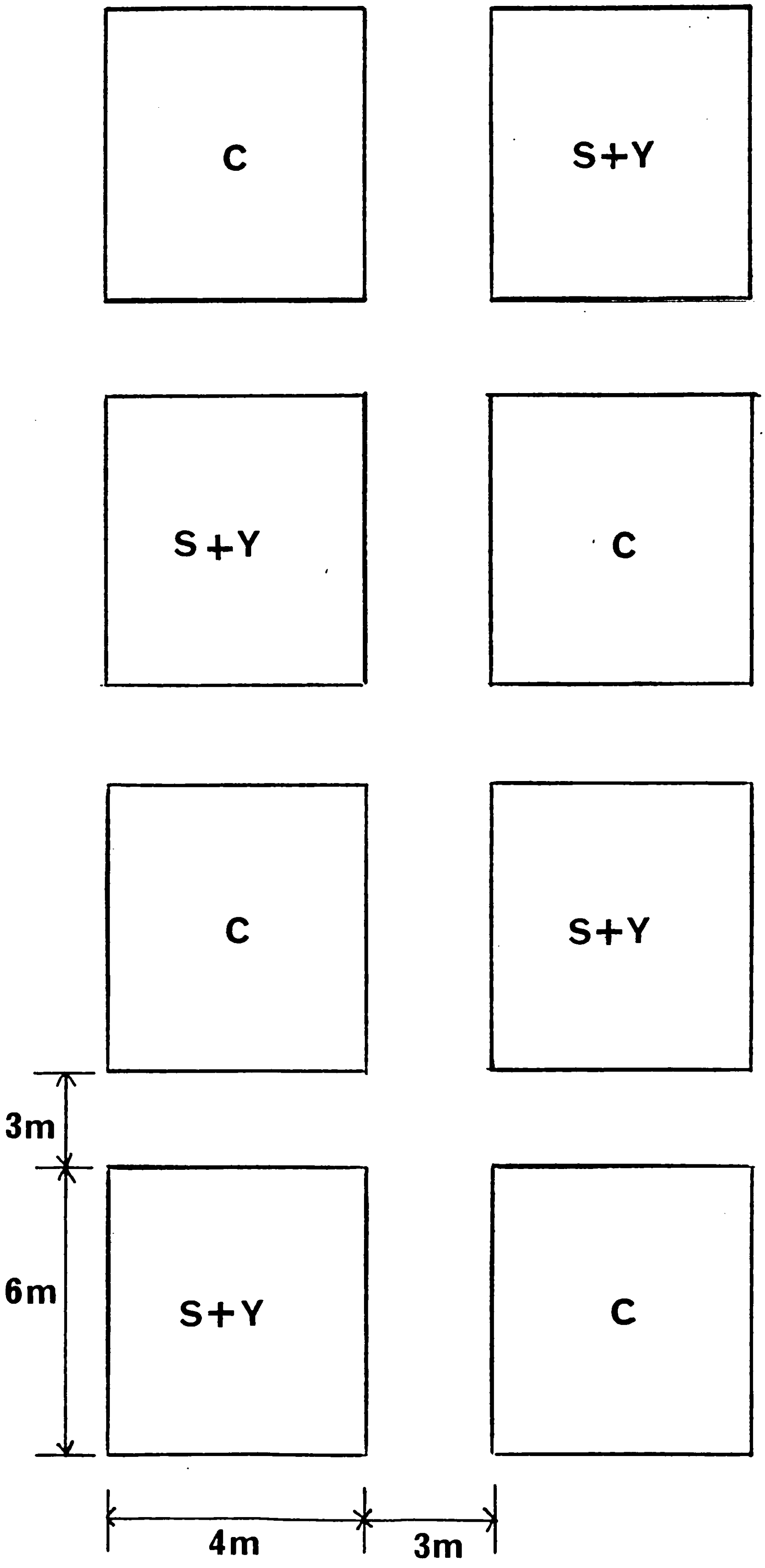
All syrphid eggs, larvae and pupae were removed from the plants and transferred to the laboratory for identification. Eggs were stored in Pampel's fluid (6 parts 35% formaldehyde:15 parts 95% ethanol: 2 parts glacial acetic acid:30 parts distilled water) prior to identification. Eggs were identified using Chandler's (1968d) egg key. The larvae were identified using Dixon's (1960) key and by rearing them through to the imaginal stage in the laboratory. Pupae were identified following the emergence of the adult.

Figure 7.2: <u>Experimental design for Field Trial 2</u>

Key

C - Control

S+Y - Sucrose + 'Yeastrel'


C
S+Y
S+Y
C
C
S+Y
S+Y
C
3m
6m
4m
3m

7.2.2 Field Trial 2

7.2.2.1 Experimental design

The second field trial was carried out in plots of red cabbage (cv Meteor Original) during September 1981. The crop was planted out as seedlings in May 1981.

The experimental design comprised eight plots of plants arranged as shown in Figure 7.2. Each plot consisted of 24 plants arranged in a 6 x 4 grid.

The plants were naturally infested with low numbers of the cabbage aphid, B. brassicae at the time of the experiment.

7.2.2 Food spray treatments

On the basis of results obtained in Field Trial 1, two treatments only were applied:

1. Sucrose + 'Yeastrel' solution.
   10 g sucrose + 2 g 'Yeastrel' per 100 ml distilled water.
2. Distilled water.

Each treatment was replicated four times (see Figure 7.2).

7.2.2.3 Application of food sprays

The treatments were applied as sprays using the 'Herbi' ultra-low volume spinning disc sprayer (as in Field Trial 1). The rate of application was 20 l/ha.

Initially, it had been planned to apply a series of three sprays and sample at two and four-day intervals after the application of each spray. However, adverse weather conditions throughout most of September prevented the application of the second and third sprays. The first spray was applied on 6.9.81; the weather conditions at the time of spraying are given in Table F3 (Appendix F).

7.2.2.4 Sampling of plants

The dates of each sample occasion are given in Table F4 (Appendix F). Two pre-spray and two post-spray samples were carried out. The post-spray samples were made 2 days and 4 days after spray application respectively. The weather conditions for the period between the spray date and each sample data are given in Table F4 (Appendix F).

Five plants from each plot were selected at random and labelled. These plants were inspected on each sample date and the following information recorded:

1. Total number of syrphid eggs per plant.
2. Number of eggs laid singly per plant.
3. Number of eggs laid in batches per plant.
4. Number of egg batches per plant.
5. Number of syrphid larvae per plant.
6. Number of syrphid pupae per plant.
7. Number of aphids per plant.

Only unhatched eggs were recorded. All syrphid eggs, larvae and pupae were transferred to the laboratory for identification as described in Section 7.2.1.4.

7.2.3 Field Trial 3

7.2.3.1 Experimental design

The third field trial was carried out in plots of cauliflower (cv All The Year Round) during August and September 1982. The cauliflowers were initially grown in cold frames and were planted out in the field as eight-week old seedlings in late May.

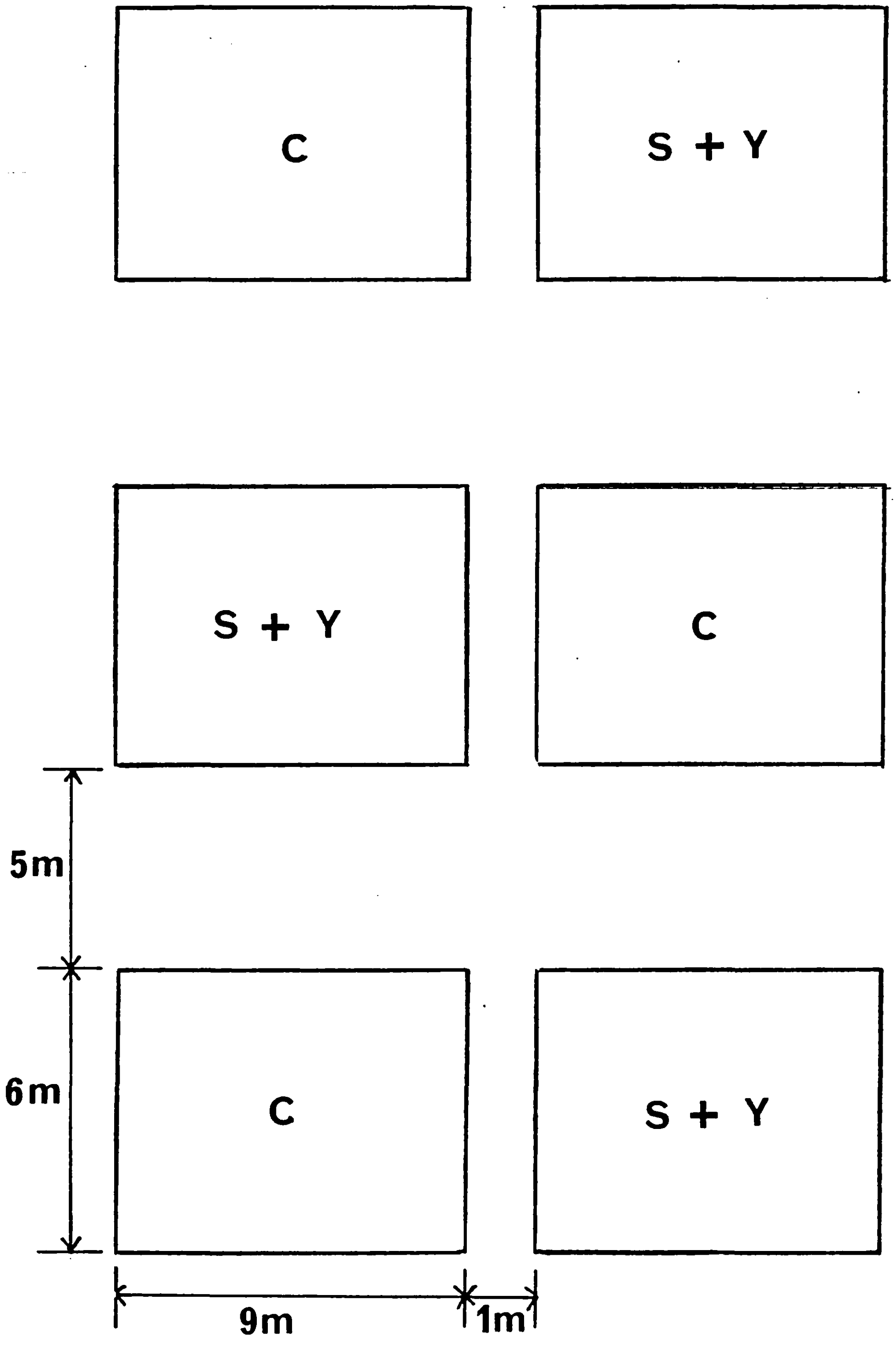
The experimental design comprised three blocks, each consisting of two plots of plants (see Figure 7.3).

Figure 7.3: Experimental design for Field Trial 3

Key

C - Control

S+Y - Sucrose + 'Yeastrel'


C
S + Y
S + Y
C
C
S + Y
5m
6m
9m
1m

All plants were naturally infested with low levels of the cabbage aphid, B. brassicae throughout the experiment.

7.2.3.2 Food spray treatments

Two treatments were applied as in Field Trial 2:

1. Sucrose + 'Yeastrel' solution
   10 g sucrose + 2 g 'Yeastrel' per 100 ml water
2. Distilled water

Each treatment was replicated three times (see Figure 7.3).

7.2.3.3 Application of food sprays

As in the two previous trials, the treatments were applied using a 'Herbi' ultra-low volume sprayer with an application rate of 20 l/ha.

Two sprays were applied on 21.8.82 and 25.8.82, respectively. Both sprays were applied at 0900. The weather conditions at the time of application of each spray are given in Table F5 (Appendix F).

7.2.3.4 Sampling of plants

The dates of each sample occasion are given in Table F6 (Appendix F). Two pre-spray and two post-spray samples were carried out. The post-spray samples were made 24 h after the application of each spray. The weather conditions for the period between the date of spray application and each sample date are given in Table F6 (Appendix F).

Ten plants in each plot were selected at random and labelled. These plants were inspected on each sample occasion and the following information was recorded:

1. Total number of syrphid eggs per plant.
2. Number of eggs laid singly per plant.
3. Number of eggs laid in batches per plant.

4. Number of egg batches per plant.
5. Number of syrphid larvae per plant.
6. Number of syrphid pupae per plant.
7. Number of aphids per plant.

Only unhatched eggs were recorded. As in the previous trials, all eggs, larvae and pupae were removed from the plants and transferred to the laboratory for identification as described in Section 7.2.1.4.

7.3 RESULTS AND DISCUSSION

7.3.1 Field Trial 1

Table 7.1 summarizes the effect of different food spray treatments on syrphid oviposition on the Brussels sprout plants. Pre- and post-spray samples have been analysed separately. Analysis of variance showed that there was no significant difference in the number of syrphid eggs laid per plant in different plots before the spray was applied ($F = 0.19$, 2 df, ns). However, following spray application, significantly more eggs were laid on plants that had been sprayed with the two food solutions than on the control plots ($F = 72.96$, 2 df, $p < 0.05$). More eggs were laid on plants that had been sprayed with sucrose + 'Yeastrel' than on these that had been sprayed with sucrose solution only.

The analysis of variance also indicated that there were significant differences between rows. The experimental area was bordered on three sides by agricultural crops (Wheat and Brussels sprouts) and on the fourth side by a grass verge containing flowering weeds. Fewer eggs were laid on the three experimental plots closest to this verge than on the other plots. It seems likely that syrphid adults entering the experimental area from the direction of the weedy verge may have been arrested within the verge before they encountered the sprayed plants.

Table 7.1: The number of syrphid eggs laid on control and treated plots on pre- and post-spray sample occasions during Field Trial 1

a)

Treatment	Number of eggs/plant (± SE)	
	Pre-spray	Post-spray
Control	0.13 ± 0.06	0.85 ± 0.12
Sucrose	0.17 ± 0.07	1.65 ± 0.20
Sucrose + Yeastrel	0.12 ± 0.07	1.86 ± 0.18

b)

Sample	Source of variation	df	SS	MS	F-ratio
Pre-spray	Rows	2	4.23	2.12	0.51 ns
	Columns	2	5.56	2.78	0.68 ns
	Treatments	2	1.56	0.78	0.19 ns
	Error	2	8.21	4.11	
	Total	8	19.56		
Post-spray	Rows	2	3472.23	1736.12	41.23 *
	Columns	2	1500.23	750.12	17.81 ns
	Treatments	2	6144.89	3072.45	72.96
	Error	2	84.21	42.11	
	Total	8	11201.56		

* $p < 0.05$

Eggs belonging to eight different syrphid species were recorded from the experimental plots. These included Episyrphus balteatus, Metasyrphus luniger, Syrphus ribesii, Sphaerophoria scripta, Platycheirus peltatus, Platycheirus albimanus, Platycheirus clypeatus and Melanostoma mellinum. The most abundant species recorded was Sphaerophoria scripta.

Table 7.2 shows the total number of eggs laid by each species on different experimental plots before and after spraying. Unfortunately, the numbers of eggs laid by individual species on all pre-spray sample occasions were too low to permit statistical analysis. These low egg counts were due mainly to adverse weather conditions (ie prolonged periods of heavy rain) during the pre-spray period. Such conditions depress adult syrphid activity. For all species, there was a significant difference in the number of eggs laid on different experimental plots on all post-spray sample occasions: significantly more eggs were laid on plots treated with the two food sprays than on the control plots.

Table 7.2: The number of eggs laid by different syrphid species on control and treated plots before and after spraying Field Trial 1

Sample occasion	Species	Number of eggs laid			χ^2 (2 df)
		C	S	S+Y	
Pre-spray	Episyrphus balteatus	1	2	1	a
	Metasyrphus luniger	-	1	-	a
	Syrphus ribesii	2	-	-	a
	Sphaerophoria scripta	-	2	1	a
	Platycheirus peltatus	-	1	-	a
	Platycheirus albimanus	3	2	4	a
	Platycheirus clypeatus	-	-	-	a
	Melanostoma mellinum	2	2	1	a
	Total	8	10	7	
Post-spray	Episyrphus balteatus	20	31	51	14.52 ***
	Metasyrphus luniger	-	-	-	
	Syrphus ribesii	9	18	30	11.68 **
	Sphaerophoria scripta	46	91	76	14.94 ***
	Platycheirus peltatus	26	45	50	7.75 *
	Platycheirus albimanus	25	51	61	15.11 ***
	Platycheirus clypeatus	13	35	28	9.99 **
	Melanostoma mellinum	14	26	39	11.88 **
	Total	153	297	335	

C - Control; S - Sucrose; S+Y - Sucrose + 'Yeastrel'

a - Number too low to permit statistical analysis

7.3.2 Field Trial 2

The results for the food-spray trial carried out in the red cabbage crop are summarised in Tables 7.3-7.5. The data for each pre- and post-spray sample occasion have been analysed separately using a nested analysis of variance.

Table 7.3 shows the total number of eggs laid on each sample occasion. Very few syrphid eggs were recorded throughout the experiment. Low egg counts were due mainly to:

1. Adverse weather conditions and
2. Time of year

(overall syrphid abundance declined rapidly during mid-September). In addition, it was demonstrated in Section 4.2.2.6 that oviposition by several syrphids, particularly batch-laying species, tends to be low on red cabbage in comparison to oviposition on other brassica crops.

The results presented in Table 7.3 indicate that there was no significant difference in the number of eggs recorded on different experimental plots before spraying. After spraying, however, syrphid oviposition on plots treated with the food spray was significant higher than on the control plots ($F = 10.14$, $p < 0.01$). However, this effect was only observed on the first post-spray sample occasion (ie 2 days after spray application). On the second post-spray sample date (ie 4 days after spraying), similar numbers of eggs were laid on both food-spray and control plots ($F = 3.33$, ns). It seems probable that the prolonged periods of heavy rainfall on the second and third day after spraying were responsible for washing the food spray from the plants, thereby rendering its effect useless.

Table 7.4 summarizes the effect of the food spray treatments on the number of syrphid eggs laid singly. More eggs were laid on plots treated with the sucrose + 'Yeastrel' food spray than on the control plots on both post-spray sample occasions. However, analysis of variance showed that these differences were not statistically significant.

Table 7.3: The total number of syrphid eggs recorded on control and treated plots on each pre- and post-spray sample occasion during Field Trial 2.

a)

Sample occasion	Number of eggs/plant (± SE)	
	Control	Food spray
Pre-spray 1	1.45 ± 0.33	1.40 ± 0.38
2	0.45 ± 0.19	0.90 ± 0.40
Post-spray 1	0.70 ± 0.22	1.95 ± 0.32
2	0.25 ± 0.12	0.65 ± 0.17

b) Anova Table

Sample occasion	Source of variation	df	SS	MS	F-ratio
Pre-spray 1	Among treatments	1	0.90	0.90	2.09 ns
	Among plots	6	0.78	0.13	0.30 ns
	Within plots	32	13.60	0.43	
	Total	39	15.28		
Pre-spray 2	Among treatments	1	1.45	1.45	2.90 ns
	Among plots	6	1.20	0.20	0.40 ns
	Within plots	32	16.10	0.50	
	Total	39	18.75		
Post-spray 1	Among treatments	1	15.62	15.62	10.14 **
	Among plots	6	7.95	1.33	0.86 ns
	Within plots	32	49.20	1.54	
	Total	39	72.77		
Post-spray 2	Among treatments	1	1.60	1.60	3.33 ns
	Among plots	6	1.10	0.18	0.38 ns
	Within plots	32	15.20	0.48	
	Total	39	17.90		

** $p < 0.01$

Table 7.4: The number of syrphid eggs laid singly on control and treated plots on each pre- and post-spray sample occasion during Field Trial 2

a)

Sample occasion	Number of eggs/plant (± SE)	
	Control	Food spray
Pre-spray 1	0.90 ± 0.22	1.00 ± 0.30
2	0.30 ± 0.13	0.57 ± 0.25
Post-spray 1	0.70 ± 0.22	1.35 ± 0.22
2	0.25 ± 0.12	0.45 ± 0.13

b) Anova Table

Sample occasion	Source of variation	df	SS	MS	F-ratio
Pre-spray 1	Among treatments	1	0.10	0.10	0.17 ns
	Among plots	6	6.40	1.07	1.81 ns
	Within plots	32	18.76	0.59	
	Total	39	25.26		
Pre-spray 2	Among treatments	1	2.16	2.16	4.60 ns
	Among plots	6	4.21	0.70	1.49 ns
	Within plots	32	15.15	0.47	
	Total	39	21.52		
Post-spray 1	Among treatments	1	4.23	4.23	4.07 ns
	Among plots	6	3.55	0.59	0.57 ns
	Within plots	32	33.20	1.04	
	Total	39	40.98		
Post-spray 2	Among treatments	1	0.40	0.40	1.05 ns
	Among plots	6	0.70	0.12	0.32 ns
	Within plots	32	12.00	0.38	
	Total	39	13.10		

Table 7.5: The number of syrphid eggs laid in batches on control and treated plots on each pre- and post-spray sample occasion during Field Trial 2

a)

Sample occasion	Number of eggs/plant (± SE)	
	Control	Food spray
Pre-spray 1	0.60 ± 0.28	0.40 ± 0.23
2	0.30 ± 0.21	0.65 ± 0.11
Post-spray 1	-	0.60 ± 0.25
2	-	0.20 ± 0.14

b) Anova Table

Sample occasion	Source of variation	df	SS	MS	F-ratio
Pre-spray 1	Among treatments	1	0.35	0.35	1.25 ns
	Among plots	6	3.72	0.62	2.21 ns
	Within plots	32	8.95	0.28	
	Total	39	14.02		
Pre-spray 2	Among treatments	1	0.36	0.36	0.86 ns
	Among plots	6	0.75	0.13	0.31 ns
	Within plots	32	13.50	0.42	
	Total	39	14.61		
Post-spray 1	Among treatments	1	3.60	3.60	5.54 *
	Among plots	6	4.00	0.67	1.03 ns
	Within plots	32	20.80	0.65	
	Total	39	28.40		
Post-spray 2	Among-treatments	1	0.40	0.40	2.00 ns
	Among plots	6	0.80	0.13	0.65 ns
	Within plots	32	6.40	0.20	
	Total	39	7.60		

* $p < 0.05$

The effect of the food spray treatments on the number of syrphid eggs laid in batches is shown in Table 7.5. No batched eggs were recorded from the control plots on either post-spray sample occasion. Analysis of variance showed that significantly more batched eggs were laid on plots treated with food-spray 2 days after spraying ($F = 5.54$, $p < 0.05$), but this difference was not significant 4 days after spraying ($F = 2.00$, ns). In section 4.2.2.6, it was demonstrated that oviposition on red cabbage by batch-laying syrphid species was often much lower than on other brassica crops; it was suggested that the red colour of the plant may inhibit egg-laying. It was interesting to note, therefore, that food-spray application may partly counteract this inhibitory effect by increasing oviposition on red cabbage plants by batch-laying species.

Eggs belonging to seven different syrphid species were recorded from the red cabbage plants during the experiment. These species are listed in Table 7.6. The table shows the number of eggs laid by each species on different experimental plots before and after spraying. Following spray application, Platycheirus peltatus and P. albimanus laid significantly more eggs on plots treated with the sucrose + 'Yeastrel' food spray than on the control plots.

The number of aphids per plant recorded on control and food-spray-treated plots for each sample occasion are given in Table F7 (Appendix F). Low numbers of aphids were recorded in the crop throughout the experiment.

Table 7.6: The number of eggs laid by different syrphid species on control and treated plots on pre- and post-spray sample occasions during Field Trial 2

Sample occasion	Species	Number of eggs laid		χ^2 (1df)	p
		C	S+Y		
Pre-spray	Episyrphus balteatus	4	6	0.40	ns
	Syrphus ribesii	5	9	1.14	ns
	Sphaerophoria scripta	4	4	b	$p = 0.27$
	Platycheirus peltatus	6	4	0.40	ns
	Platycheirus albimanus	11	11	0	ns
	Platycheirus clypeatus	4	3	b	$p = 0.27$
	Melanostoma scalare	5	8	0.70	ns
	Total	39	45		
Post-spray	Episyrphus balteatus	4	4	b	$p = 0.27$
	Syrphus ribesii	4	5	b	$p = 0.25$
	Sphaerophoria scripta	-	-		
	Platycheirus peltatus	2	14	9.00	$p < 0.01$
	Platycheirus albimanus	9	21	4.80	$p < 0.05$
	Platycheirus clypeatus	-	4	a	
	Melanostoma scalare	-	4	a	
	Total	19	52		

C - Control; S+Y - Sucrose + 'Yeastrel'

a - Numbers too low to permit statistical analysis

b - Exact probability of binomial

7.3.3 Field Trial 3

The results for the food-spray trial carried out in the cauliflower crop are summarized in Tables 7.7-7.9. The data for each pre- and post-spray sample occasion have been analysed separately using a nested analysis of variance.

Table 7.7 shows the total number of eggs laid on each sample occasion. Analysis of variance showed that there was no significant difference in egg numbers on different experimental plots before spraying. In addition, similar numbers of eggs were recorded on control and food-spray-treated plots 24 h after the application of the first spray. Again, it seems likely that heavy rainfall immediately after spray application may have washed the spray from the treated plants thereby rendering the treatment useless. Following the second spray application, however, significantly more eggs were recorded on food-spray-treated plots than on control plots.

Table 7.8 summarizes the effect of the food spray treatments on the number of syrphid eggs laid singly. Significantly more eggs were laid on plots treated with the sucrose + 'Yeastrel' food solution than on the control plots on both post-spray sample occasions.

The effect of the food spray treatments on the number of syrphid eggs laid in batches is shown in Table 7.9. More eggs were laid on plots treated with the food-spray than on the control plots on both post-spray sample occasions. However, analysis of variance showed that these differences were only statistically significant on the second sample date.

Table 7.10 shows that eggs belonging to ten different syrphid species were recovered from the cauliflower crop during the experiment. The table compares the number of eggs laid on different experimental plots before and after spraying. Following spray application, most species laid significantly more eggs on plots treated with the sucrose + 'Yeastrel' food spray than on control plots. The one exception was Melanostoma scalare which laid similar numbers of eggs on both control and food-spray-treated plants.

The number of aphids per plant recorded on different experimental plots is given in Table F8 (Appendix F) for each sample occasion. A low level of aphid infestation was present in the crop throughout the experiment.

In all three trials, adult syrphids were frequently observed feeding on the food solution present on the surface of sprayed plants.

Table 7.7: The total number of syrphid eggs recorded on control and treated plots on each pre- and post-spray sample occasion during Field Trial 3

a)

Sample occasion	Number of eggs/plant (± SE)	
	Control	Food spray
Pre-spray 1	16.27 ± 2.18	16.00 ± 1.71
2	6.38 ± 0.97	8.10 ± 0.93
Post-spray 1	6.30 ± 1.42	5.60 ± 1.25
2	2.03 ± 0.51	4.57 ± 0.63

b) Anova Table

Sample occasion	Source of variation	df	SS	MS	F-ratio
Pre-spray 1	Among treatments	1	1.06	1.06	0.01 ns
	Among plots	4	528.67	132.17	1.16 ns
	Within plots	54	6155.20	113.99	
	Total	59	6684.93		
Pre-spray 2	Among treatments	1	45.06	45.06	1.77 ns
	Among plots	4	207.07	51.77	2.04 ns
	Within plots	54	1372.60	25.42	
	Total	59	1624.73		
†Post-spray 1	Among treatments	1	4.90	4.90	0.15 ns
	Among plots	2	208.80	104.40	3.28 *
	Within plots	36	1146.20	31.84	
	Total	39	1359.90		
Post-spray 2	Among treatments	1	101.40	101.40	10.72 ***
	Among plots	4	13.33	3.33	0.35 ns
	Within plots	54	511.00	9.46	
	Total	59	625.73		

† 2 plots per treatment only sampled due to heavy rain

*** $p < 0.001$

* $p < 0.05$

Table 7.8: The number of syrphid eggs laid singly on control and treated plots on each pre- and post-spray sample occasion during Field Trial 3

a)

Sample occasion	Number of eggs/plant (± SE)	
	Control	Food spray
Pre-spray 1	1.17 ± 0.21	1.80 ± 0.30
2	1.33 ± 0.27	1.53 ± 0.27
Post-spray 1	0.65 ± 0.20	2.10 ± 0.52
2	0.27 ± 0.09	1.00 ± 0.21

b) Anova Table

Sample occasion	Source of variation	df	SS	MS	F-ratio
Pre-spray 1	Among treatments	1	6.01	6.01	3.89 ns
	Among plots	4	5.47	1.37	0.91 ns
	Within plots	54	81.50	1.51	
	Total	59	92.98		
Pre-spray 2	Among treatments	1	1.35	1.35	0.58 ns
	Among plots	4	4.33	1.08	0.46 ns
	Within plots	54	126.50	2.34	
	Total	59	132.18		
†Post-spray 1	Among treatments	1	21.02	21.02	8.65 **
	Among plots	2	28.85	14.43	5.94 **
	Within plots	36	87.50	2.43	
	Total	39	137.37		
Post-spray 2	Among treatments	1	8.06	8.06	9.83 **
	Among plots	4	1.47	0.37	0.45 ns
	Within plots	54	44.40	0.82	
	Total	59	53.93		

† 2 plots per treatment only sampled due to heavy rain

** $p < 0.01$

Table 7.9: The number of syrphid eggs laid in batches on control and treated plots on each pre- and post-spray sample occasion during Field Trial 3

a)

Sample occasion	Number of eggs/plant (± SE)	
	Control	Food spray
Pre-spray 1	15.10 ± 2.12	14.20 ± 1.68
2	5.10 ± 0.86	6.57 ± 0.81
Post-spray 1	5.65 ± 1.35	3.50 ± 0.83
2	1.83 ± 0.50	3.57 ± 0.58

b) Anova Table

Sample occasion	Source of variation	df	SS	MS	F-ratio
Pre-spray 1	Among treatments	1	12.15	12.15	1.11 ns
	Among plots	4	476.80	119.20	10.91 ***
	Within plots	54	590.27	10.93	
	Total	59	1079.22		
Pre-spray 2	Among treatments	1	33.75	33.75	1.80 ns
	Among plots	4	175.33	43.83	2.34 ns
	Within plots	54	1013.10	18.76	
	Total	59	1222.18		
† Post-spray 1	Among treatments	1	46.22	46.22	1.93 ns
	Among plots	2	91.25	45.63	1.90 ns
	Within plots	36	864.30	24.01	
	Total	39	1001.77		
Post-spray 2	Among treatments	1	45.07	45.07	4.95 *
	Among plots	4	25.13	6.28	0.69 ns
	Within plots	54	490.40	9.08	
	Total	59	560.60		

† 2 plots per treatment only sampled due to heavy rain

*** $p < 0.001$

* $p < 0.05$

Table 7.10: The number of eggs laid by different syrphid species on control and treated plots on pre- and post-spray sample occasions during Field Trial 3

Sample	Species	Number of eggs laid		χ^2 (1df)	p
		C	S+Y		
Pre-spray	Episyrphus balteatus	107	140	4.40	*
	Metasyrphus luniger	4	-	a	
	Syrphus ribesii	15	25	2.50	ns
	Sphaerophoria scripta	82	81	0.01	ns
	Platycheirus peltatus	134	146	0.51	ns
	Platycheirus albimanus	42	61	3.50	ns
	Platycheirus clypeatus	105	98	0.24	ns
	Platycheirus manicatus	17	29	3.14	ns
	Melanostoma mellinum	126	129	0.02	ns
	Melanostoma scalare	21	14	1.40	ns
	Total	653	723		
Post-spray	Episyrphus balteatus	35	60	6.58	$p < 0.05$
	Metasyrphus luniger	1	-	a	
	Syrphus ribesii	6	19	6.76	$p < 0.01$
	Sphaerophoria scripta	13	31	7.36	$p < 0.01$
	Platycheirus peltatus	94	126	4.65	$p < 0.05$
	Platycheirus albimanus	19	7	5.54	$p < 0.05$
	Platycheirus clypeatus	25	-	25.00	$p < 0.001$
	Platycheirus manicatus	-	-	-	
	Melanostoma mellinum	2	-	a	
	Melanostoma scalare	14	6	3.20	ns
	Total	209	249		

C - Control

S + Y - Sucrose + 'Yeastrel'

a - Numbers too low to permit statistical analysis

7.4 GENERAL DISCUSSION AND CONCLUSIONS

The results of the three field trials described above indicate that nutritional food sprays may be useful in increasing the effectiveness of syrphids as biological control agents of aphids. More syrphid eggs were laid on brassica plants that had been sprayed with a food solution of sucrose or sucrose plus 'Yeastrel' than on control plants.

Food spray application significantly increased oviposition by both aphidozetic and phytozetic syrphid species. Aphidozetic species normally oviposit in crops only when the aphid population is already well-established. However, food spray application significantly increased oviposition by these species at low aphid densities. Thus, food sprays may be a useful way of improving synchronisation between pest and predator populations.

Studies on the mode of action of these food sprays have demonstrated that sucrose alone serves only to arrest adult syrphids in the field whereas a spray consisting of sucrose plus a yeast hydrolysate acts as an attractant (Hagen et al, 1971). The attractive components of the yeast hydrolysate have been shown to be amino acids: tryptophan has been isolated as a powerful attractant for adults of Chrysopa carnea (Hagen et al, 1976).

An effective food spray should include both nutritive and attractive components, together with an oviposition stimulant. It is important that the food spray contains the nutritional components necessary for egg production. Artificial honeydews developed for the mass-rearing of Chrysopa carnea have been shown to significantly enhance both the fecundity and longevity of this insect (Hagen et al, 1971). The addition of tryptophan to artifical honeydews has been shown to increase the efficiency of food sprays in manipulating the oviposition behaviour of adult C. carnea. In alfalfa fields infested with low aphid populations, food sprays including tryptophan attracted adults from an area of at least 2.6 acres into a 0.001 acre area. The third component of a successful food spray is an oviposition stimulant.

An earlier study by Ben Saad and Bishop (1976) showed that artifical honeydews did not stimulate oviposition in syrphid flies unless a small aphid stimulus was also present. This problem may be overcome if the specific compounds that stimulate oviposition could be isolated from the honeydew and identified.

In the present study, adult syrphids were frequently observed feeding on the food spray on treated plants. However, further work is needed to determine whether the spray was simply acting as an arrestant to syrphids already present in the treated plots or whether it also attracted flies into the sprayed plots from other areas.

The effectiveness of food sprays may be affected by several factors. Firstly, it is important that there is a naturally-occurring predator population already present in the vicinity of the sprayed crop. Secondly, climatic factors may influence the effectiveness of the spray. In the present study, all three field trials were disrupted by prolonged periods of heavy rain and this washed the food spray off the plants, thereby rendering the treatment useless. Previous studies have shown that the food sprays may need to be regularly and frequently reapplied if they are to remain effective (Hagen _et al_, 1976). Thirdly, the effects of food sprays may be considerably reduced in the presence of high aphid populations. This may prove a particular problem with polyphagous predators when aphid populations in adjacent crops are high: such predators are likely to be attracted into the neighbouring crops.

One possible side-effect of food spray application may be the development of fungal pathogens on the treated plants. This problem may be overcome by incorporating an antifungal compound (eg sorbic acid) into the spray (Hagen _et al_, 1971).

In conclusion, food sprays appear to be a useful means of attracting adult syrphids into a crop and stimulating them to oviposit at a time when the level of aphid infestation is low. This technique may be of value as part of an integrated control programme for enhancing the effectiveness of syrphids as biological control agents of aphids.

CHAPTER 8

GENERAL DISCUSSION

8.1 INTRODUCTION

In this chapter, I will attempt to draw together the main findings of the previous chapters and to present a holistic view of oviposition strategies in aphidophagous syrphids. I will first discuss the general factors that affect the spatial and temporal activity patterns of adult syrphids in the field.

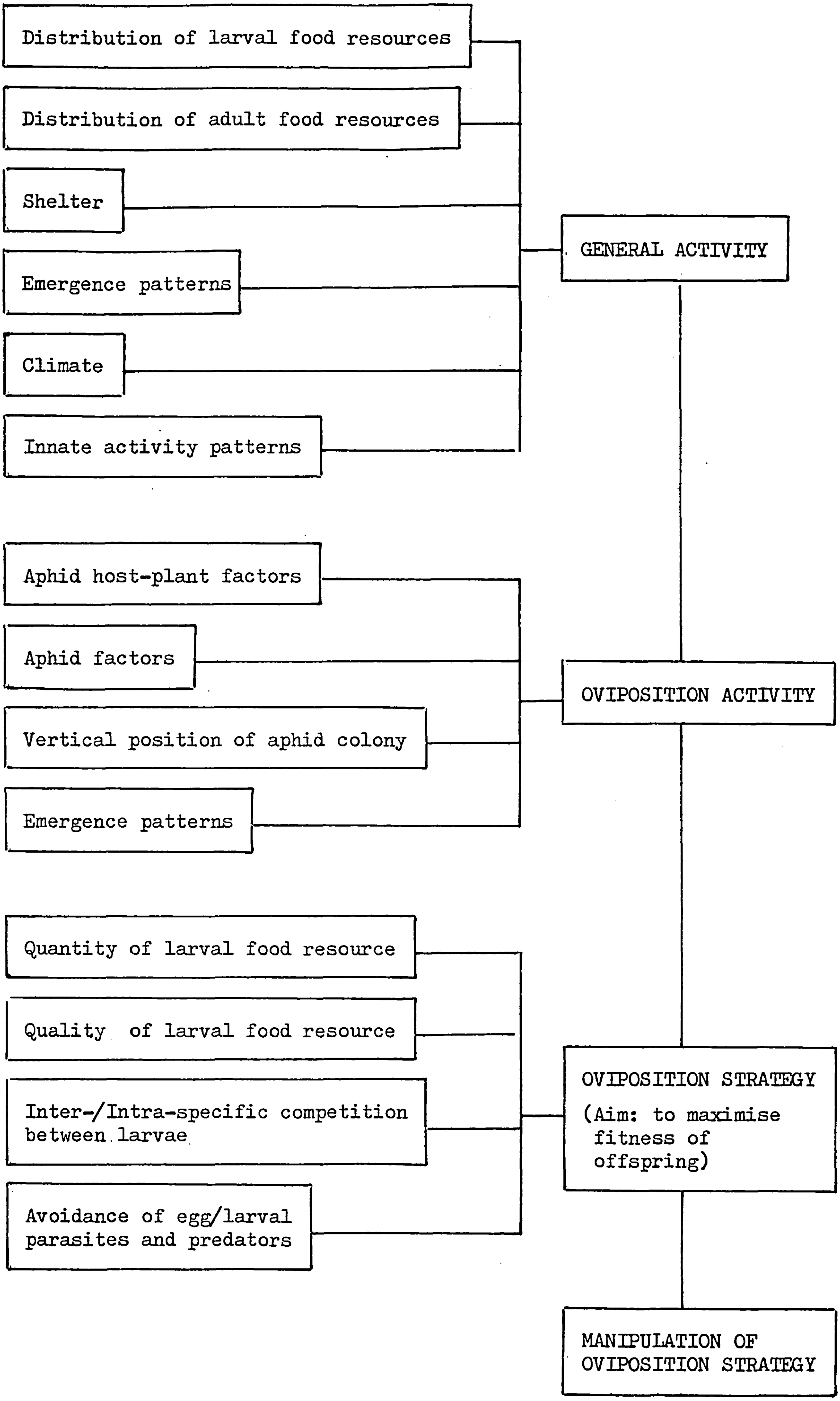
From a discussion of general syrphid activity, I will proceed to concentrate specifically on oviposition activity and to consider factors that influence oviposition site selection by different syrphid species.

I will then go on to discuss oviposition behaviour within the context of reproductive strategies. The goal of an ovipositing syrphid female should be to maximise her reproductive output in terms of both the number of eggs laid and/or the survival of her offspring. Factors influencing larval fitness are discussed in relation to the oviposition strategy of the adult female.

Finally, I will consider ways in which oviposition behaviour may be manipulated in the field so as to improve the effectiveness of syrphids as biological control agents of aphids.

The general outline of this discussion is presented in Figure 8.1.

Figure 8.1: Outline of General Discussion


Distribution of larval food resources
Distribution of adult food resources
Shelter
Emergence patterns
Climate
Innate activity patterns
GENERAL ACTIVITY
Aphid host-plant factors
Aphid factors
Vertical position of aphid colony
Emergence patterns
OVIPOSITION ACTIVITY
Quantity of larval food resource
Quality of larval food resource
Inter-/Intra-specific competition between larvae
Avoidance of egg/larval parasites and predators
OVIPOSITION STRATEGY
(Aim: to maximise fitness of offspring)
MANIPULATION OF OVIPOSITION STRATEGY

8.2 FACTORS INFLUENCING THE SPATIAL AND TEMPORAL ACTIVITY PATTERNS OF ADULT SYRPHIDS

The spatial and temporal distribution patterns of adult syrphids were studied in annual crop and natural habitats over a six-month field season (see Chapter 2).

A number of factors were shown to influence adult activity. These factors were:

1. Distribution of larval food resources
2. Distribution of adult food resources
3. Shelter
4. Emergence patterns
5. Climate
6. Innate activity patterns

8.2.1 Distribution of larval food resources

The syrphid communities associated with both crop and natural habitats were dominated by species with an aphidophagous larval stage. This suggested that aphids were an important larval food resource.

There was a considerable amount of indirect evidence to suggest that adult syrphid activity was closely related to the distribution of aphids. Two main peaks of syrphid activity were recorded during the study period (Figure 2.4). The first peak occurred during the spring when aphid populations are usually still present on their overwintering host-plants (ie shrubs and trees). The second peak occurred during the summer when aphid populations normally migrate to their secondary host-plants (ie annual crops, herbs and grasses). The mid-season lull in syrphid activity coincided with the period during which aphids migrate from their overwintering sites to their summer host-plants.

In the present study, more syrphids were taken in the edgegrowth than in the crops during May and June. Throughout this period, aphid populations were high on broom bushes (Cytisus scoparius) in the edgegrowth but few aphids were recorded in the crops. During July, similar numbers of adult syrphids were taken in both types of habitat and this corresponded to a build-up of aphid populations both in the annual crops and on perennial herbs and grasses in the edgegrowth. In August, more adult syrphids were taken in the crops. During September and October, similar numbers of syrphids were recorded in both crop and edgegrowth sites: aphid populations in both habitats were now starting to migrate back to their overwintering host-plants. These seasonal changes in adult syrphid activity in different crop and edgegrowth sites are summarized in Table A5 (Appendix A),

Within individual crops, patterns of syrphid activity were found to be related to aphid abundance (Figures 2.6 - 2.9). In all crops, the development of aphid populations resulted in a corresponding increase in adult syrphid activity.

8.2.2 Adult food resources

Several authors have noted the importance of adult feeding in the syrphidae (eg Schneider, 1948; Doucette and Eide, 1955; Adeshkevich and Karelin, 1972). Pollen is essential for ovarial maturation. Pollen-feeding by males may also be a necessary pre-requisite for sexual maturation (eg Gilbert, 1981a).

Some authors (eg van Emden, 1963) have reported increased syrphid oviposition close to flowers, although other studies have shown that the presence of flowers has no effect on oviposition activity (eg Chandler, 1968c; Pollard, 1971). These conflicting results may be explained by the particular flower species involved. Some hoverflies have been shown to be selective in the flowers they visit (eg Pollard, 1971; Gilbert, 1981b; Haslett, 1981): most aphidophagous species feed mainly on pollen and the distribution of suitable pollen sources may be a critical factor influencing syrphid activity.

In the present study, adult feeding and oviposition sites frequently occurred in close proximity to each other and it was difficult to assess their relative effects on adult syrphid distribution patterns. This problem has already been discussed in Section 2.4.7. During spring and early summer, the only floral resources available for adult feeding occurred in the edgegrowth and this may have been a contributory factor in concentrating syrphid activity in the edgegrowth during this time. Later on in the summer, flowering weeds also developed in the wheat and this may have contributed to the overwhelming attraction of this crop to the adults of both aphidophagous and non-aphidophagous syrphid species.

Some studies have shown that adult syprhids utilize different habitats for feeding and oviposition activities (eg Maier and Waldbauer, 1979a). Adult syrphids are highly mobile and are capable of flying considerable distances (up to 5 km) between night resting sites and day-time feeding sites (Schneider, 1958).

In the present study, adult syrphids were frequently observed both feeding and ovipositing on the same plant (eg on _Cytisus scoparius_ and _Heracleum sphondylium_).

8.2.3 Shelter

The importance of shelter in influencing adult syrphid activity is not clear. Lewis (1965) found concentrations of syrphids close to artificial barriers. Chandler (1968c) has suggested that van Emden's (1963) observations of increased syrphid oviposition on Brussels sprout plants close to a flowery field edge may be due to a shelter effect. Shelter may have a more important influence on the activity patterns of woodland syrphid species than on species associated with more open habitats.

In the present study, the importance of shelter was difficult to assess. Certainly, adult syrphid activity was restricted mainly to the edgegrowth during the early stages of crop development and it seems possible that this may be related to a shelter effect although there was no direct evidence to confirm this.

8.2.4 Emergence patterns

The spatial distribution patterns of individual syrphid species were found to be influenced by the time of year when they occur. Early-season species (eg Episyrphus balteatus, Epistrophe nitidicollis and E. eligans) were usually restricted to the edgegrowth whereas summer-occurring species (eg Sphaerophoria scripta and Meliscaeva cinctella) were taken more frequently in the crops. Species that had several generations during the season were usually found in the edgegrowth during the spring but also occurred in the crops during the summer (Table 2.7). The relationship between these habitat preferences and seasonal changes in the distribution of aphids has already been discussed (Section 8.2.1).

8.2.5 Climate

Climatic factors influence the diel periodicity of insect activity. The most important climatic factors are temperature, light intensity, relative humidity and wind-velocity; these act by imposing thresholds that limit the duration of the activity (Corbet, 1966).

In this study, temperature was demonstrated to be the most important climatic factor influencing syrphid flight activity. (Table 3.4). Different syrphid species were found to have different threshold temperatures above which they became flight-active (Figures 3.17 - 3.22) with larger species usually becoming active at lower temperatures than smaller species.

These results indicated that the time for which adult syrphids may be active in the field is largely constrained by the prevailing climatic conditions. However, some syrphid species are capable of elevating their body-temperatures above the ambient temperature by behavioural (eg sun-basking) and/or endothermic (eg 'shivering') means and are therefore able to fly at lower temperatures (Heinrich and Pantle, 1975). Such mechanisms allow these species to increase the time available for flight activity.

8.2.6 Innate activity patterns

Climatic factors were shown to constrain the time for which adult syrphids may be active in the field. However, laboratory studies on Episyrphus balteatus show that a very large proportion of their time is spent resting despite the absence of climatic restraints. This has important implications with regard to optimal foraging theory. Most optimal foraging models take little account of activity budgets and assume that foraging is the sole activity. Herbers (1981) has developed a model which assumes that the animal's main objective is simply to remain alive. Thus, resting may be a behaviour that avoids risks and constitutes an important part of an optimal foraging strategy.

8.3 FACTORS INFLUENCING OVIPOSITION SITE SELECTION

The discussion so far has considered factors influencing the general activity patterns of adult syrphids in the field. I now propose to concentrate specifically on oviposition activity and to discuss the factors that may affect oviposition site selection by different syrphid species.

These factors include:-

1. Aphid-host-plant factors;
2. Aphid factors;
3. Vertical position of the aphid colony; and
4. Emergence patterns

8.3.1 Aphid host-plant factors

The oviposition patterns of different syrphid species were studied in a range of different brassica crops infested with the cabbage aphid, Brevicoryne brassicae (see Chapter 4). Oviposition site selection by phytozetic syrphid species was found to be significantly influenced by crop type: factors such as the colour, size and spatial complexity of different crop plants may be important in determining their relative attractiveness to phytozetic syrphids. In contrast, the oviposition responses of aphidozetic species were found to be relatively independent of crop type (Table 4.17).

The effect of plant background on syrphid oviposition was investigated by comparing the numbers of eggs laid on aphid-infested potted Brussels sprout plants placed in different habitats (Section 4.3). Plant background significantly influenced oviposition site selection by several phytozetic species but had less effect on the oviposition responses of aphidozetic syrphids (Table 4.20). The presence of weeds in a crop may affect oviposition site selection in two ways:

1. By altering the optical attractiveness of the crop to ovipositing females, and
2. By providing alternative oviposition sites.

8.3.2 Aphid factors

The effect of aphid density on the oviposition patterns of different syrphid species was examined in a range of brassica crops (Chapter 4). Oviposition site selection by aphidozetic species was found to be significantly influenced by the size of aphid population present on a plant. In contrast, oviposition by phytozetic species was relatively independent of aphid density. There was some evidence to suggest that different syrphid species prefer different sizes of aphid population for maximal oviposition.

Laboratory studies on the aphidozetic species, Episyrphus balteatus, showed that oviposition by this species increases in response to increasing aphid density reaching a maximum beyond which egg numbers declined with increasing aphid density (Figure 6.3). The behavioural mechanism of this density-dependent oviposition response was investigated. Gravid females made more landings on higher density plants, each landing resulted in a more or less fixed number of eggs laid.

This mechanism may also explain the differential oviposition responses of some syrphid species to different crops: more landings may be made on the more attractive crop plants and so, eventually, more eggs will be laid on these crops.

8.3.3 Vertical position of the aphid colony

In the present study, the effect of the vertical position of aphid colonies on oviposition site-selection was not investigated. However, Chandler (1968d) demonstrated that some syrphid species prefer to oviposit at a particular height above the ground and have well-defined searching-zones. Aphid colonies occurring outside these preferred searching zones may therefore escape exploitation.

8.3.4 Emergence patterns

Spring-occurring syrphid species usually search for aphid colonies at a height of 1-2 metres above the ground. Thus, they are well-adapted for locating aphid colonies on shrubs and trees. In contrast, summer-occurring species usually search for aphids near the ground where they are more likely to encounter aphid populations on herbs and grasses (Chandler, 1968d). Species that occur throughout the year tend to have no particular preferred searching zone. This enables them to locate aphids on a range of host-plants at varying heights.

In the present study the relationship between the emergence patterns of different syrphid species and the vertical distribution of aphid colonies on different host-plants was not investigated.

Differential responses by different syrphid species to the four factors discussed above may be important in reducing inter-specific competition between the larvae.

8.4 FACTORS INFLUENCING EGG/LARVAL FITNESS

Some of the more important factors influencing egg/larval survival include:

1. Quantity of the larval food resource
2. Quality of the larval food resource
3. Inter- and intra-specific competition between larvae
4. Parasites and predators

The following section considers how the oviposition strategy of the adult female may influence the survival of her offspring. Because few studies have focussed on this relationship, much of the ensuing discussion is speculative in nature.

8.4.1 Quantity of the larval food resource

Laboratory studies on larval voracity have demonstrated how larval fitness is related to the number of aphids consumed. Periods of prolonged starvation during the larval stage may result in the production of 'dwarf' adults (Scott, 1939; Wilkening, 1961; Růžička and Cairo, 1976) which, in the case of females, have lowered fecundity and may even be sterile (Cornelius and Barlow, 1980).

Different syrphid species have been shown to prefer different sizes of aphid populations for maximal oviposition (Chandler, 1968a). These 'preferences' may be related to the voracity of the larvae.

The larvae of aphidozetic species tend to be obligate entomophages, often requiring large numbers of aphids to complete development. Thus, the adults of aphidozetic species usually oviposit only in response to well-established aphid populations. In contrast, the larvae of phytozetic syrphids tend to be only facultatively entomophagous and require relatively fewer aphids to complete development. (Rotheray, unpubl). Eggs of phytozetic species are frequently found on plants that are only lightly-infested with aphids or sometimes with no aphids at all. Phytozetic species also frequently lay eggs in small batches. This strategy ensures survival of at least one member of the batch if alternative food material is unavailable. Thus, phytozetic species are able to exploit small aphid infestations that would be inadequate to support the more voracious aphidozetic larvae.

8.4.2 Quality of the larval food resource

Different aphid species have been shown to vary in their nutritional value to syrphid larvae (Růžička, 1975).

In the present study, different syrphid species preferred different crops for oviposition: it seems possible that these preferences may be related to the suitability of different aphid species found on these crops for larval development.

Many of the more abundant aphidophagous species have a polyphagous larval stage and will oviposit in response to a wide range of different aphid species. However, it is not clear if the adult female is capable of assessing the nutritional value of a particular aphid species for larval development.

It was stated earlier that some syrphid species prefer to oviposit at a particular height above the ground and exhibit well-defined searching zones. Aphid species occurring outside these zones will not be exploited by these syrphids. Thus, the possible range of aphid species utilized by syrphid larvae may be restricted by the behaviour of the ovipositing female.

It has been demonstrated in coccinellids that the nutritional value of a particular aphid species may vary with both the aphid host-plant and the time of year. No similar studies have been carried out on syrphids.

8.4.3 Inter- and intra-specific competition between larvae

Inter-specific competition between syrphid larvae has been shown to have an important effect on the bionomics of the species (Hagvar, 1972, 1973). Rotheray (unpubl) has shown that an obligate aphidophage (Syrphus ribesii) has a higher attack rate, lower handling time and a greater speed of movement at every larval instar, and for every aphid instar than a facultative aphidophage (Melanostoma mellinum).

Inter-specific competition between larvae may be reduced if oviposition strategies differ between syrphid species. This may consist of differential responses to aphid and aphid host-plant factors, differences in the preferred searching heights of ovipositing females and the temporal separation of oviposition periods (see Chapter 4). Despite such possible mechanisms, however, larvae of different species are frequently found together on the same aphid host-plant, utilizing the same aphid resource, and it seems inevitable that some element of inter-specific competition must occur.

In the present study, observations on laboratory cultures of Episyrphus balteatus larvae indicated that cannibalism may be very high if aphid food is scarce. However, it is not known to what extent intra-specific competition occurs in the field.

8.4.4 Parasites and predators

Several parasites of syrphid eggs and larvae locate their hosts by responding to aphid-associated cues (Rotheray, 1981). It has been noted that some ovipositing syrphid females tend to avoid heavy aphid infestations (Banks, 1953; Chandler, 1968c) and this may be associated with reducing risks of parasitism and predation. However, this avoidance may also be due to deterioration of plant quality and the development of fungal pathogens on the aphid honeydew.

It must be stressed that there is no real evidence to suggest that oviposition site selection by adult females is influenced by risks due to parasites and predators.

8.5 MANIPULATION OF OVIPOSITION BEHAVIOUR

Syrphids have been demonstrated to have considerable potential as biological control agents of aphids. However, their effectiveness in controlling aphid populations is often limited by poor synchronisation. The application of nutritional food sprays may be a useful means of attracting syrphids into a crop during the initial stages of aphid infestation. In the present study, syrphid oviposition was significantly increased in crops that had been sprayed with a sucrose plus protein food solution.

APPENDIX A

Table A1: Plant species recorded in the edge growth

HERBS AND SHRUBS				
Family	Species	Life-form	Location	Flowering period
Caryophyllaceae	Silene alba (Miller)	P	U	May - October
	Spergula arvensis L.	A	U	May - September
	Stelleria media (L,) Vill.	A	U	All year
Chenopodiaceae	Chenopodium album L.	A	U	June - October
Compositae	Achillea millefolium L.	P	U	June - November
	Cirsium arvense (L.) Scop.	P	BrE	June - September
	Cirsium vulgare (Savi) Ten.	B	U	July - September
	Crepis capillaris (L.) Wallr.	A	U	June - November
	Hieracium pilosella L.	P	U	June - August
	Leucanthemum vulgare L.	P	U	May - September
	Matricaria matricarioides (Less.) Porter	A	U	May - November
	Senecio jacobaea L.	P	U	June - November
	Senecio vulgaris L.	A	U	All year
	Sonchus oleraceus L.	A	U	May - November
	Tanacetum vulgare L.	P	WE	July - October
	Taraxacum officinale Weber	P	U	April - June
	Tussilago farfara L.	P	U	February - April
Cruciferae	Capsella bursa-pastoris (L.) Medicus	A	U	All year
	Raphanus raphanistrum L.	A	U	May - September
	Sinapis arvensis L	A	U	April - October
Leguminosae	Cytisus scoparius (L.) Link	S	BE	April - June
	Lotus corniculatus L.	P	U	June - July

Cont/. . .

Table A1: continued

Family	Species	Life-form	Location	Flowering period
	Trifolium campestre Schreb.	A	U	May - September
	Trifolium pratensis L.	P	U	April - May
	Trifolium repens L.	P	U	May - August
	Vicia sativa L.	A	WE, BE	April - September
Onagraceae	Chamaenerion angustifolium (L.) Scop.	P	U	June - August
	Epilobium montanum L.	P	U	June - August
Plantaginaceae	Plantago lanceolata L.	P	U	April - October
	Plantago major L.	P	U	June - October
Polygonaceae	Polygonum persicaria L.	A	U	June - October
	Rumex acetosa L.	P	U	May - August
	Rumex spp.			
Ranunculaceae	Rununculus repens L.	P	U	May - September
Scrophulariaceae	Veronica arvensis L.	A	U	March - October
	Veronica chamaedrys L.	P	U	April - June
	Veronica persica Poir.	A	U	All year
Umbelliferae	Angelica sylvestris L.	P	U	July - September
	Anthriscus sylvestris (L.) Bernh.	P	U	April - June
	Heracleum sphondylium L.	B	BrE	August - October
Urticaceae	Urtica dioica L.	P	PE, BrE	June - September

Cont/. . .

Table A1: continued

GRASSES				
Family	Species	Life-form	Location	Flowering period
Graminae	Agrostis stolonifera L.	P	U	
	Dactylis glomerata L.	P	U	May - June
	Festuca rubra L.	P	U	June - July
	Holcus lanatus L.	P	U	June - July
	Holcus mollis L.	P	U	
	Phleum pratense L.	P	U	July - August
	Poa annua	A	U	All year
	Poa pratensis L.	P	U	May - June
	Poa trivialis L.	P	U	July - August

Key

Life-form

A - Annual
B - Biennial
P - Perennial
S - Shrub

Location

U - Ubiquitous
BrE - Edgegrowth adjoining Brussels sprout crop
BE - Edgegrowth adjoining Bean crop
PE - Edgegrowth adjoining Potato crop
WE - Edgegrowth adjoining Wheat crop

Table A2: The syrphid species recorded during this study

Tribe	Species	Number Recorded
	Subfamily: Syrphinae	
Syrphini	Syrphus ribesii (Linnaeus)	106
	Syrphus torvus (Osten-Sacken)	2
	Syrphus vitripennis (Meigen)	3
	Epistrophe eligans (Harris)	11
	Epistrophe nitidicollis (Meigen)	11
	Metasyrphus corollae (Fabricius)	26
	Metasyrphus latifasciatus (Macquart)	8
	Metasyrphus luniger (Meigen)	14
	Dasysyrphus albostriatus (Fallen)	6
	Dasysyrphus lunulatus (Meigen)	2
	Dasysyrphus tricinctus (Fallen)	3
	Dasysyrphus venustus (Meigen)	22
	Scaeva selenitica (Meigen)	13
	Leucozona lucorum (Linnaeus)	4
	Meligramma cincta (Fallen)	18
	Meligramma triangulifera (Zetterstedt)	2
	Episyrphus balteatus (Degeer)	47
	Sphaerophoria menthastri (Linnaeus)	2
	Sphaerophoria scripta (Linnaeus)	604
	Xanthogramma pedissequum (Harris)	5
	Parasyrphus punctulatus (Verrall)	2
	Meliscaeva auricollis (Meigen)	3
	Meliscaeva cinctella (Zetterstedt)	68
Chrysotoxini	Chrysotoxum bicinctum (Linnaeus)	77
	Chrysotoxum cautum (Harris)	6
	Chrysotoxum festivum (Linnaeus)	6
	Chrysotoxum verralli (Collin)	2
Bacchini	Baccha obscuripennis (Meigen)	17
	Melanostoma mellinum (Linnaeus)	427
	Melanostoma scalare (Fabricius)	141
	Platycheirus albimanus (Fabricius)	246
	Platycheirus angustatus (Zetterstedt)	268
	Platycheirus clypeatus (Meigen)	77
	Platycheirus fulviventris (Macquart)	3
	Platycheirus manicatus (Meigen)	8
	Platycheirus peltatus (Meigen)	198
	Platycheirus scambus (Staeger)	1
	Platycheirus scutatus (Meigen)	61
	Platycheirus tarsalis (Schummel)	1
	Pyrophaena granditarsa (Forster)	2
	Pyrophaena rosarum (Fabricius)	1

Cont/. . .

Table A2: continued

Tribe	Species	Number Recorded
	<u>Subfamily: Milesiinae</u>	
Cheilosini	Cheilosia bergenstammi (Becker)	3
	Cheilosia illustrata (Harris)	2
	Cheilosia variabilis (Panzer)	8
	Cheilosia vernalis (Fallen)	3
	Rhingia campestris (Meigen)	14
Chrysogastrini	Neoascia podagrica (Fabricius)	5
Eristalini	Eristalis arbustorum (Linnaeus)	5
	Eristalis nemorum (Linnaeus)	2
	Eristalis pertinax (Scopoli)	2
	Helophilus pendulus (Linnaeus)	24
	Parhelophilus frutetorum (Fabricius)	2
Merodontini	Merodon equestris (Fabricius)	2
Pipizini	Pipizella varipes (Meigen)	1
	Heringia heringi (Zetterstedt)	2
Xylotini	Xylota florum (Fabricius)	4
	Xylota nemorum (Fabricius)	4
	Xylota sylvarum (Linnaeus)	1
	Syritta pipiens (Linnaeus)	119

Table A3: Feeding habits of the larvae of syrphid species encountered in this study

Species	Type	Records of larval feeding sites
Syrphus ribesii	Aphidophagous	Obligate aphidophage, polyphagous. Crops and herbs (Malinowska, 1979); shrubs and trees (Rotheray, unpubl)
Syrphus torvus	Aphidophagous	On Spiraea sp and plum seedlings (Metcalf, 1916)
Syrphus vitripennis	Aphidophagous	Obligate aphidophage. Crops and herbs (Malinowska, 1979)
Epistrophe eligans	Aphidophagous	Obligate aphidophage. Shrubs and trees (Schneider, 1969); herbs (Rotheray, unpubl)
Epistrophe nitidicollis	Aphidophagous?	On Sarothamnus scoparius L. (Dixon, 1959)
Metasyrphus corollae	Aphidophagous	Obligate aphidophage, polyphagous. Crops and herbs (Malinowska, 1979). On Rubus sp (Rotheray, unpubl)
Metasyrphus latifasciatus	Aphidophagous?	Unknown
Metasyrphus luniger	Aphidophagous	Obligate aphidophage. Shrubs and herbs (Rotheray, unpubl)
Dasysyrphus albostriatus	Aphidophagous	Obligate aphidophage. On Acer sp and Silene sp (Rotheray, unpubl)
Dasysyrphus lunulatus	Aphidophagous	Obligate aphidophage On Pinus, Quercus spp (Chandler, 1968d)
Dasysyrphus tricinctus	Aphidophagous?	Unknown
Dasysyrphus venustus	Aphidophagous	Herbs (Goeldlin, 1974)

Cont/. . .

Table A3: continued

Species	Type	Records of larval feeding sites
Scaeva selenitica	Aphidophagous?	Unknown
Leucozona lucorum	Aphidophagous	Obligate aphidophage. On *Rumex* sp (Dixon, 1960). 'Wide host acceptance' (Chandler, 1968d)
Meligramma cincta	Aphidophagous	*Phyllaphis fagi* L. on *Fagus sylvatica* and *Tuberculoides annulatus* (Hortig) on *Quercus robur* (Rotheray, unpubl); on *Tilia* (Dixon, unpubl)
Meligramma triangulifera	Aphidophagous?	Unknown
Episyrphus balteatus	Aphidophagous	Obligate aphidophage, polyphagous. Widespread (Schneider, 1948; Pollard, 1971); crops (Bańkowska *et al*, 1978; Malinowska, 1979)
Sphaerophoria menthastri	Aphidophagous	On *Silene* sp (Rotheray, unpubl)
Sphaerophoria scripta	Aphidophagous	Obligate aphidophage. On herbs (Goeldlin, 1974; Rotheray, unpubl)
Xanthogramma pedissequum	Aphidophagous?	Unknown
Parasyrphus punctulatus	Aphidophagous	*Pinus* and *Picea* spp (Chandler, 1968d)
Meliscaeva auricollis	Aphidophagous	Obligate apidophage. *Sarothamnus* sp (Dixon, 1960); *Heracleum* sp (Rotheray, unpubl)
Meliscaeva cinctella	Aphidophagous	Obligate aphidophage. On *Picea*, *Pinus*, *Quercus* spp (Chandler, 1968d)
Chrysotoxum bicinctum	Aphidophagous?	Subterranean aphids? (Speight *et al*, 1975)

Cont/. . .

Table A3: continued

Species	Type	Records of larval feeding sites
Chrysotoxum cautum	Aphidophagous?	Subterranean aphids? (Speight *et al*, 1975)
Chrysotoxum festivum	Aphidophagous?	Unknown
Chrysotoxum verralli	Aphidophagous?	Unknown
Baccha obscuripennis	Aphidophagous	Obligate aphidophage. On *Centaurea*, *Aconitum* spp (Dušek and Láska, 1960); *Rosa*, *Silene* spp (Rotheray, unpubl), Widespread (Chandler, 1968d)
Melanostoma mellinum	Phyto-/Aphidophagous	Facultative aphidophage. Aphid colonies, herbs, crops (Giard, 1896; Malinowska, 1979)
Melanostoma scalare	Phyto-/Aphidophagous	Facultative aphidophage. Aphid colonies, leaf litter of *Acer* sp (Rotheray, unpubl)
Platycheirus albimanus	Phyto-/Aphidophagous	Facultative aphidophage? On herbs (Goeldlin, 1974; Rotheray, unpubl)
Platycheirus angustatus	Phyto-/Aphidophagous	Unknown
Platycheirus clypeatus	Phyto-/Aphidophagous	Facultative aphidophage? On herbs (Goeldlin, 1974)
Platycheirus fulviventris	Aphidophagous?	Unknown
Platycheirus manicatus	Phyto-/Aphidophagous	Facultative aphidophage? On herbs (Goeldlin, 1974); crops (Dunn, 1949)
Platycheirus peltatus	Phyto-/Aphidophagous	Facultative aphidophage? On herbs (Goeldlin, 1974)
Platycheirus scambus	Aphidophagous?	Unknown

Cont/. . .

Table A3: continued

Species	Type	Records of larval feeding sites
Platycheirus scutatus	Aphidophagous	Obligate aphidophage. On herbs and shrubs (Rotheray, unpubl); crops (Dunn, 1949)
Platycheirus tarsalis	Phyto-/Aphidophagous	Facultative aphidophage?
Pyrophaena granditarsa	Aphidophagous?	Unknown
Pyrophaena rosarum	Aphidophagous?	Unknown
Cheilosia bergenstammi	Phytophagous	On Senecio jacobaea (Smith, 1980)
Cheilosia illustrata	Phytophagous	Unknown
Cheilosia variabilis	Phytophagous	In roots of Scrophularia nodosa (Fryer, 1915; Dusek, 1962); on composites (Smith, 1980)
Cheilosia vernalis	Phytophagous?	In roots of Achillea millefolium (on root galls of the tephritid Dithryca guttularis (Mg)) questionably on Matricaria recutita and Verbascum pulverulentum (Smith, 1980)
Rhingia campestris	Coprophagous	Cow dung (Krüger, 1926; Hammer, 1941; Coe, 1942)
Neoascia podagrica	Coprophagous	Wet, decaying manure (Hartley, 1961)
Eristalis arbustorum	Filter-feeder	Polluted water, drains (Hartley, 1961)
Eristalis nemorum	Filter-feeder	Drains, contaminated ponds (Hartley, 1961)
Eristalis pertinax	Filter-feeder	Drains, wet manure (Hartley, 1961)
Helophilus pendulus	Filter-feeder	Cesspits (Lindroth, 1931) drains, wet manure (Hartley, 1961)

Cont/. . .

Table A3: continued

Species	Type	Records of larval feeding sites
Parhelophilus frutetorum	Filter-feeder?	
Merodon equestris	Phytophagous	In bulbs (Doucette *et al*, 1942)
Pipizella varipes	Aphidophagous	On subterranean root aphids associated with *Pastinaca sativa* (Dixon, 1959) and *Chamaenerion angustifolium* (qv in Stubbs and Falk, 1983)
Heringia heringi	Aphidophagous	On galls formed by *Schizoneura lanuginosa* on *Ulmus* sp (Wachtl, 1882); also on apid galls on *Salix* (P Chandler, 1969)
Xylota florum	Saprophagous?	Unknown
Xylota nemorum	Saprophagous	In rotting beech bark (Lundbeck, 1916)
Xylota sylvarum	Saprophagous	Wet sawdust, under rotting beech bark (Hartley, 1961)
Syritta pipiens	Saprophagous	Rotting *Narcissus* bulbs (Hodson, 1931). Manure, silage (Hartley, 1961)

Table A4: Number of syrphid adults recorded at each trap site

Species	Crop					Edgegrowth					Total
	W	B	P	Br	Total	WE	BE	PE	BrE	Total	
Syrphus ribesii	24	1	8	4	37	5	33	6	25	69	106
Syrphus torvus	-	-	-	-	-	-	-	1	1	2	2
Syrphus vitripennis	-	-	1	1	2	-	-	1	-	1	3
Epistrophe eligans	2	1	1	2	6	1	2	2	-	5	11
Epistrophe nitidicollis	-	-	2	-	2	-	3	6	-	9	11
Metasyrphus corollae	8	-	4	5	17	1	1	1	6	9	26
Metasyrphus latifasciatus	2	-	1	1	4	1	1	-	2	4	8
Metasyrphus luniger	-	2	2	2	6	2	3	-	3	8	14
Dasysyrphus albostriatus	1	-	-	1	2	-	-	1	3	4	6
Dasysyrphus lunulatus	1	-	-	-	1	-	-	-	1	1	2
Dasysyrphus tricinctus	-	-	-	1	1	-	1	1	1	3	4
Dasysyrphus venustus	7	4	2	-	13	1	4	2	2	9	22
Scaeva selenitica	2	-	-	1	3	1	2	5	2	10	13
Leucozona lucorum	-	-	1	-	1	-	2	1	-	3	4
Meligramma cincta	2	5	4	4	15	1	2	-	-	3	18
Meligramma triangulifera	-	-	1	1	2	-	-	-	-	-	2
Episyrphus balteatus	7	3	7	1	18	5	15	2	7	29	47
Sphaerophoria menthastri	-	-	1	-	1	1	-	-	-	1	2
Sphaerophoria scripta	277	-	41	79	397	98	26	9	74	207	604
Xanthogramma pedissequum	-	-	2	-	2	2	1	-	-	3	5
Parasyrphus punctulatus	-	2	-	-	2	-	-	-	-	-	2
Meliscaeva auricollis	1	1	1	-	3	-	-	-	-	-	3
Meliscaeva cinctella	40	1	5	1	47	5	4	2	10	21	68
Chrysotoxum bicinctum	20	-	2	3	25	21	7	4	20	52	77
Chrysotoxum cautum	-	-	-	-	-	1	4	-	1	6	6
Chrysotoxum festivum	4	-	-	-	4	-	-	1	1	2	6

Cont/. . .

Table A4: continued

Species	Crop					Edgegrowth					Total
	W	B	P	Br	Total	WE	BE	PE	BrE	Total	
Chrysotoxum verralli	-	-	-	-	-	-	-	2	-	2	2
Baccha obscuripennis	4	1	-	2	7	3	5	-	2	10	17
Melanostoma mellinum	61	5	46	39	151	50	98	38	90	276	427
Melanostoma scalare	9	3	1	5	18	11	38	28	46	123	141
Platycheirus albimanus	38	-	67	42	147	2	25	12	60	99	246
Platycheirus angustatus	20	8	9	18	55	24	112	30	47	213	268
Platycheirus clypeatus	2	1	1	24	28	2	20	7	20	49	77
Platycheirus fulviventris	-	-	-	-	-	-	2	-	-	2	2
Platycheirus manicatus	-	1	1	1	3	-	3	1	1	5	8
Platycheirus peltatus	21	3	14	52	90	8	43	23	34	108	198
Platycheirus scambus	-	-	-	1	1	-	-	-	-	-	1
Platycheirus scutatus	6	3	11	13	33	-	8	6	14	28	61
Platycheirus tarsalis	-	-	1	-	1	-	-	-	-	-	1
Pyrophaena granditarsa	-	-	-	1	1	-	-	-	-	-	1
Pyrophaena rosarum	1	-	-	-	1	-	-	-	1	1	2
Cheilosia bergenstammi	-	-	-	-	-	-	-	-	3	3	3
Cheilosia illustrata	-	-	-	-	-	1	-	-	-	1	1
Cheilosia variabilis	1	-	-	2	3	-	3	-	2	5	8
Cheilosia vernalis	-	-	-	1	1	-	1	-	1	2	3
Rhingia campestris	3	-	-	1	4	3	-	7	-	10	14
Neoascia podagrica	1	-	1	-	2	-	-	1	2	3	5
Eristalis arbustorum	5	-	-	-	5	-	-	-	-	-	5
Eristalis nemorum	-	-	-	-	-	-	-	-	2	2	2
Eristalis pertinax	-	-	1	-	1	-	-	1	-	1	2
Helophilus pendulus	7	-	2	-	9	-	9	2	4	15	24
Parhelophilus frutetorum	1	-	-	-	1	-	-	1	-	1	2

Cont/. . .

Table A4: continued

Species	Crop					Edgegrowth					Total
	W	B	P	Br	Total	WE	BE	PE	BrE	Total	
Merodon equestris	-	-	-	-	-	-	-	-	2	2	2
Pipizella varipes	-	-	-	-	-	-	-	-	1	1	1
Heringia heringi	2	-	-	-	2	-	-	-	-	-	2
Xylota florum	-	-	1	-	1	-	1	1	-	2	3
Xylota nemorum	-	1	-	-	1	2	1	-	-	3	4
Xylota sylvarum	-	-	-	-	-	-	-	1	-	1	1
Syritta pipiens	32	3	23	6	64	5	7	11	32	55	119
Total Number of Individuals	612	49	266	318	1245	258	488	217	525	1488	2733
Total Number of Species	32	19	32	30	49	26	32	33	36	51	59

Key W - Wheat; B - Beans; P - Potato; Br - Brussels Sprouts; WE - Wheat Edge; BE - Bean Edge;

PE - Potato Edge: BrE - Brussels Sprout Edge

Table A5: Changes in syrphid community structure during the study period

	Number of species	Number of individuals	Dominance index	Dominant species	Number of species	Number of individuals	Dominance index	Dominant species
Date	WHEAT				BRUSSELS SPROUT			
12.5- 6.6	9	27	0.37	Platycheirus angustatus	9	21	0.33	Platycheirus angustatus
9.6- 4.7	8	12	0.33	Platycheirus angustatus	14	32	0.26	Platycheirus angustatus
7.7- 1.8	11	93	0.59	Sphaerophoria scripta	15	62	0.23	Platycheirus clypeatus
4.8-29.8	23	389	0.49	Sphaerophoria scripta	14	158	0.34	Sphaerophoria scripta
1.9-26.9	15	91	0.36	Sphaerophoria scripta	10	42	0.40	Platycheirus albimanus
29.9-17.10	-	-	-	-	3	4	0.50	Platycheirus albimanus
	POTATO				BEANS			
12.5- 6.6	11	18	0.24	Platycheirus angustatus	12	29	0.21	Platycheirus angustatus
9.6- 4.7	16	31	0.33	Platycheirus scutatus	8	15	0.20	Platycheirus peltatus
7.7- 1.8	8	11	0.18	Melanostoma mellinum Platycheirus angustatus Platycheirus albimanus	4	5	0.40	Metasyrphus luniger
4.8-29.8	12	126	0.27	Melanostoma mellinum	-	-	-	-
1.9-26.9	14	79	0.51	Platycheirus albimanus	-	-	-	-
29.9-17.10	1	1	1.00	Platycheirus albimanus	-	-	-	-
	EDGE GROWTH (4 sites)				ALL SITES			
12.5- 6.6	25	161	0.48	Platycheirus angustatus	29	256	0.41	Platycheirus angustatus
9.6- 4.7	30	194	0.35	Platycheirus angustatus	39	284	0.30	Platycheirus angustatus
7.7- 1.8	25	193	0.25	Melanostoma mellinum	31	364	0.30	Sphaerophoria scripta
4.8-29.8	30	641	0.31	Melanostoma mellinum	34	1314	0.28	Sphaerophoria scripta
1.9-26.9	23	287	0.18	Melanostoma scalare	29	499	0.22	Platycheirus albimanus
29.9-17.10	9	12	0.25	Platycheirus albimanus	9	17	0.35	Platycheirus albimanus

Table A6: Number of syrphid adults recorded each week from May until October 1980

Species	12.5	19.5	26.5	2.6	9.6	16.6	23.6	30.6	7.7	14.7	21.7	28.7	4.8	11.8	18.8	25.8	1.9	8.9	15.9	22.9	29.9	6.10	13.10	Total
Syrphus ribesii	1	-	1	1	1	-	-	4	-	2	3	-	8	2	8	25	26	13	7	3	1	-	-	106
Syrphus torvus	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Syrphus vitripennis	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	3
Epistrophe eligans	3	1	3	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Epistrophe nitidicollis	-	-	2	4	1	-	-	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	11
Metasyrphus corollae	-	-	-	3	-	1	2	1	-	1	1	1	1	3	9	1	-	-	1	-	1	-	-	26
Metasyrphus latifasciatus	-	-	-	1	-	-	-	1	-	-	1	-	-	-	2	-	1	1	-	1	-	-	-	8
Metasyrphus luniger	-	-	-	-	-	-	-	-	1	1	3	-	-	-	-	1	4	4	-	-	-	-	-	14
Dasysyrphus albostriatus	1	1	-	-	-	-	-	1	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	6
Dasysyrphus lunulatus	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Dasysyrphus tricinctus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	-	-	3
Dasysyrphus venustus	3	3	4	11	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22
Scaeva selenitica	-	-	-	-	-	-	4	-	-	-	-	1	2	3	2	-	-	1	-	-	-	-	-	13
Leucozona lucorum	-	-	-	-	-	-	-	2	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	4
Meligramma cincta	1	3	2	7	-	-	-	3	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	18
Meligramma triangulifera	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2
Episyrphus balteatus	1	-	-	2	3	4	12	3	-	1	3	-	2	2	1	2	3	4	1	2	-	-	1	47
Sphaerophoria menthastri	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Sphaerophoria scripta	1	-	-	9	3	1	4	2	-	1	35	72	78	79	149	68	74	12	11	3	2	-	-	604
Xanthogramma pedissequum	-	-	-	-	-	-	1	1	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	5
Parasyrphus punctulatus	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Meliscaeva auricollis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	3
Meliscaeva cinctella	1	1	-	-	2	-	-	-	-	-	-	1	6	3	13	19	20	2	-	-	-	-	-	68
Chrysotoxum bicinctum	-	-	-	-	-	-	1	3	-	8	8	11	20	10	3	7	4	2	-	-	-	-	-	77
Chrysotoxum cautum	-	-	-	3	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6

Cont/. . .

Table A6: continued

Species	12.5	19.5	26.5	2.6	9.6	16.6	23.6	30.6	7.7	14.7	21.7	28.7	4.8	11.8	18.8	25.8	1.9	8.9	15.9	22.9	29.9	6.10	13.10	Total
Chrysotoxum festivum	-	-	-	-	-	-	-	-	-	-	1	1	2	1	1	-	-	-	-	-	-	-	-	6
Chrysotoxum verralli	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2
Baccha obscuripennis	-	-	-	-	-	-	-	1	-	-	5	1	2	-	1	2	-	1	1	1	2	-	-	17
Melanostoma mellinum	1	1	1	11	6	5	1	1	-	1	19	49	102	105	70	26	5	12	3	6	1	-	1	427
Melanostoma scalare	-	1	-	6	4	-	1	-	-	1	2	5	2	17	28	21	26	21	4	2	-	-	-	141
Platycheirus albimanus	-	-	1	7	3	4	-	1	-	-	9	19	26	30	20	12	35	25	22	26	4	2	-	246
Platycheirus angustatus	7	15	12	69	27	12	27	18	-	4	10	15	10	7	6	5	11	4	4	4	1	-	-	268
Platycheirus clypeatus	-	-	-	3	1	1	1	-	-	-	8	20	11	9	8	4	7	2	1	1	-	-	-	77
Platycheirus fulviventris	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	3
Platycheirus manicatus	-	-	-	3	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Platycheirus peltatus	-	-	-	15	9	9	5	7	2	2	2	1	13	21	51	41	11	4	1	4	-	-	-	198
Platycheirus scambus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Platycheirus scutatus	-	1	1	3	7	2	5	12	2	1	4	3	5	4	2	3	3	2	1	-	-	-	-	61
Platycheirus tarsalis	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Pyrophaena granditarsa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Pyrophaena rosarum	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2
Cheilosia bergenstammi	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	3
Cheilosia illustrata	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	2
Cheilosia variabilis	-	-	-	5	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	8
Cheilosia vernalis	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	3
Rhingia campestris	-	-	-	-	1	-	-	-	-	-	-	-	-	-	6	5	2	-	-	-	-	-	-	14
Neoascia podagrica	-	1	-	1	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	5
Eristalis arbustorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	2	-	-	-	-	-	-	5
Eristalis nemorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2
Eristalis pertinax	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2

Cont/. . .

Table A6: continued

Species	12.5	19.5	26.5	2.6	9.6	16.6	23.6	30.6	7.7	14.7	21.7	28.7	4.8	11.8	18.8	25.8	1.9	8.9	15.9	22.9	29.9	6.10	13.10	Total
Helophilus pendulus	-	-	-	-	-	-	-	1	-	-	-	2	-	-	3	5	4	6	1	2	-	-	-	24
Parhelophilus frutetorum	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Merodon equestris	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Pipizella varipes	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Heringia heringi	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2
Xylota florum	-	-	-	-	2	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	4
Xylota nemorum	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	-	1	-	-	-	-	-	-	4
Xylota sylvarum	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Syritta pipiens	-	-	1	2	5	8	2	4	-	-	-	-	12	10	19	33	20	1	-	1	-	1	-	119
Unidentified species	-	-	-	4	1	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	8
Total number of individuals	23	30	29	174	86	52	68	77	5	27	120	212	305	312	403	294	263	121	58	57	12	3	2	2733
Total number of identified individuals	23	30	29	170	85	52	68	75	5	27	120	212	305	312	403	293	263	121	58	57	12	3	2	2725
Total number of identified species	12	12	11	18	23	15	15	26	3	15	21	21	20	22	21	27	23	22	13	14	7	2	2	59
Dominance index	0.30	0.50	0.41	0.40	0.31	0.23	0.40	0.23	0.40	0.30	0.29	0.34	0.33	0.34	0.37	0.23	0.28	0.21	0.38	0.46	0.33	0.67	0.50	

Table A7: Records of the phenologies of some aphidophagous syrphids

Species	Number of emergence periods			Overwintering stage	
	Present study	Other studies			
Syrphus ribesii	2+	2	Sundby (1966)	Larva	Scott (1939); Schneider (1948); Dušek and Láska (1974); Rotheray (unpubl)
		2+	Pollard (1971)		
		3	Rotheray (unpubl)		
		3+	Bhatia (1939)		
		2 - 4	Schneider (1948)	Larva/ Adult	Pollard (1971)
		3 - 4	Bänsch (1964)		
		Many	Goeldlin (1974)		
Metasyrphus corollae	1	1	Pollard (1971); Rotheray (unpubl)	Pupa	Scott (1939);
		1 - 2	Goeldlin (1974); Grosser and Klapperstück (1977)	Adult	Pollard (1971); Rotheray (unpubl)
Dasysyrphus venustus	1	1	Speight *et al* (1975); Gilbert (1981a)		
Meliscaeva cinctella	2	2	Chandler (1968d)		
		4 - 5	Schneider (1948)		

Cont/. . .

Table A7: continued

Species	Number of emergence periods			Overwintering stage	
	Present study	Other studies			
Episyrphus balteatus	1	1	Pollard (1971); Nielsen (1971); Grosser and Klapperstück (1977); Rotheray (unpubl)	Larva/ Pupa	Bhatia (1939)
		2?	Gilbert (1981a)	Adult	Schneider (1948) Pollard (1971); Dušek and Láska (1974); Rotheray (unpubl)
		3+	Bhatia (1939)		
		4 - 5	Schneider (1948)		
		7	Gaumont (1929)		
		Many	Goeldlin (1974)		
Sphaerophoria scripta	3	2	Pollard (1971)	Larva	Scott (1939); Dušek and Láska (1974); Rotheray (unpubl)
		3	Bhatia (1939); Grosser and Klapperstück (1977); Gilbert (1981a)	Larva/ Pupa	Bhatia (1939)
		Many	Bánkowska (1964); Goeldlin (1974)	Adult	Schneider (1948)
Chrysotoxum bicinctum	1				

Cont/. . .

Table A7: continued

Species	Number of emergence periods		Overwintering stage
	Present study	Other studies	
Melanostoma mellinum	2	2 Zimina (1957b); Pollard (1971); Claussen (1980); Gilbert (1981a) Many Goeldlin (1974)	
Melanostoma scalare	2	2 Pollard (1971); Claussen (1980); Gilbert (1981a) 2 - 3 Grosser and Klapperstück (1977)	
Platycheirus albimanus	2	2 Pollard (1971); Nielsen (1971); Claussen (1980); Gilbert (1981a) 2 - 3 Goeldlin (1974)	Larva Scott (1939)
Platycheirus angustatus	2+		

Cont/. . .

Table A7: continued

Species	Number of emergence periods		Overwintering stage
	Present study	Other studies	
Platycheirus clypeatus	2	2 Pollard (1971); Nielsen (1971); Claussen (1980) 2 - 3 Goeldlin (1974)	Larva Scott (1939)
Platycheirus peltatus	2	2 Zimina (1957b); Pollard (1971); Goeldlin (1974); Claussen (1980); Gilbert (1981a)	Larva Scott (1939); Dušek and Láska (1974)
Platycheirus scutatus	2+	2 Pollard (1971); Claussen (1980) 2 - 3 Dunn (1949) 2 - 3+ Goeldlin (1974) 3 Rotheray (unpubl) 3+ Bhatia (1939)	Larva Scott (1939); Dunn (1949); Pollard (1971); Dušek and Láska (1974); Rotheray (unpubl)

APPENDIX B

Table B1: Average times of sunrise and sunset for weeks in June, August and September 1980 (GMT)

Date	Sunrise	Sunset
2.6 - 6.6	0343 h	2014 h
9.6 - 13.6	0340 h	2019 h
16.6 - 20.6	0339 h	2022 h
23.6 - 27.6	0342 h	2024 h
30.6 - 4.7	0345 h	2022 h
11.8 - 15.8	0441 h	1928 h
18.8 - 22.8	0452 h	1913 h
25.8 - 29.8	0504 h	1858 h
1.9 - 5.9	0520 h	1835 h
8.9 - 12.9	0528 h	1820 h

Table B2: Average temperature recorded at different times of day for seven days in August and September 1980

Date	Mean temperature for each period (^{o}C)				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	7.8	16.5	19.8	20.5	19.8
26.8.80	11.1	18.0	21.5	22.7	22.0
27.8.80	9.6	16.2	21.4	23.9	23.2
28.8.80	16.0	16.8	18.9	20.8	21.1
4.9.80	11.5	15.0	18.0	19.4	18.1
5.9.80	12.2	14.8	17.3	15.6	14.9
6.9.80	11.9	16.8	19.3	20.5	18.3

Table B3: Average relative humidity recorded at different times of day for seven days in August and September 1980

Date	Mean relative humdidity for each period (%)				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	90	61	48	46	49
26.8.80	90	78	56	50	52
27.8.80	94	82	61	52	58
28.8.80	90	94	88	69	65
4.9.80	93	91	80	70	70
5.9.80	92	91	83	88	84
6.9.80	92	79	67	64	73

Table B4: Average incoming solar radiation recorded at different times of day for seven days in August and September 1980

Date	Mean radiation for each period (Wm^{-2})				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	81.6	298.4	353.3	310.4	142.0
26.8.80	65.6	277.1	291.8	250.9	103.6
27.8.80	72.1	270.0	325.8	288.5	93.9
28.8.80	21.3	72.0	174.2	236.1	136.4
4.9.80	34.8	75.4	138.2	142.7	63.9
5.9.80	23.6	152.3	210.2	137.5	65.8
6.9.80	80.5	290.4	314.6	280.3	105.4

Table B5: Average net radiation recorded at the soil surface at different times of day for seven days in August and September 1980

Date	Mean radiation for each period (Wm^{-2})				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	-15.10	-1.36	5.94	3.61	-5.32
26.8.80	-13.93	-3.72	3.25	0.83	-4.14
27.8.80	-15.36	-0.77	9.37	9.00	-0.73
28.8.80	- 8.55	-4.72	1.78	2.28	-3.01
4.9.80	-12.92	-5.41	-0.46	-0.29	-5.67
5.9.80	-11.07	-4.38	4.33	-2.05	-7.54
6.9.80	-10.89	-1.46	6.94	4.47	-5.10

Table B6: Average net radiation recorded at a height of 1 m above the ground at different times of day for seven days in August and September 1980

Date	Mean radiation for each period (Wm^{-2})				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	359.2	397.3	422.7	401.8	360.7
26.8.80	356.3	396.7	404.1	395.9	359.7
27.8.80	358.4	395.1	418.9	400.9	362.2
28.8.80	350.7	355.3	402.9	399.2	367.3
4.9.80	356.1	367.6	379.5	372.5	357.2
5.9.80	345.3	377.9	397.9	359.5	356.1
6.9.80	363.5	395.1	424.7	404.2	362.2

Table B7: Average wind velocity recorded at different times of day for seven days in August and September 1980

Date	Mean wind velocity for each period (ms^{-1})				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	0.16	1.87	2.71	2.44	2.16
26.8.80	1.00	2.27	3.06	2.25	1.49
27.8.80	0.26	0.80	1.21	1.58	1.20
28.8.80	1.44	2.14	2.12	2.66	2.35
4.9.80	0.30	0.59	1.32	1.47	2.25
5.9.80	1.58	1.63	1.68	2.57	1.80
6.9.80	1.51	2.60	2.69	3.01	2.88

Table B8: Average rainfall recorded at different times of day for seven days in August and September 1980

Date	Mean rainfall for each period (hours)				
	Sunrise -0800	0800-1030	1030-1300	1300-1530	1530-Sunset
25.8.80	-	-	-	-	-
26.8.80	-	-	-	-	-
27.8.80	-	-	-	-	-
28.8.80	-	0.7	-	-	-
4.9.80	-	-	-	-	-
5.9.80	1.2	-	0.1	0.4	-
6.9.80	-	-	-	-	-

APPENDIX C

Table C1: Number of plants in each aphid infestation category on different sample dates in August and September 1981

Crop	Sample date	Aphid infestation category							
		1.	2	3.	4	5	6.	7	Total
Cauliflower	4.8.81	1	14	4	-	-	-	1	20
	11.8.81	1	15	1	1	1	1	-	20
	18.8.81	-	12	2	4	1	1	-	20
	25.8.81	-	13	-	3	3	1	-	20
	1.9.81	-	14	-	3	2	-	1	20
Brussels sprout	4.8.81	-	3	6	3	2	4	2	20
	11.8.81	-	2	7	3	2	4	2	20
	18.8.81	-	2	7	3	3	3	2	20
	25.8.81	-	2	6	2	3	4	3	20
	1.9.81	-	3	9	1	2	3	2	20
White Cabbage	4.8.81	4	14	2	-	-	-	-	20
	11.8.81	2	15	2	1	-	-	-	20
	18.8.81	1	12	4	2	1	-	-	20
	25.8.81	1	14	2	2	1	-	-	20
	1.9.81	1	15	2	1	1	-	-	20
Red Cabbage	4.8.81	-	7	9	3	1	-	-	20
	11.8.81	1	10	6	2	1	-	-	20
	18.8.81	2	14	4	-	-	-	-	20
	25.8.81	2	15	3	-	-	-	-	20
	1.9.81	-	19	1	-	-	-	-	20
Chinese Cabbage	4.8.81	12	6	2	-	-	-	-	20
	11.8.81	12	7	1	-	-	-	-	20
	18.8.81	13	5	2	-	-	-	-	20
	25.8.81	12	6	2	-	-	-	-	20
	1.9.81	15	3	2	-	-	-	-	20
Swede	4.8.81	7	12	1	-	-	-	-	20
	11.8.81	8	12	-	-	-	-	-	20
	18.8.81	12	8	-	-	-	-	-	20
	25.8.81	6	14	-	-	-	-	-	20
	1.9.81	14	6	-	-	-	-	-	20
Radish	4.8.81	18	2	-	-	-	-	-	20
	11.8.81	17	2	1	-	-	-	-	20
	18.8.81	15	4	1	-	-	-	-	20
	25.8.81	15	2	3	-	-	-	-	20
	1.9.81	18	1	1	-	-	-	-	20

Table C2: The effect of aphid density on the number of eggs laid per plant

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.26 ±0.08	0.86 ±0.46	2.09 ±0.83	4.14 ±0.49	6.00 ±1.15	6.50 ±2.50
Brussels Sprout	*	0.58 ±0.23	1.46 ±0.23	2.75 ±0.69	4.58 ±1.09	7.06 ±0.94	9.09 ±1.37
White Cabbage	0.11 ±0.11	0.40 ±0.10	1.67 ±0.67	3.17 ±1.05	6.33 ±2.03	*	*
Red Cabbage	0.20 ±0.20	0.52 ±0.12	0.96 ±0.28	1.00 ±0.45	2.00 ±2.00	*	*
Chinese Cabbage	0.19 ±0.09	0.44 ±0.15	1.22 ±0.60	*	*	*	*
Swede	0.13 ±0.06	0.52 ±0.17	2.00 ±0.00	*	*	*	*
Radish	0.18 ±0.05	0.36 ±0.24	1.33 ±0.49	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	256.15 114.36	42.69 1.23	34.72	0.001
Brussels Sprout	Among groups Within groups	5 94	835.09 766.62	167.02 8.16	20.48	0.001
White Cabbage	Among groups Within groups	4 95	149.45 169.86	37.36 1.79	20.90	0.001
Red Cabbage	Among groups Within groups	4 95	8.47 113.97	2.12 1.20	1.76	ns
Chinese Cabbage	Among groups Within groups	2 97	8.78 71.97	4.39 0.74	5.92	0.001
Swede	Among groups Within groups	2 97	6.54 82.22	3.27 0.85	3.86	0.01
Radish	Among groups Within groups	2 97	7.54 32.17	3.77 0.33	11.37	0.001

In this and subsequent tables of this type * denotes that no plants were recorded in this aphid infestation category

Table C3: The effect of aphid density on the number of eggs laid per plant by Sphaerophoria scripta

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.15 ±0.04	1.00 ±0.38	2.18 ±0.50	3.00 ±0.69	4.00 ±0.58	4.50 ±1.50
Brussels Sprout	*	0.83 ±0.27	1.09 ±0.21	2.58 ±0.61	4.08 ±1.14	5.06 ±0.91	5.18 ±1.21
White Cabbage	-	0.20 ±0.09	0.50 ±6.26	2.17 ±0.65	3.33 ±1.76	*	*
Red Cabbage	-	0.06 ±0.03	0.39 ±0.20	1.00 ±0.77	-	*	*
Chinese Cabbage	0.19 ±0.08	0.30 ±0.14	1.11 ±0.51	*	*	*	*
Swede	0.09 ±0.04	0.21 ±0.07	-	*	*	*	*
Radish	0.05 ±0.03	-	0.50 ±0.34	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	143.44 68.67	23.91 0.74	32.38	0.001
Brussels Sprout	Among groups Within groups	5 94	323.42 700.82	64.68 7.46	8.68	0.001
White Cabbage	Among groups Within groups	4 95	48.81 75.70	12.20 0.80	15.31	0.001
Red Cabbage	Among groups Within groups	4 95	5.53 35.23	1.38 0.37	3.73	0.01
Chinese Cabbage	Among groups Within groups	2 97	6.73 56.27	3.37 0.58	5.80	0.001
Swede	Among groups Within groups	2 97	0.42 18.33	0.21 0.19	1.10	ns
Radish	Among groups Within groups	2 97	1.21 9.31	0.60 0.10	6.27	0.001

Table C4: The effect of aphid density on the number of eggs laid per plant by *Syrphus ribesii*

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.06 ±0.03	0.86 ±0.34	1.82 ±0.38	2.43 ±0.48	3.67 ±1.86	4.50 ±0.50
Brussels Sprout	*	-	0.17 ±0.08	2.08 ±0.51	3.58 ±0.79	4.22 ±0.82	5.45 ±1.28
White Cabbage	-	0.13 ±0.04	-	1.00 ±0.52	1.67 ±0.88	*	*
Red Cabbage	-	-	0.17 ±0.10	-	-	*	*
Chinese Cabbage	0.06 ±0.04	0.07 ±0.07	0.78 ±0.28	*	*	*	*
Swede	-	0.19 ±0.02	-	*	*	*	*
Radish	-	-	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	118.97 55.14	19.83 0.59	33.44	0.001
Brussels Sprout	Among groups Within groups	5 94	414.36 512.64	82.87 5.45	15.20	0.001
White Cabbage	Among groups Within groups	4 95	11.49 20.51	2.87 0.22	13.31	0.001
Red Cabbage	Among groups Within groups	4 95	0.54 5.30	0.13 0.06	2.40	ns
Chinese Cabbage	Among groups Within groups	2 97	4.15 15.16	2.08 0.16	13.29	0.001
Swede	Among groups Within groups	2 97	0.01 0.98	0.005 0.010	0.46	ns
Radish	Among groups Within groups	-	-	-	-	-

Table C5: The effect of aphid density on the number of eggs laid per plant by *Metasyrphus luniger*

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	-	-	0.18 ±0.12	0.57 ±0.30	2.67 ±0.88	2.50 ±0.50
Brussels Sprout	*	-	-	-	-	0.56 ±0.28	1.64 ±0.56
White Cabbage	-	-	-	0.50 ±0.50	0.33 ±0.33	*	*
Red Cabbage	-	-	0.09 ±0.06	0.40 ±0.40	2.50 ±2.50	*	*
Chinese Cabbage	-	-	-	*	*	*	*
Swede	-	-	-	*	*	*	*
Radish	-	-	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	32.87 10.52	5.48 0.11	48.45	0.001
Brussels Sprout	Among groups Within groups	5 94	27.17 58.99	5.43 0.63	8.66	0.001
White Cabbage	Among groups Within groups	4 95	1.67 8.17	0.42 0.09	4.87	0.01
Red Cabbage	Among groups Within groups	4 95	12.66 17.33	3.17 0.18	17.16	0.001
Chinese Cabbage	Among groups Within groups	-	-	-	-	-
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	-	-	-	-	-

Table C6: The effect of aphid density on the number of eggs laid per plant by Metasyrphus corollae

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	-	-	-	-	0.33 ±0.33	1.00 ±1.00
Brussels Sprout	*	-	-	-	-	0.11 ±0.11	0.73 ±0.45
White Cabbage	-	-	-	0.17 ±0.17	-	*	*
Red Cabbage	-	-	0.40 ±0.04	0.20 ±0.20	1.00 ±1.00	*	*
Chinese Cabbage	-	-	-	*	*	*	*
Swede	-	-	-	*	*	*	*
Radish	-	-	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 95	2.24 2.67	0.37 0.03	13.04	0.001
Brussels Sprout	Among groups Within groups	5 94	5.04 25.97	1.01 0.27	3.69	0.01
White Cabbage	Among groups Within groups	4 95	0.99	0.25		
Red Cabbage	Among groups Within groups	4 95	2.08 3.76	0.52 0.04	13.17	0.001
Chinese Cabbage	Among groups Within groups	-	-	-	-	-
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	-	-	-	-	-

Table C7: The effect of aphid density on the number of eggs laid per plant by Platycheirus manicatus

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.53 ±0.12	1.86 ±0.55	0.91 ±0.31	-	-	-
Brussels Sprout	*	1.17 ±0.37	1.74 ±0.38	0.92 ±0.33	0.58 ±0.31	-	-
White Cabbage	0.22 ±0.22	0.97 ±0.23	0.33 ±0.33	-	-	*	*
Red Cabbage	0.20 ±0.20	0.37 ±0.10	-	-	-	*	*
Chinese Cabbage	0.25 ±0.13	0.93 ±0.26	-	*	*	*	*
Swede	0.02 ±0.02	0.02 ±0.02	-	*	*	*	*
Radish	0.07 ±0.04	0.09 ±0.09	0.17 ±0.17	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups	6	17.48	2.91	3.20	0.01
	Within groups	93	84.71	0.91		
Brussels Sprout	Among groups	5	50.32	10.06	4.42	0.01
	Within groups	94	214.19	2.28		
White Cabbage	Among groups	4	13.07	3.27	1.15	ns
	Within groups	95	270.17	2.84		
Red Cabbage	Among groups	4	2.81	0.70	1.45	ns
	Within groups	95	45.94	0.48		
Chinese Cabbage	Among groups	2	10.34	5.17	4.33	0.01
	Within groups	97	115.85	1.19		
Swede	Among groups	2	0.001	0.001	0.01	ns
	Within groups	97	1.960	0.020		
Radish	Among groups	2	0.05	0.03	0.22	ns
	Within groups	97	11.31	0.12		

Table C8: The effect of aphid density on the number of eggs laid per plant by Platycheirus albimanus

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.16 ±0.05	1.71 ±0.92	2.55 ±0.73	0.86 ±0.46	-	-
Brussels Sprout	*	0.58 ±0.26	0.63 ±0.18	1.17 ±0.46	1.75 ±0.55	3.67 ±0.83	1.73 ±0.81
White Cabbage	0.22 ±0.22	0.56 ±0.17	0.25 ±0.25	0.17 ±0.17	-	*	*
Red Cabbage	0.20 ±0.20	0.02 ±0.02	-	0.80 ±0.58	-	*	*
Chinese Cabbage	0.06 ±0.04	0.07 ±0.06	0.44 ±0.29	*	*	*	*
Swede	0.02 ±0.02	0.04 ±0.03	-	*	*	*	*
Radish	0.01 ±0.01	0.27 ±0.20	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	66.28 114.23	11.05 1.23	8.99	0.001
Brussels Sprout	Among groups Within groups	5 94	123.80 399.19	24.76 4.25	5.83	0.001
White Cabbage	Among groups Within groups	4 95	2.84 153.91	0.71 1.62	0.44	ns
Red Cabbage	Among groups Within groups	4 95	3.06 8.58	0.76 0.09	8.45	0.001
Chinese Cabbage	Among groups Within groups	2 97	1.18 13.82	0.59 0.14	4.13	0.05
Swede	Among groups Within groups	2 97	0.01 2.90	0.004 0.300	0.14	ns
Radish	Among groups Within groups	2 97	0.67 5.17	0.34 0.05	6.29	0.01

Table C9: The effect of aphid density on the number of eggs laid per plant by Platycheirus scutatus

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.04 ±0.03	0.57 ±0.43	-	1.00 ±0.72	-	-
Brussels Sprout	*	0.17 ±0.17	0.23 ±0.10	0.83 ±0.42	1.17 ±0.44	0.72 ±0.35	-
White Cabbage	-	0.04 ±0.02	0.25 ±0.25	0.50 ±0.50	-	*	*
Red Cabbage	-	-	-	-	-	*	*
Chinese Cabbage	0.03 ±0.02	-	0.11 ±0.11	*	*	*	*
Swede	-	0.04 ±0.03	-	*	*	*	*
Radish	-	0.09 ±0.09	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	7.46 32.58	1.24 0.35	3.55	0.01
Brussels Sprout	Among groups Within groups	5 94	14.13 100.78	2.83 1.07	2.64	0.05
White Cabbage	Among groups Within groups	4 95	1.57 18.62	0.39 0.20	2.00	ns
Red Cabbage	Among groups Within groups	2 97	0.08 2.83	0.04 0.03	1.43	ns
Chinese Cabbage	Among groups Within groups	2 97	0.08 2.83	0.04 0.03	1.43	ns
Swede	Among groups Within groups	2 97	0.04 1.92	0.02 0.02	0.93	ns
Radish	Among groups Within groups	2 97	0.08 0.91	0.04 0.01	4.32	0.05

Table C10: The effect of aphid density on the number of eggs laid per plant by Platycheirus peltatus

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	1.65 ±0.31	0.71 ±0.47	0.55 ±0.39	1.86 ±0.96	-	-
Brussels Sprout	*	2.75 ±1.23	1.23 ±0.37	4.08 ±1.11	2.50 ±0.88	0.94 ±0.70	1.09 ±0.48
White Cabbage	0.11 ±0.11	0.69 ±0.19	3.08 ±1.08	1.33 ±0.62	1.00 ±1.00	*	*
Red Cabbage	-	0.19 ±0.09	0.35 ±0.25	-	-	*	*
Chinese Cabbage	0.19 ±0.08	0.15 ±0.10	1.78 ±0.70	*	*	*	*
Swede	0.38 ±0.19	1.42 ±0.37	3.00 ±0.00	*	*	*	*
Radish	0.12 ±0.06	1.00 ±0.43	0.67 ±0.42	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	30.50 504.50	5.08 5.43	0.94	ns
Brussels Sprout	Among groups Within groups	5 94	109.25 740.19	21.85 7.87	2.77	0.05
White Cabbage	Among groups Within groups	4 95	66.69 352.22	16.67 3.71	4.50	0.01
Red Cabbage	Among groups Within groups	4 95	1.00 67.00	0.25 0.71	0.35	ns
Chinese Cabbage	Among groups Within groups	2 97	21.05 70.71	10.52 0.73	14.44	0.001
Swede	Among groups Within groups	2 97	30.95 433.80	15.48 4.47	3.46	0.05
Radish	Among groups Within groups	2 97	8.62 52.13	4.31 0.54	8.02	0.001

Table C11: The effect of aphid density on the number of eggs laid per plant by *Platycheirus clypeatus*

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.24 ±0.13	0.13 -	0.36 ±0.36	-	-	-
Brussels Sprout	*	1.00 ±0.52	1.09 ±0.34	1.50 ±0.54	0.83 ±0.44	0.33 ±0.24	0.36 ±0.36
White Cabbage	-	0.54 ±0.20	1.17 ±0.63	0.33 ±0.33	-	*	*
Red Cabbage	-	0.06 ±0.06	-	-	-	*	*
Chinese Cabbage	0.06 ±0.04	0.44 ±0.25	0.44 ±0.44	*	*	*	*
Swede	0.11 ±0.08	-	-	*	*	*	*
Radish	-	0.36 ±0.36	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	1.22 36.78	0.20 1.04	0.20	ns
Brussels Sprout	Among groups Within groups	5 94	14.61 273.95	2.92 2.91	1.00	ns
White Cabbage	Among groups Within groups	4 95	8.47 244.37	2.12 2.57	0.82	ns
Red Cabbage	Among groups Within groups	4 95	0.09 15.75	0.02 0.17	0.13	ns
Chinese Cabbage	Among groups Within groups	2 97	3.36 66.64	1.68 0.69	2.45	ns
Swede	Among groups Within groups	2 97	0.28 12.47	0.14 0.13	1.10	ns
Radish	Among groups Within groups	2 97	1.30 14.55	0.65 0.15	4.32	0.05

Table C12: The effect of aphid density on the number of eggs laid per plant by Melanostoma mellinum

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.99 ±0.21	-	1.27 ±0.51	1.00 ±0.72	2.67 ±1.33	-
Brussels Sprout	*	1.08 ±0.71	2.14 ±0.45	0.50 ±0.36	1.25 ±0.55	0.72 ±0.33	0.27 ±0.27
White Cabbage	-	1.11 ±0.24	1.50 ±0.56	2.67 ±1.69	1.00 ±1.00	*	*
Red Cabbage	0.40 ±0.40	0.26 ±0.10	0.35 ±0.21	-	-	*	*
Chinese Cabbage	0.16 ±0.08	1.74 ±0.55	0.56 ±0.38	*	*	*	*
Swede	0.15 ±0.11	0.65 ±0.19	-	*	*	*	*
Radish	0.05 ±0.03	0.27 ±0.27	0.50 ±0.50	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	20.01 263.83	3.33 2.84	1.18	ns
Brussels Sprout	Among groups Within groups	5 94	50.50 404.25	10.10 4.30	2.35	ns
White Cabbage	Among groups Within groups	4 95	27.41 410.63	6.85 4.32	1.59	ns
Red Cabbage	Among groups Within groups	4 95	0.74 64.97	0.19 0.68	0.27	ns
Chinese Cabbage	Among groups Within groups	2 97	47.72 249.84	23.86 2.58	0.27	0.001
Swede	Among groups Within groups	2 97	6.46 119.73	3.23 1.23	2.62	0.05
Radish	Among groups Within groups	2 97	1.51 23.49	0.76 0.24	3.12	0.05

Table C13: The effect of aphid density on the number of eggs laid per plant by Melanostoma scalare

a)

Crop	Mean number of eggs per plant at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	0.38 ±0.15	-	0.18 ±0.18	0.57 ±0.37	-	-
Brussels Sprout	*	1.75 ±0.78	0.86 ±0.32	0.50 ±0.36	1.17 ±0.53	0.11 ±0.11	-
White Cabbage	-	0.14 ±0.07	-	-	-	*	*
Red Cabbage	-	0.03 ±0.03	-	-	-	*	*
Chinese Cabbage	-	0.48 ±0.24	-	*	*	*	*
Swede	0.04 ±0.04	0.27 ±0.11	-	*	*	*	*
Radish	-	-	0.33 ±0.33	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	6 93	2.35 107.41	0.39 1.15	0.34	ns
Brussels Sprout	Among groups Within groups	5 94	28.73 260.98	5.75 2.78	2.07	ns
White Cabbage	Among groups Within groups	4 95	0.43 24.57	0.11 0.26	0.41	ns
Red Cabbage	Among groups Within groups	4 95	0.02 3.94	0.01 0.04	0.13	ns
Chinese Cabbage	Among groups Within groups	2 97	4.57 40.74	2.29 0.42	5.44	0.001
Swede	Among groups Within groups	2 97	1.29 34.15	0.65 0.35	1.84	ns
Radish	Among groups Within groups	2 97	0.63 3.33	0.31 0.03	9.12	0.001

Table C14: The effect of aphid population size on the size of egg batches laid by Episyrphus balteatus

a)

Crop	Mean egg batch size laid at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	2.00 ±0.00	-	2.00 ±0.00	-	-	-
Brussels Sprout	-	-	-	2.00 ±0.00	3.00 ±0.41	2.78 ±0.22	2.67 ±0.21
White Cabbage	-	-	-	-	-	*	*
Red Cabbage	-	-	-	-	-	*	*
Chinese Cabbage	-	-	2.00 ±0.00	*	*	*	*
Swede	-	2.00 ±0.00	-	*	*	*	*
Radish	-	2.00 ±0.00	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	1 2	0.00 0.00	0.00 0.00	-	-
Brussels Sprout	Among groups Within groups	3 18	1.88 6.89	0.63 0.38	1.64	ns
White Cabbage	Among groups Within groups	-	-	-	-	-
Red Cabbage	Among groups Within groups	-	-	-	-	-
Chinese Cabbage	Among groups Within groups	-	-	-	-	-
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	-	-	-	-	-

Table C15: The effect of aphid population size on the size of egg batches laid by Platycheirus peltatus

a)

Crop	Mean egg batch size laid at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	3.59 ±0.22	2.50 ±0.50	3.00 ±1.00	3.50 ±0.50	-	-
Brussels Sprout	-	3.38 ±0.18	3.50 ±0.27	3.39 ±0.18	4.20 ±0.20	4.25 ±0.48	3.00 ±0.41
White Cabbage	-	3.00 ±0.17	2.64 ±0.20	2.67 ±0.33	3.00 ±0.00	*	*
Red Cabbage	-	2.00 ±1.00	4.00 ±1.00	-	-	*	*
Chinese Cabbage	2.40 ±0.25	2.00 ±0.00	2.29 ±0.18	*	*	*	*
Swede	3.60 ±0.25	2.47 ±0.12	3.00 ±0.00	*	*	*	*
Radish	2.00 ±0.00	2.75 ±0.25	2.00 ±0.00	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	3 31	2.71 42.03	0.90 1.36	0.67	ns
Brussels Sprout	Among groups Within groups	5 36	5.90 16.50	1.18 0.46	2.58	0.05
White Cabbage	Among groups Within groups	3 29	1.03 13.88	0.34 0.48	0.72	ns
Red Cabbage	Among groups Within groups	1 3	1.20 8.00	1.20 2.67	0.45	ns
Chinese Cabbage	Among groups Within groups	2 11	0.23 2.63	0.11 0.24	0.48	ns
Swede	Among groups Within groups	2 33	5.64 14.67	2.82 0.44	6.34	0.01
Radish	Among groups Within groups	2 7	1.35 0.75	0.68 0.11	6.30	0.05

Table C16: The effect of aphid population size on the size of egg batches laid by Platycheirus clypeatus

a)

Crop	Mean egg batch size laid at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	5.33 ±0.33	-	4.00 ±0.00	-	-	-
Brussels Sprout	-	3.00 ±0.58	3.17 ±0.32	3.60 ±0.25	3.33 ±0.33	3.00 ±1.00	4.00 ±0.00
White Cabbage	-	2.92 ±0.35	3.50 ±0.29	2.00 ±0.00	-	*	*
Red Cabbage	-	4.00 ±0.00	-	-	-	*	*
Chinese Cabbage	2.00 ±0.00	2.40 ±0.25	4.00 ±0.00	*	*	*	*
Swede	2.50 ±0.50	-	-	*	*	*	*
Radish	-	2.00 ±0.00	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	1 2	1.33 0.67	1.33 0.33	4.00	ns
Brussels Sprout	Among groups Within groups	5 21	1.65 21.53	0.33 1.03	0.32	ns
White Cabbage	Among groups Within groups	2 15	2.08 19.92	1.04 1.33	0.78	ns
Red Cabbage	Among groups Within groups	-	-	-	-	-
Chinese Cabbage	Among groups Within groups	2 5	2.80 1.20	1.40 0.24	5.83	ns
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	-	-	-	-	-

Table C17: <u>The effect of aphid population size on the size of egg batches laid by Melanostoma mellinum</u>

a)

Crop	Mean egg batch size laid at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	2.71 ±0.13	-	2.33 ±0.21	4.00 ±0.00	2.67 ±0.67	-
Brussels Sprout	-	2.67 ±0.33	2.91 ±0.14	2.00 ±0.00	3.33 ±0.33	3.25 ±0.25	3.00 ±0.00
White Cabbage	-	2.26 ±0.10	2.57 ±0.20	3.20 ±0.37	3.00 ±0.00	*	*
Red Cabbage	2.00 ±0.00	2.14 ±0.14	3.50 ±0.50	-	-	*	*
Chinese Cabbage	2.00 ±0.00	2.35 ±0.11	2.50 ±0.50	*	*	*	*
Swede	2.33 ±0.33	2.13 ±0.09	-	*	*	*	*
Radish	2.00 ±0.00	3.00 ±0.00	3.00 ±0.00	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	4 30	2.59 12.96	0.65 0.43	1.50	ns
Brussels Sprout	Among groups Within groups					
White Cabbage	Among groups Within groups	3 40	4.35 14.45	1.45 0.36	4.01	0.05
Red Cabbage	Among groups Within groups	2 7	3.04 1.36	1.53 0.19	7.85	0.05
Chinese Cabbage	Among groups Within groups	2 24	0.58 5.05	0.29 0.21	1.38	ns
Swede	Among groups Within groups	1 17	0.11 2.42	0.11 0.14	0.77	ns
Radish	Among groups Within groups	2 1	1.00 0.00	0.50 0.00	-	-

Table C18: The effect of aphid population size on the size of egg laid by Melanostoma scalare

a)

Crop	Mean egg batch size laid at each aphid density (± SE)						
	1	2	3	4	5	6	7
Cauliflower	-	2.60 ±0.22	-	2.00 ±0.00	2.00 ±0.00	-	-
Brussels Sprout	-	2.33 ±0.17	2.73 ±0.20	3.00 ±1.00	3.00 ±0.41	2.00 ±0.00	-
White Cabbage	-	2.50 ±0.29	-	-	-	*	*
Red Cabbage	-	2.00 ±0.00	-	-	-	*	*
Chinese Cabbage	-	2.60 ±0.25	-	*	*	*	*
Swede	2.00 ±0.00	2.33 ±0.21	-	*	*	*	*
Radish	-	-	2.00 ±0.00	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	2 10	0.83 4.	0.42 0.	0.94	ns
Brussels Sprout	Among groups Within groups	4 22	2.11 10.18	0.53 0.46	1.14	ns
White Cabbage	Among groups Within groups	1 2	0.00 0.00	0.00 0.00	-	-
Red Cabbage	Among groups Within groups		0.00 0.00	0.00 0.00	-	
Chinese Cabbage	Among groups Within groups		0.00 0.00	0.00 0.00	-	
Swede	Among groups Within groups	1 5	0.10 1.33	0.10 0.27	0.36	ns
Radish	Among groups Within groups		0.00 0.00	0.00 0.00	-	

Table C19: The effect of aphid density on the number of eggs laid per aphid by Episyrphus balteatus

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0145 ±0.0052	0.0114 ±0.0060	0.0143 ±0.0033	0.0153 ±0.0041	0.0100 ±0.0058	0.0500 ±0.0010
Brussels Sprout	0.0133 ±0.0051	0.0186 ±0.0029	0.0192 ±0.0047	0.0142 ±0.0032	0.0117 ±0.0016	0.0076 ±0.0011
White Cabbage	0.0356 ±0.0110	0.0249 ±0.0107	0.0208 ±0.0062	0.0197 ±0.0043	*	*
Red Cabbage	0.0246 ±0.0059	0.0146 ±0.0043	0.0062 ±0.0030	0.0050 ±0.0050	*	*
Chinese Cabbage	0.095 ±0.044	0.016 ±0.008	*	*	*	*
Swede	0.106 ±0.0562	0.029 ±0.000	*	*	*	*
Radish	0.0279 ±0.0019	0.0178 ±0.0066	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.00029 0.12703	0.00006 0.00138	0.04	ns
Brussels Sprout	Among groups Within groups	5 94	0.00150 0.01888	0.00030 0.00020	1.40	ns
White Cabbage	Among groups Within groups	3 87	0.00268 0.59865	0.00089 0.00688	00.1	ns
Red Cabbage	Among groups Within groups	3 91	0.00347 0.15327	0.00114 0.00168	0.68	ns
Chinese Cabbage	Among groups Within groups	1 34	0.0418 1.3703	0.0418 0.0403	1.04	ns
Swede	Among groups Within groups	1 51	0.0060 8.3770	0.0060 0.1640	0.04	ns
Radish	Among groups Within groups	1 15	0.0004 0.0415	0.0004 0.0028	0.14	ns

Table C20: The effect of aphid density on the number of eggs laid per aphid by Sphaerophoria scripta

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0062 ±0.0020	0.0141 ±0.0058	0.0148 ±0.0035	0.0113 ±0.0033	0.0070 ±0.0006	0.0035 ±0.0005
Brussels Sprout	0.0233 ±0.0077	0.0149 ±0.0032	0.0188 ±0.0042	0.0138 ±0.0037	0.0087 ±0.0017	0.0039 ±0.0009
White Cabbage	0.023 ±0.0147	0.007 ±0.0038	0.015 ±0.0045	0.012 ±0.0058	*	*
Red Cabbage	0.017 ±0.0015	0.0064 ±0.0033	0.0062 ±0.0045	-	*	*
Chinese Cabbage	0.040 ±0.0264	0.016 ±0.0073	*	*	*	*
Swede	0.0192 ±0.0076	-	*	*	*	*
Radish	-	0.0083 ±0.0063	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups	5	0.00112	0.00023	0.95	ns
	Within groups	92	0.02186	0.00024		
Brussels Sprout	Among groups	5	0.00299	0.00060	2.22	ns
	Within groups	94	0.02530	0.00027		
White Cabbage	Among groups	3	0.0028	0.0009	0.08	ns
	Within groups	87	1.0456	0.0120		
Red Cabbage	Among groups	3	0.00076	0.00025	0.08	ns
	Within groups	91	0.28893	0.00318		
Chinese Cabbage	Among groups	1	0.0038	0.0038	0.26	ns
	Within groups	34	0.4954	0.0146		
Swede	Among groups	1	0.00036	0.00036	0.12	ns
	Within groups	51	0.15399	0.00302		
Radish	Among groups	1	0.00027	0.00027	3.45	ns
	Within groups	15	0.00117	0.00008		

Table C21: The effect of aphid density on the number of eggs laid per per aphid by Syrphus ribesii

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0060 ±0.0047	0.0109 ±0.0040	0.0128 ±0.0021	0.0090 ±0.0027	0.0053 ±0.0027	0.0035 ±0.0005
Brussels Sprout	-	0.00208 ±0.0009	0.0152 ±0.0043	0.0125 ±0.0032	0.0065 ±0.0012	0.0047 ±0.0013
White Cabbage	0.0076 ±0.0027	-	0.0067 ±0.0036	0.0067 ±0.0040	*	*
Red Cabbage	-	0.0026 ±0.0017	-	-	*	*
Chinese Cabbage	0.0026 ±0.0026	0.0110 ±0.0041	*	*	*	*
Swede	0.0013 ±0.0013	-	*	*	*	*
Radish	-	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.00059 0.10053	0.00012 0.00109	0.11	ns
Brussels Sprout	Among groups Within groups	5 94	0.00251 0.00536	0.00050 0.00006	8.82	0.001
White Cabbage	Among groups Within groups	3 87	0.00059 0.03703	0.00020 0.00043	0.46	ns
Red Cabbage	Among groups Within groups	3 91	0.00011 0.00141	0.00004 0.00002	2.47	ns
Chinese Cabbage	Among groups Within groups	1 34	0.00048 0.00582	0.00048 0.00017	2.81	ns
Swede	Among groups Within groups	1 51	0.000002 0.004403	0.000002 0.000086	0.02	ns
Radish	Among groups Within groups	-	-	-	-	-

Table C22: The effect of aphid density on the number of eggs laid per aphid by Metasyrphus luniger

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	-	-	0.0010 ±0.0007	0.0019 ±0.0009	0.0050 ±0.0021	0.0035 ±0.0005
Brussels Sprout	-	-	-	-	0.0009 ±0.0005	0.0013 ±0.0004
White Cabbage	-	-	0.0027 ±0.0027	0.0010 ±0.0010	*	*
Red Cabbage	-	0.0016 ±0.0011	0.0022 ±0.0022	0.0065 ±0.0065	*	*
Chinese Cabbage	-	-	*	*	*	*
Swede	-	-	*	*	*	*
Radish	-	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.000113 0.000111	0.000023 0.000001	18.68	0.001
Brussels Sprout	Among groups Within groups	5 94	0.000023 0.000086	0.0000046 0.0000009	5.04	0.001
White Cabbage	Among groups Within groups	3 87	0.000042 0.000219	0.000014 0.000003	5.51	0.01
Red Cabbage	Among groups Within groups	3 91	0.000127 0.000775	0.000042 0.000009	4.98	0.01
Chinese Cabbage	Among groups Within groups	-	-	-	-	-
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	-	-	-	-	-

Table C23: The effect of aphid density on the number of eggs laid per aphid by Metasyrphus corollae

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	-	-	-	-	0.0003 ±0.0003	0.0010 ±0.0010
Brussels Sprout	-	-	-	-	0.0002 ±0.0002	0.0005 ±0.0003
White Cabbage	-	-	0.0013 ±0.0013	-	*	*
Red Cabbage	-	0.00078 ±0.0008	0.0018 ±0.0018	0.0045 ±0.0045	*	*
Chinese Cabbage	-	-	*	*	*	*
Swede	-	-	*	*	*	*
Radish	-	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.000002 0.000003	0.0000004 0.0000000	15.47	0.001
Brussels Sprout	Among groups Within groups	5 94	0.000003 0.000024	0.000001 0.000000	2.49	0.05
White Cabbage	Among groups Within groups	3 87	0.000010 0.000053	0.0000033 0.0000006	5.42	0.01
Red Cabbage	Among groups Within groups	3 91	0.000057 0.000415	0.0000191 0.0000046	4.17	0.05
Chinese Cabbage	Among groups Within groups	-	-	-	-	-
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	-	-	-	-	-

Table C24: The effect of aphid density on the number of eggs laid per aphid by Platycheirus manicatus

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0304 ±0.0075	0.0249 ±0.0070	0.0065 ±0.0024	-	-	-
Brussels Sprout	0.0312 ±0.0097	0.0229 ±0.0051	0.0061 ±0.0022	0.0023 ±0.0013	-	-
White Cabbage	0.0690 ±0.0194	0.0060 ±0.0058	-	-	*	*
Red Cabbage	0.0243 ±0.0073	-	-	-	*	*
Chinese Cabbage	0.068 ±0.0371	-	*	*	*	*
Swede	0.0009 ±0.0009	-	*	*	*	*
Radish	0.0057 ±0.0057	0.0018 ±0.0018	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.0131 0.2577	0.0026 0.0028	0.93	ns
Brussels Sprout	Among groups Within groups	5 94	0.0143 0.0437	0.0029 0.0005	6.16	0.001
White Cabbage	Among groups Within groups	3 87	0.0708 1.8106	0.0236 0.0208	1.13	ns
Red Cabbage	Among groups Within groups	3 91	0.0121 0.2190	0.0040 0.0024	1.68	ns
Chinese Cabbage	Among groups Within groups	1 34	0.0308 0.9639	0.0308 0.0283	1.09	ns
Swede	Among groups Within groups	1 51	0.0000007 0.0019861	0.0000007 0.0000389	0.02	ns
Radish	Among groups Within groups	1 15	0.000059 0.003709	0.000059 0.000247	0.24	ns

Table C25: The effect of aphid density on the number of eggs laid per aphid by Platycheirus albimanus

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0090 ±0.0035	0.0210 ±0.0118	0.0179 ±0.0057	0.0024 ±0.0013	-	-
Brussels Sprout	0.0148 ±0.0068	0.0080 ±0.0022	0.0074 ±0.0028	0.0058 ±0.0019	0.0058 ±0.0012	0.0014 ±0.0006
White Cabbage	0.0360 ±0.0016	0.0040 ±0.0040	0.0010 ±0.0012	-	*	*
Red Cabbage	0.0007 ±0.0007	-	0.0044 ±0.0031	-	*	*
Chinese Cabbage	0.0032 ±0.0024	0.0049 ±0.0032	*	*	*	*
Swede	0.0022 ±0.0018	-	*	*	*	*
Radish	0.0288 ±0.0023	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.002500 0.064463	0.000500 0.000701	0.71	ns
Brussels Sprout	Among groups Within groups	5 94	0.001154 0.014239	0.000231 0.000151	1.52	ns
White Cabbage	Among groups Within groups	3 87	0.0183 1.3017	0.0061 0.0150	0.41	ns
Red Cabbage	Among groups Within groups	3 91	0.0000808 0.0020158	0.0000269 0.0000222	1.22	ns
Chinese Cabbage	Among groups Within groups	1 34	0.000020 0.004691	0.000020 0.000138	0.14	ns
Swede	Among groups Within groups	1 51	0.000005 0.008647	0.000005 0.000170	0.03	ns
Radish	Among groups Within groups	1 15	0.00322 0.05785	0.00322 0.00386	0.84	ns

Table C26: The effect of aphid density on the number of eggs laid per aphid by Platycheirus scutatus

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0016 ±0.0010	0.0066 ±0.0048	-	0.0031 ±0.0024	-	-
Brussels Sprout	0.0058 ±0.0058	0.0028 ±0.0012	0.0055 ±0.0028	0.0039 ±0.0014	0.0011 ±0.0005	-
White Cabbage	0.0019 ±0.0012	0.0032 ±0.0033	0.0040 ±0.0040	-	*	*
Red Cabbage	-	-	-	-	*	*
Chinese Cabbage		0.0016 ±0.0016	*	*	*	*
Swede	0.0019 ±0.0014	-	*	*	*	*
Radish	0.0061 ±0.0061	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.000226 0.005347	0.000045 0.000058	0.78	ns
Brussels Sprout	Among groups Within groups	5 94	0.000341 0.007614	0.000068 0.000081	0.84	ns
White Cabbage	Among groups Within groups	3 87	0.000055 0.008776	0.000018 0.000101	0.18	ns
Red Cabbage	Among groups Within groups	-	-	-	-	-
Chinese Cabbage	Among groups Within groups	1 34	0.000016 0.000174	0.000016 0.000005	3.19	ns
Swede	Among groups Within groups	1 51	0.000004 0.004965	0.000004 0.000097	0.04	ns
Radish	Among groups Within groups	1 15	0.000144 0.004081	0.000144 0.000272	0.53	ns

Table C27: The effect of aphid density on the number of eggs laid per aphid by Platycheirus peltatus

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.097 ±0.0207	0.012 ±0.0083	0.004 ±0.0027	0.008 ±0.0045		
Brussels Sprout	0.155 ±0.0866	0.016 ±0.0049	0.026 ±0.0067	0.007 ±0.0026	0.001 ±0.0009	0.001 ±0.0003
White Cabbage	0.049 ±0.0143	0.050 ±0.0188	0.010 ±0.0049	0.003 ±0.0029	*	*
Red Cabbage	0.008 ±0.0045	0.006 ±0.0043	*	*	*	*
Chinese Cabbage	0.011 ±0.0094	0.023 ±0.0093	*	*	*	*
Swede	0.098 ±0.0279	0.043 ±0.000	*	*	*	*
Radish	0.062 ±0.0324	0.008 ±0.0051	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.1721 1.9411	0.0344 0.0211	1.63	ns
Brussels Sprout	Among groups Within groups	5 94	0.2228 1.0268	0.0446 0.0109	4.08	0.01
White Cabbage	Among groups Within groups	3 87	0.0137 1.0401	0.0046 0.0120	0.38	ns
Red Cabbage	Among groups Within groups	3 91	0.0005 0.0924	0.0002 0.0010	0.17	ns
Chinese Cabbage	Among groups Within groups	1 34	0.0010 0.0683	0.0010 0.0020	0.50	ns
Swede	Among groups Within groups	1 51	0.0029 2.0583	0.0029 0.0404	0.07	ns
Radish	Among groups Within groups	1 15	0.0111 0.1166	0.0111 0.0078	1.43	ns

Table C28: The effect of aphid density on the number of eggs laid per aphid by Platycheirus clypeatus

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0121 ±0.0076	-	0.028 ±0.0008	-	-	-
Brussels Sprout	0.0328 ±0.0197	0.0141 ±0.0046	0.0259 ±0.0067	0.0022 ±0.0012	0.0006 ±0.0004	0.0003 ±0.0003
White Cabbage	0.0460 ±0.0214	0.0170 ±0.0092	0.0030 ±0.0029	-	*	*
Red Cabbage	0.0022 ±0.0022	-	-	-	*	*
Chinese Cabbage	0.0134 ±0.0077	0.0073 ±0.0073	*	*	*	*
Swede	-	-	*	*	*	*
Radish	0.1210 ±0.1212	-	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.0026 0.2654	0.0005 0.0029	0.18	ns
Brussels Sprout	Among groups Within groups	5 94	0.0127 0.0823	0.0025 0.0009	2.90	0.05
White Cabbage	Among groups Within groups	3 87	0.0211 2.2300	0.0070 0.0256	0.27	ns
Red Cabbage	Among groups Within groups	3 91	0.0001 0.0201	0.00003 0.00022	0.15	ns
Chinese Cabbage	Among groups Within groups	1 34	0.0003 0.0451	0.0003 0.0013	0.19	ns
Swede	Among groups Within groups	-	-	-	-	-
Radish	Among groups Within groups	1 15	0.0570 1.6150	0.0570 0.1080	0.53	ns

Table C29: The effect of aphid density on the number of eggs laid per aphid by Melanostoma mellinum

a)

Crop	Mean number of eggs per aphid at each aphid density (± SE)					
	2	3	4	5	6	7
Cauliflower	0.0583 ±0.0128		0.0097 ±0.0040	0.0037 ±0.0028	0.0053 ±0.0027	-
Brussels Sprout	0.0317 ±0.0212	0.0298 ±0.0066	0.0037 ±0.0026	0.0039 ±0.0017	0.0012 ±0.0006	0.0003 ±0.0003
White Cabbage	0.071 ±0.0241	0.022 ±0.0084	0.016 ±0.0098	0.003 ±0.0029	*	*
Red Cabbage	0.0127 ±0.0050	0.0054 ±0.0034	-	-	*	*
Chinese Cabbage	0.0760 ±0.0252	0.0070 ±0.0043	*	*	*	*
Swede	0.1950 ±0.0845	-	*	*	*	*
Radish	0.0062 ±0.0062	0.0082 ±0.0082	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.0565 0.7[illegible]77	0.0113 0.0081	1.39	ns
Brussels Sprout	Among groups Within groups	5 94	0.0198 0.1129	0.0040 0.0012	3.29	0.01
White Cabbage	Among groups Within groups	3 87	0.0479 2.8293	0.0160 0.0325	0.49	ns
Red Cabbage	Among groups Within groups	3 91	0.0017 0.1081	0.0006 0.0012	0.47	ns
Chinese Cabbage	Among groups Within groups	1 34	0.0325 0.4499	0.0325 0.0132	2.45	0.05
Swede	Among groups Within groups	1 51	0.0370 18.8840	0.0370 0.3700	0.10	ns
Radish	Among groups Within groups	1 15	0.00002 0.00620	0.00002 0.00041	0.04	ns

Table C30: The effect of aphid density on the number of eggs laid per aphid by Melanostoma scalare

a)

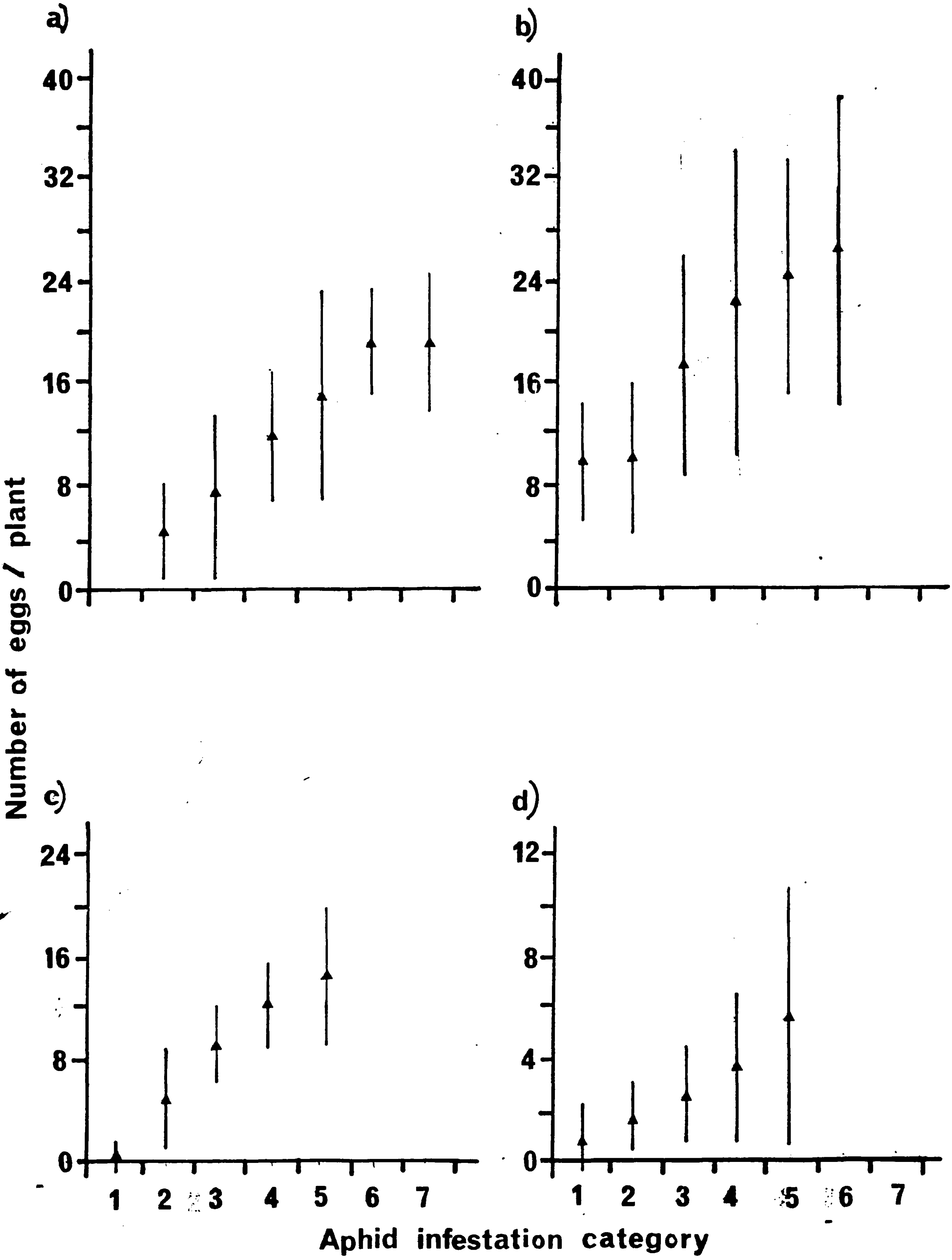
Crop	Mean number of eggs per aphid at each aphid density (SE)					
	2	3	4	5	6	7
Cauliflower	0.0291 ±0.0109	-	0.0013 ±0.0013	0.0026 ±0.0017	-	-
Brussels Sprout	0.158 ±0.1233	0.011 ±0.0041	0.003 ±0.0020	0.003 ±0.0014	-	-
White Cabbage	0.0121 ±0.0078	-	-	-	*	*
Red Cabbage	0.0020 ±0.0020	-	-	-	*	*
Chinese Cabbage	0.0309 ±0.0183	-	*	*	*	*
Swede	0.054 ±0.0039	-	*	*	*	*
Radish	-	0.0045 ±0.0045	*	*	*	*

b) Anova Table

Crop	Source of variation	df	SS	MS	F-ratio	P
Cauliflower	Among groups Within groups	5 92	0.01641 0.53897	0.00328 0.00586	0.56	ns
Brussels Sprout	Among groups Within groups	5 94	0.2472 2.0272	0.0404 0.0216	2.29	ns
White Cabbage	Among groups Within groups	3 87	0.0024 0.2953	0.0008 0.0034	0.23	ns
Red Cabbage	Among groups Within groups	3 91	0.00009 0.01742	0.00003 0.00019	0.15	ns
Chinese Cabbage	Among groups Within groups	1 34	0.0065 0.2340	0.0065 0.0069	0.94	ns
Swede	Among groups Within groups	1 51	0.0029 4.0409	0.0029 0.0792	0.04	ns
Radish	Among groups Within groups	1 15	0.000079 0.000608	0.000079 0.000041	1.94	ns

Figure C1 a-g: The relationship between aphid population size and the total number of syrphid eggs laid per plant in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
b)
c)
d)
Number of eggs / plant
0
8
16
24
32
40
0
8
16
24
32
40
0
8
16
24
0
4
8
12
1
2
3
4
5
6
7
1
2
3
4
5
6
7
Aphid infestation category

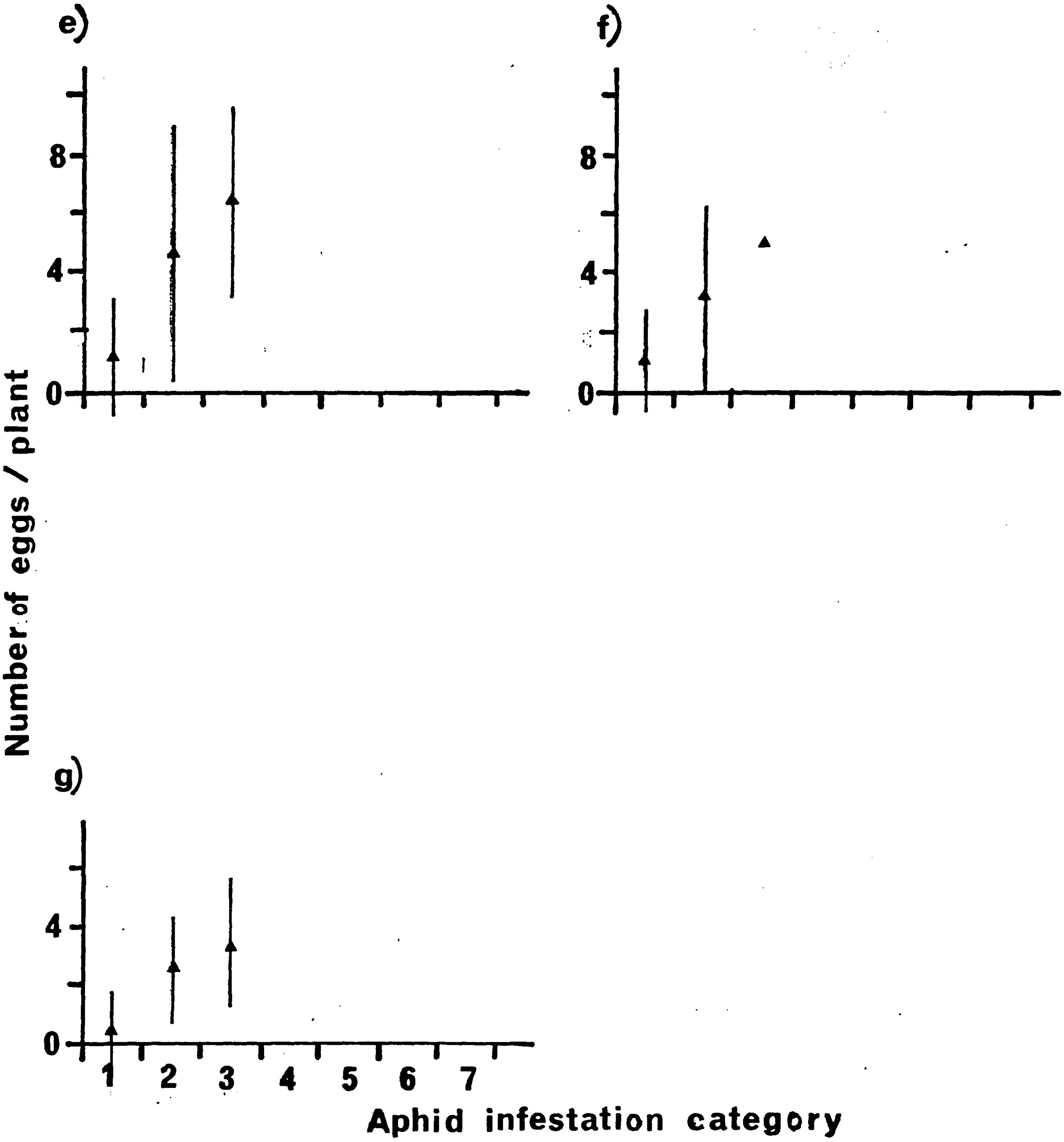
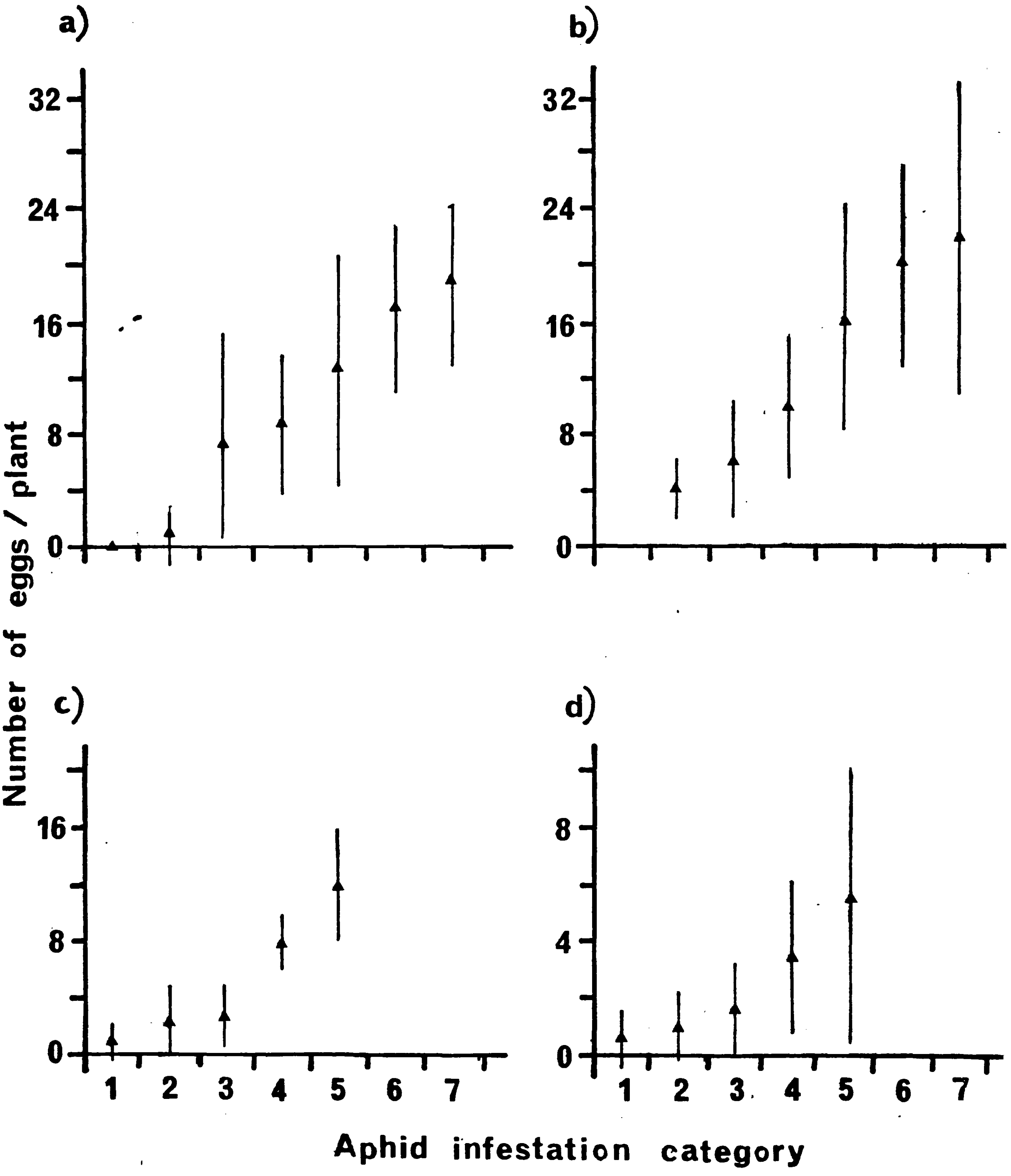

e)
f)
g)
Number of eggs / plant
0
4
8
0
4
8
0
4
1
2
3
4
5
6
7
Aphid infestation category

Figure C2 a-g: The relationship between aphid population size and the number of single syrphid eggs laid per plant in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
b)
c)
d)
32
24
16
8
0
32
24
16
8
0
16
8
0
8
4
0
Number of eggs / plant
1
2
3
4
5
6
7
1
2
3
4
5
6
7
Aphid infestation category

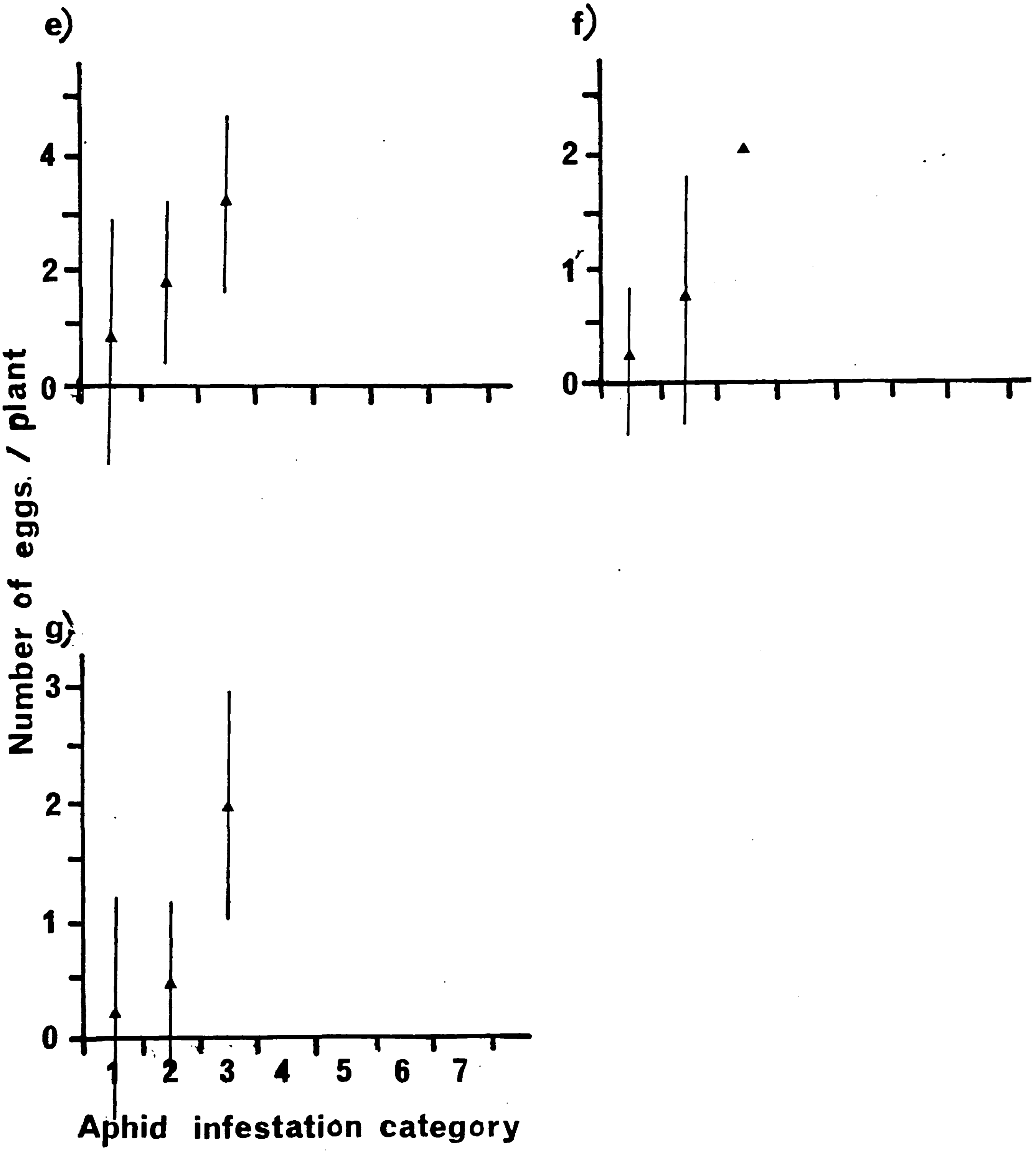
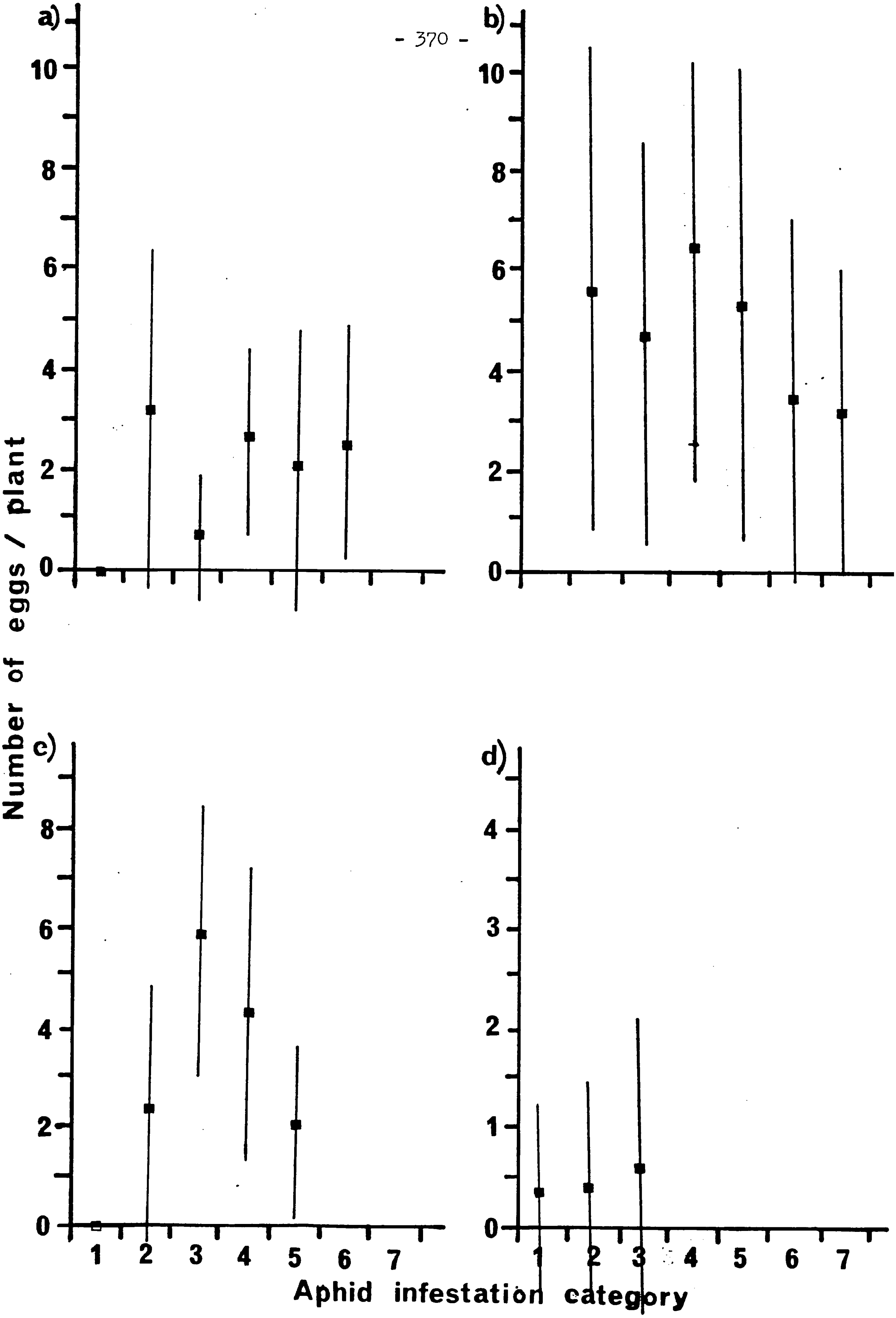

e)
f)
g)
Number of eggs / plant
0
2
4
0
1
2
0
1
2
3
1
2
3
4
5
6
7
Aphid infestation category

Figure C3 a-g: The relationship between aphid population size and the number of batched syrphid eggs laid per plant in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
b)
c)
d)
0
2
4
6
8
10
0
1
2
3
4
Number of eggs / plant
1
2
3
4
5
6
7
Aphid infestation category

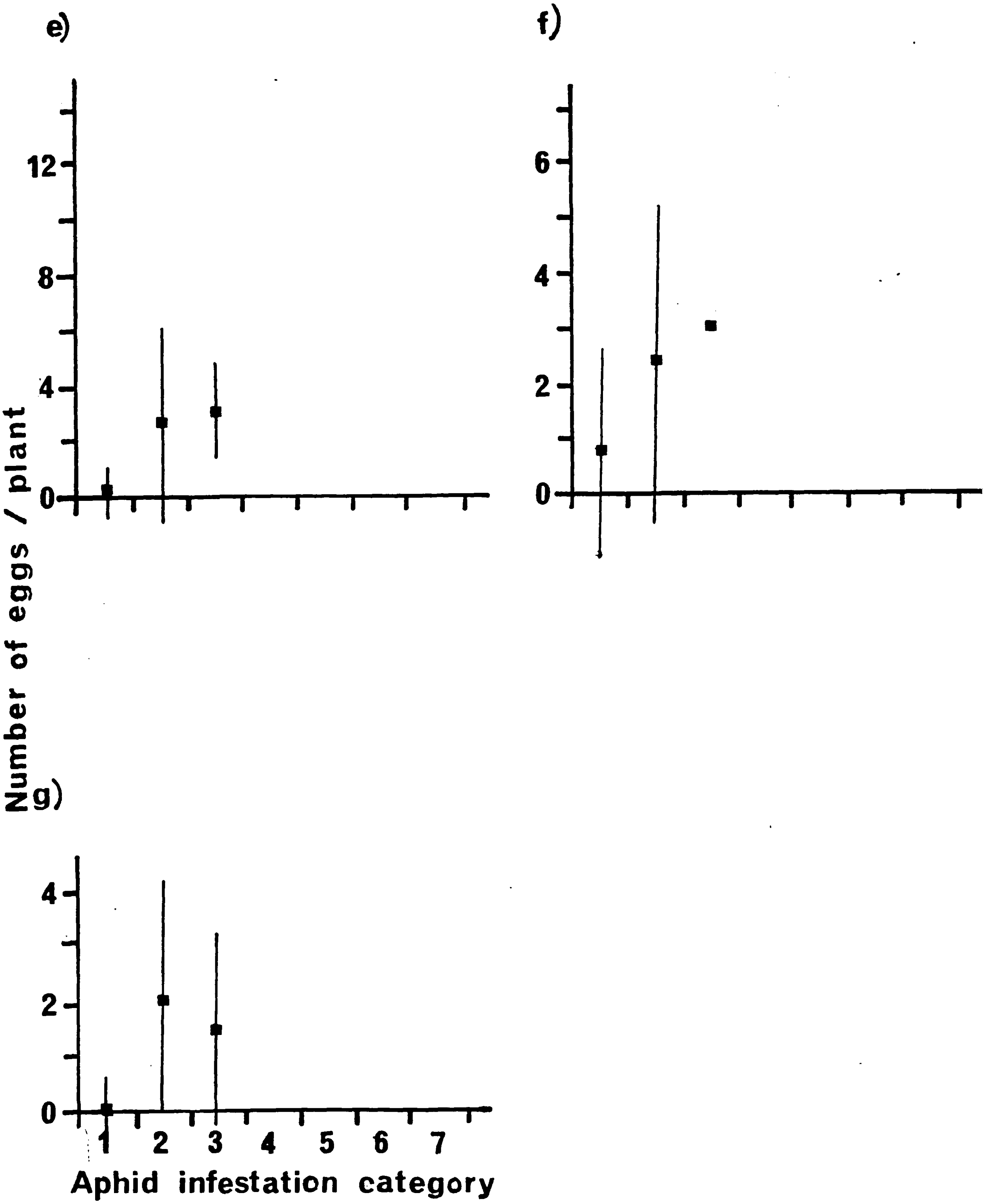
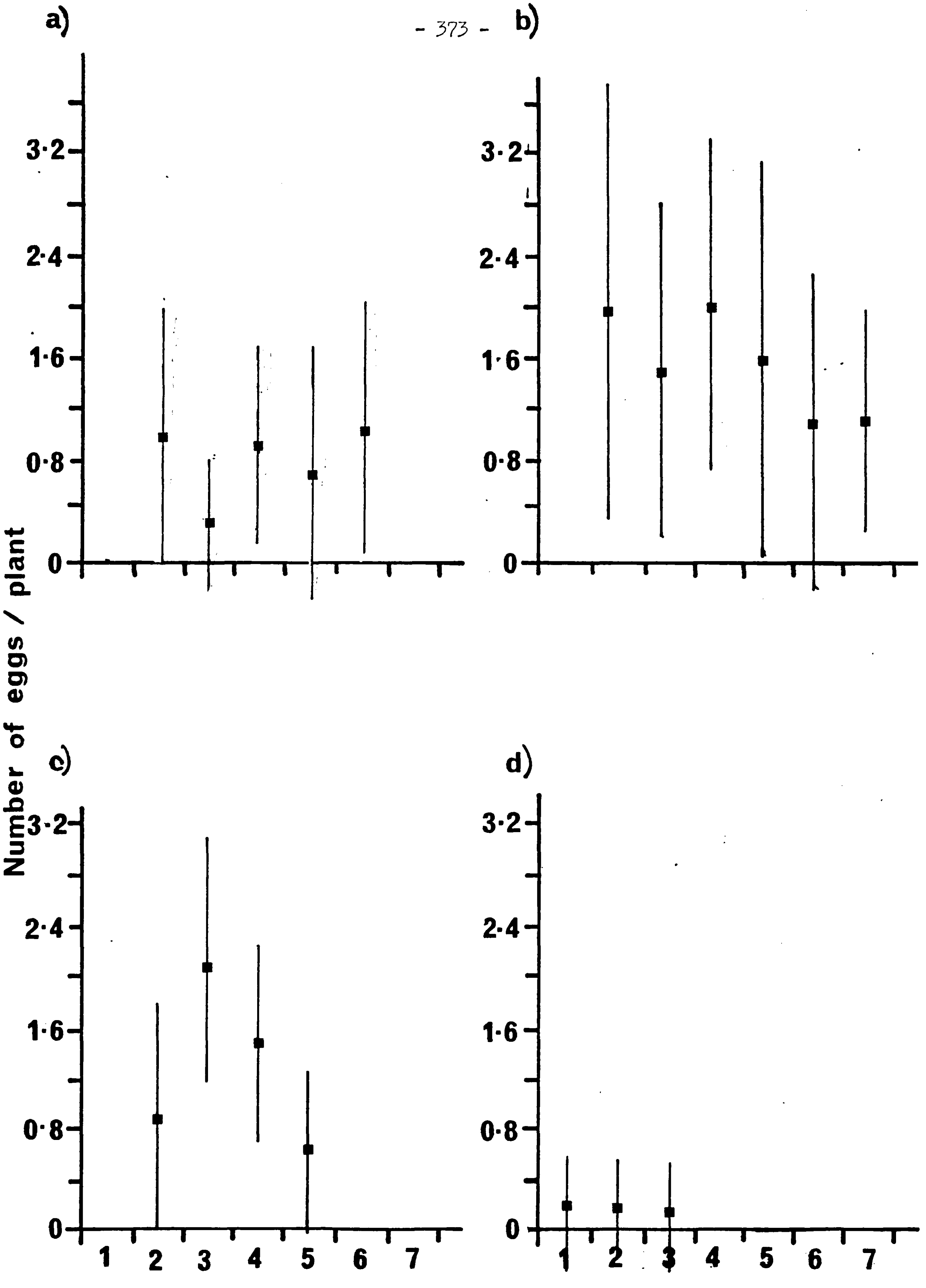

e)
f)
g)
Number of eggs / plant
12
8
4
0
6
4
2
0
4
2
0
1
2
3
4
5
6
7
Aphid infestation category

Figure C4 a-g: <u>The relationship between aphid population size and the number of egg batches per plant in</u>

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
b)
c)
d)
Number of eggs / plant
0
0·8
1·6
2·4
3·2
1
2
3
4
5
6
7
Aphid infestation category

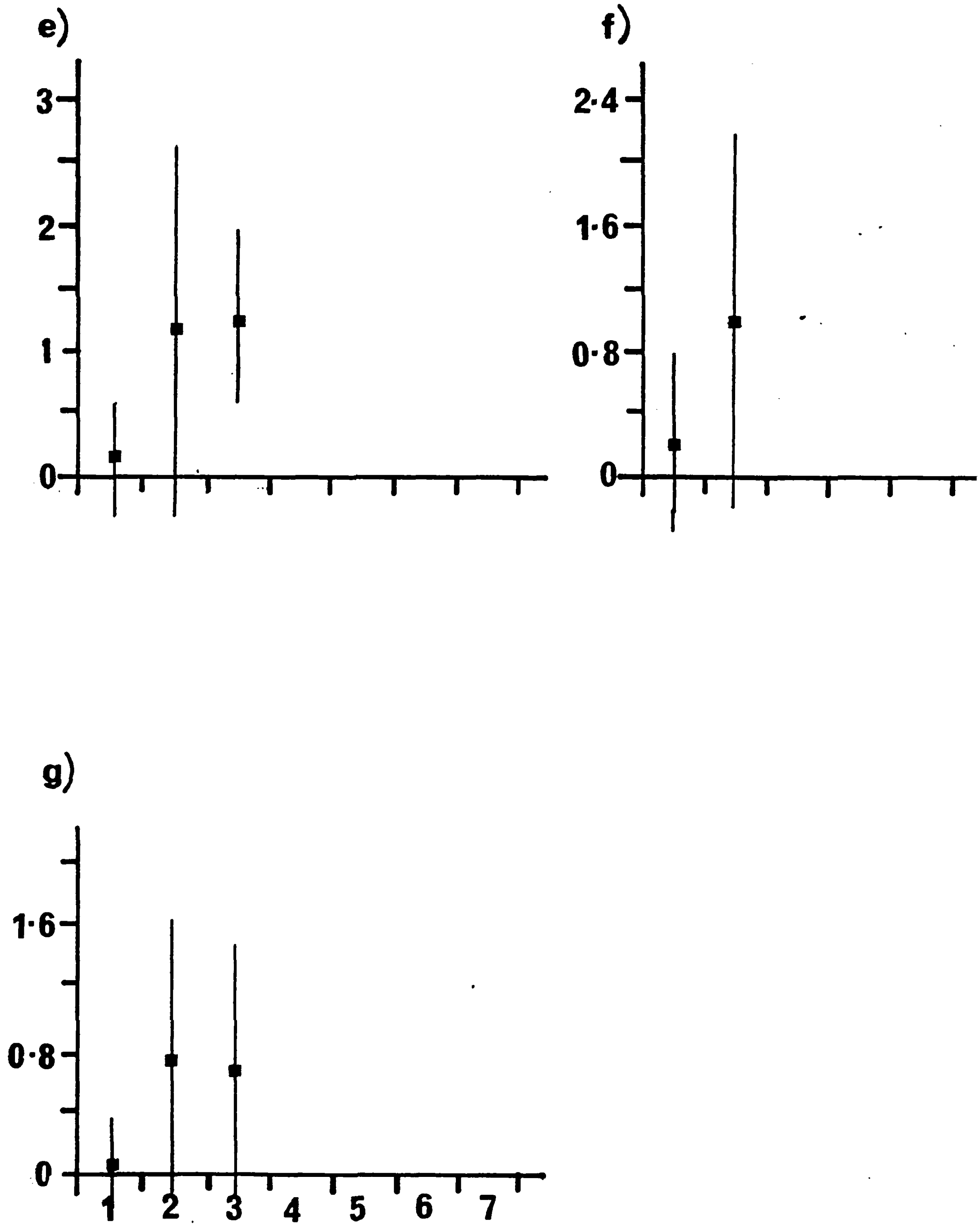
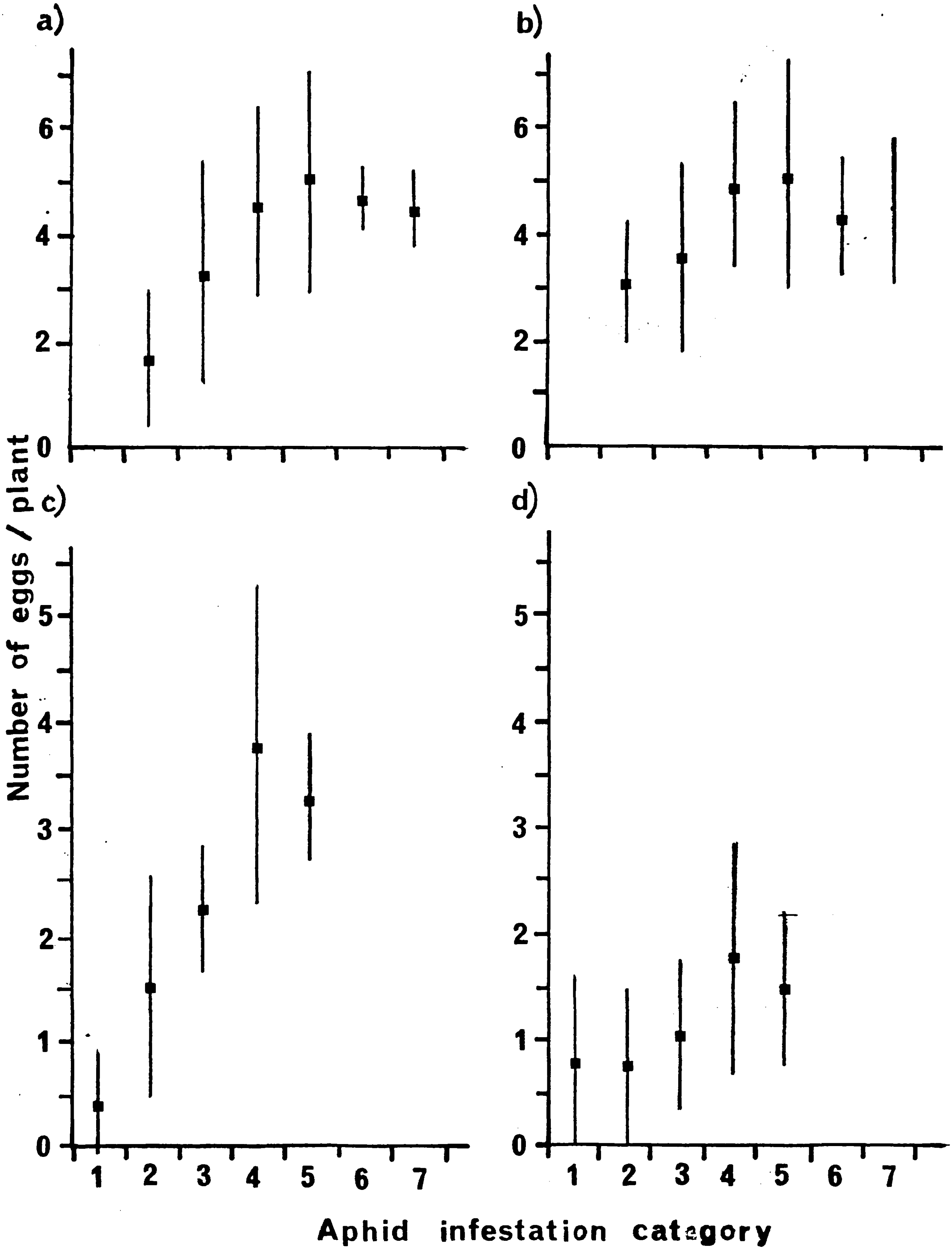

e)
3
2
1
0
f)
2·4
1·6
0·8
0
g)
1·6
0·8
0
1
2
3
4
5
6
7

Figure C5 a-g: The relationship between aphid population size and the number of syrphid species ovipositing per plant in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
b)
c)
d)
Number of eggs / plant
0
2
4
6
0
2
4
6
0
1
2
3
4
5
0
1
2
3
4
5
1
2
3
4
5
6
7
1
2
3
4
5
6
7
Aphid infestation category

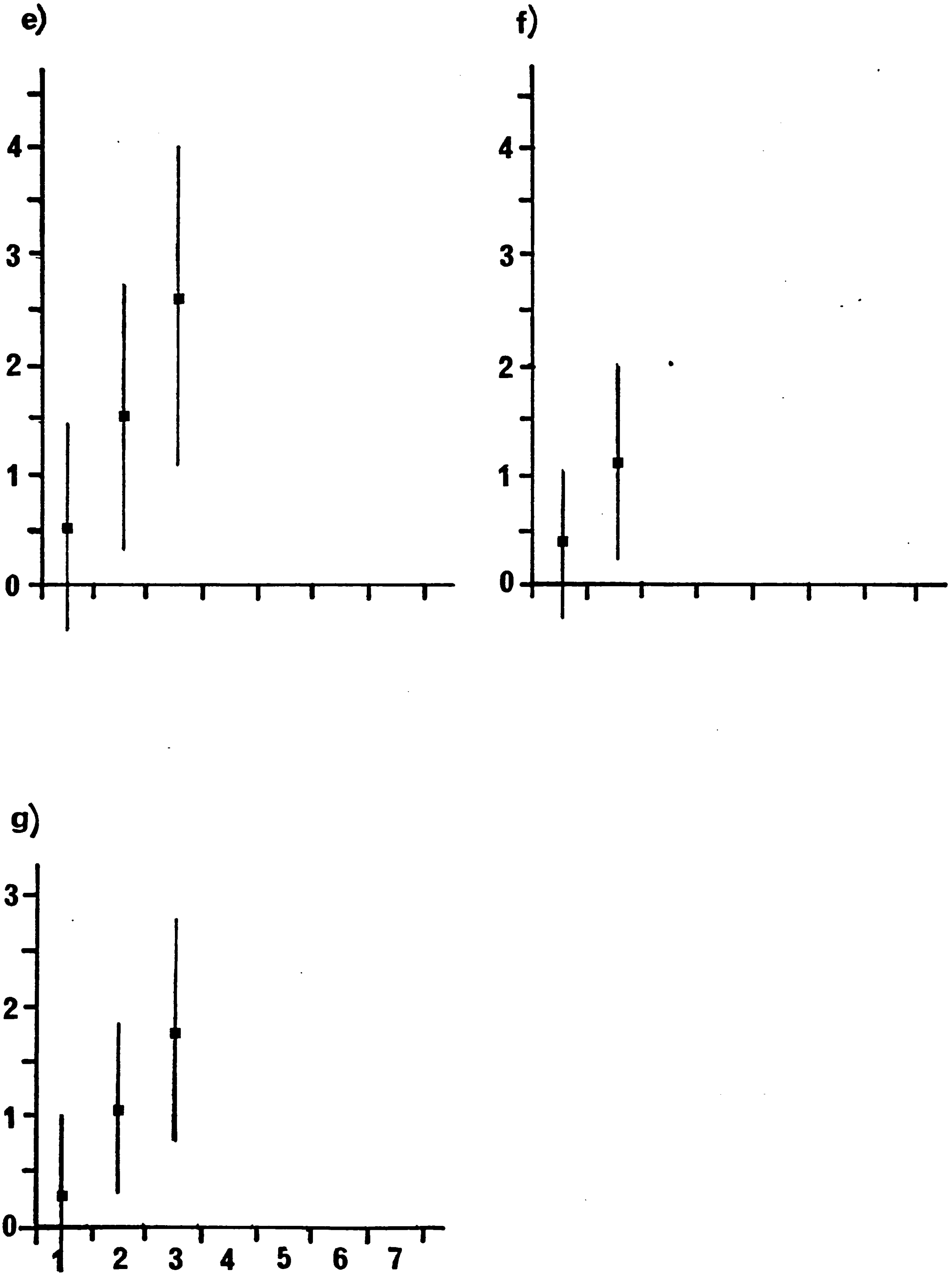
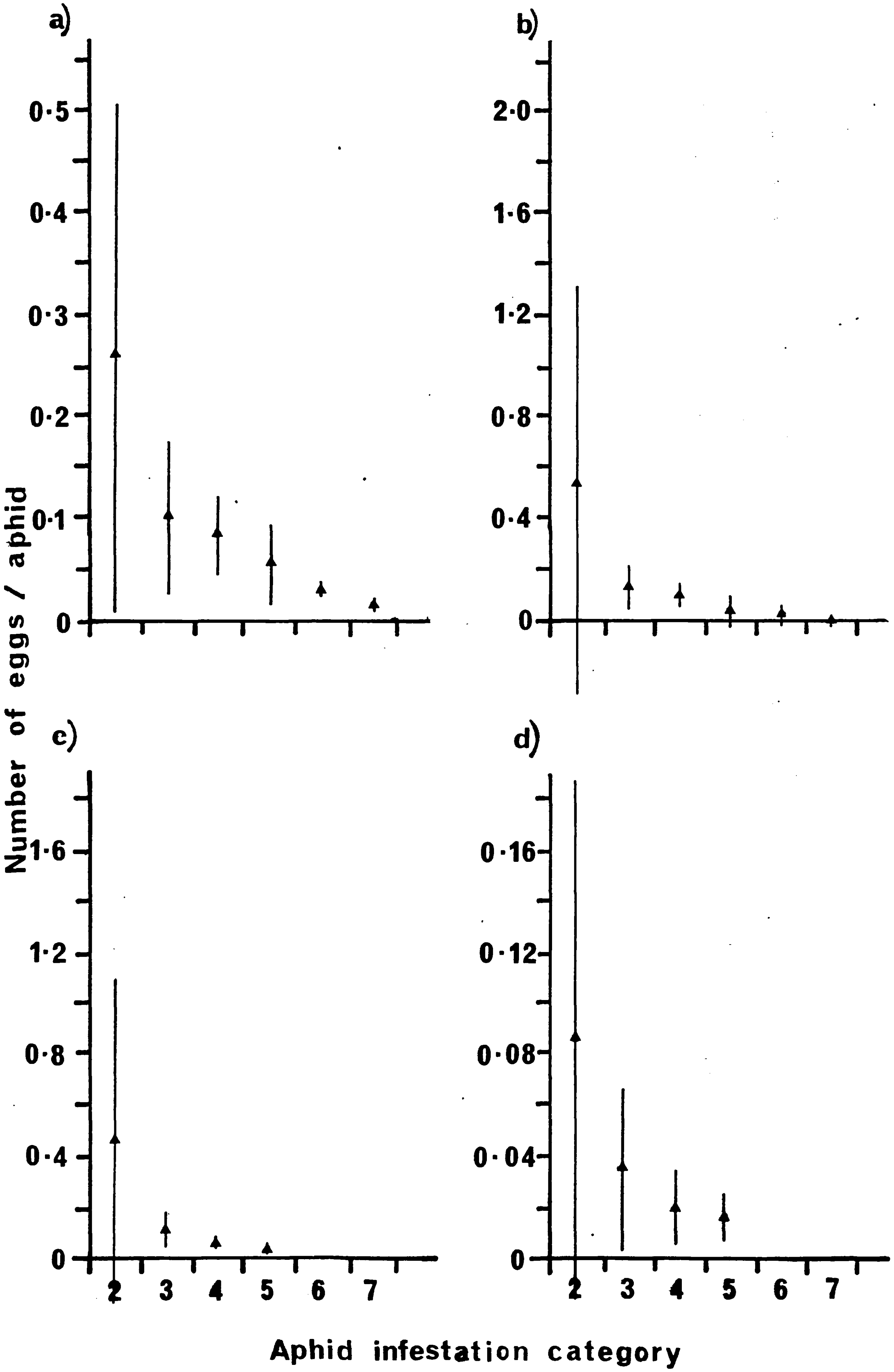

e)
4
3
2
1
0
f)
4
3
2
1
0
g)
3
2
1
0
1
2
3
4
5
6
7

Figure C6 a-g: The relationship between aphid population size and the total number of syrphid eggs laid per aphid in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
b)
c)
d)
0·5
0·4
0·3
0·2
0·1
0
2·0
1·6
1·2
0·8
0·4
0
1·6
1·2
0·8
0·4
0
0·16
0·12
0·08
0·04
0
Number of eggs / aphid
2
3
4
5
6
7
Aphid infestation category

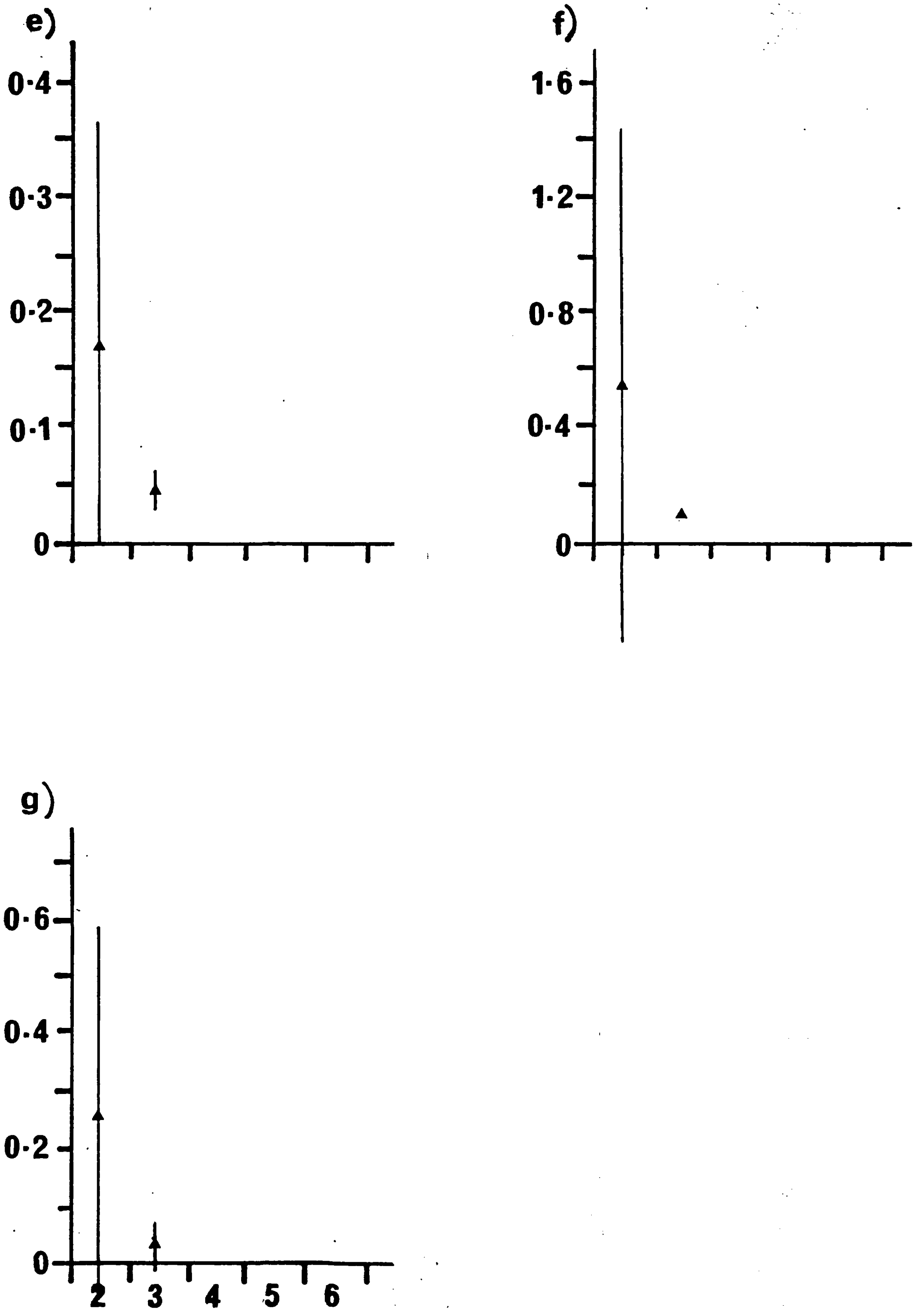
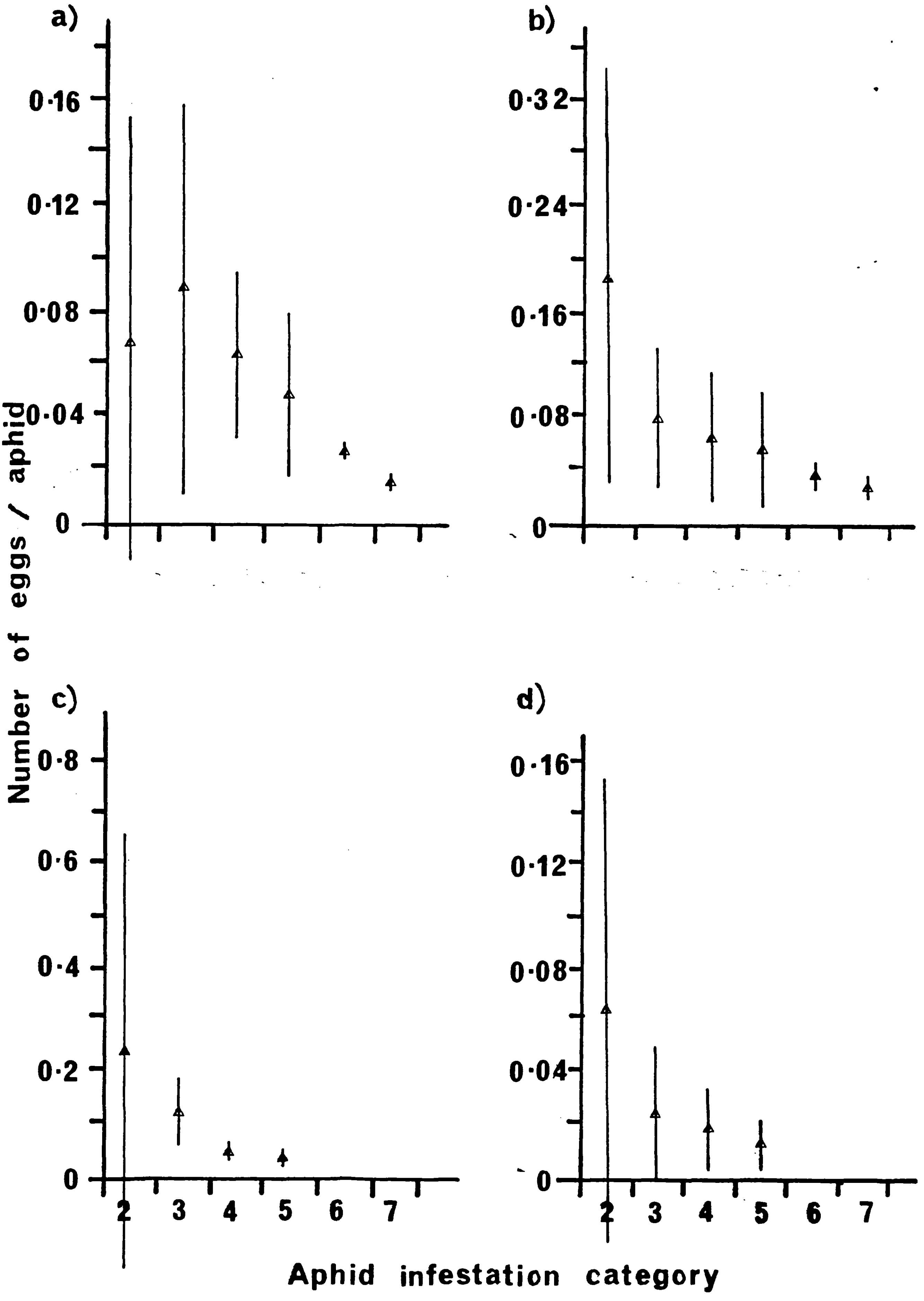
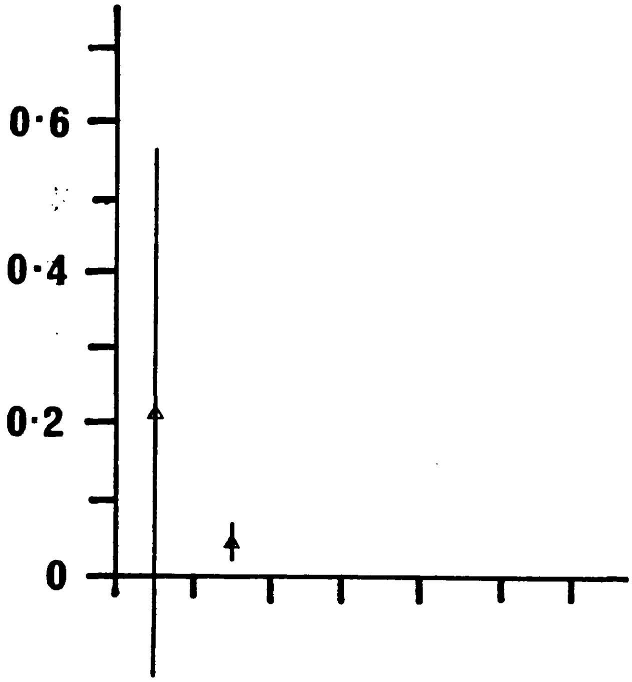

e)
0·4
0·3
0·2
0·1
0
f)
1·6
1·2
0·8
0·4
0
g)
0·6
0·4
0·2
0
2
3
4
5
6

Figure C7 a-g: The relationship between aphid population size and the number of single syrphid eggs laid per aphid in

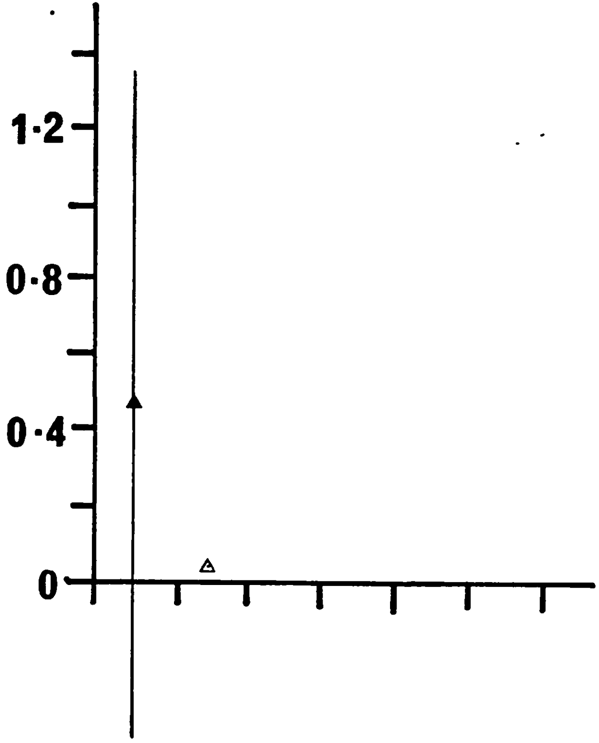
- a) cauliflower
- b) Brussels sprout
- c) white cabbage
- d) red cabbage
- e) Chinese cabbage
- f) swede
- g) radish


a)
0·16
0·12
0·08
0·04
0
b)
0·32
0·24
0·16
0·08
0
c)
0·8
0·6
0·4
0·2
0
d)
0·16
0·12
0·08
0·04
0
2
3
4
5
6
7
2
3
4
5
6
7
Number of eggs / aphid
Aphid infestation category

e)



f)



g)

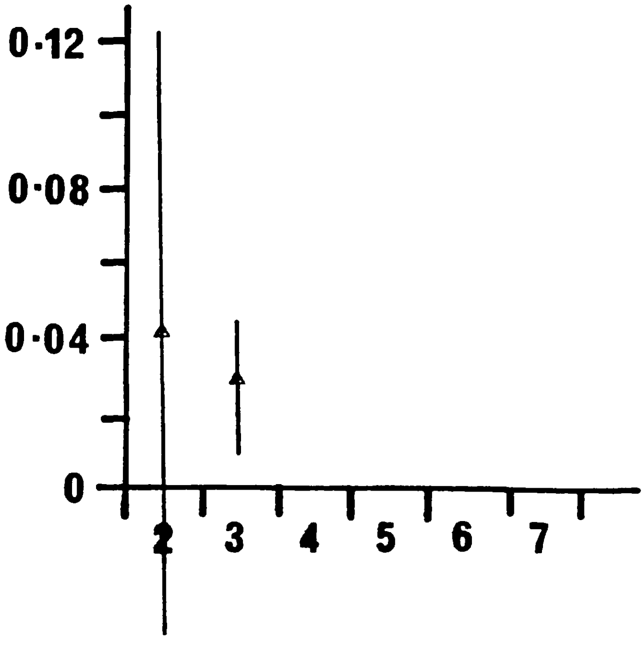
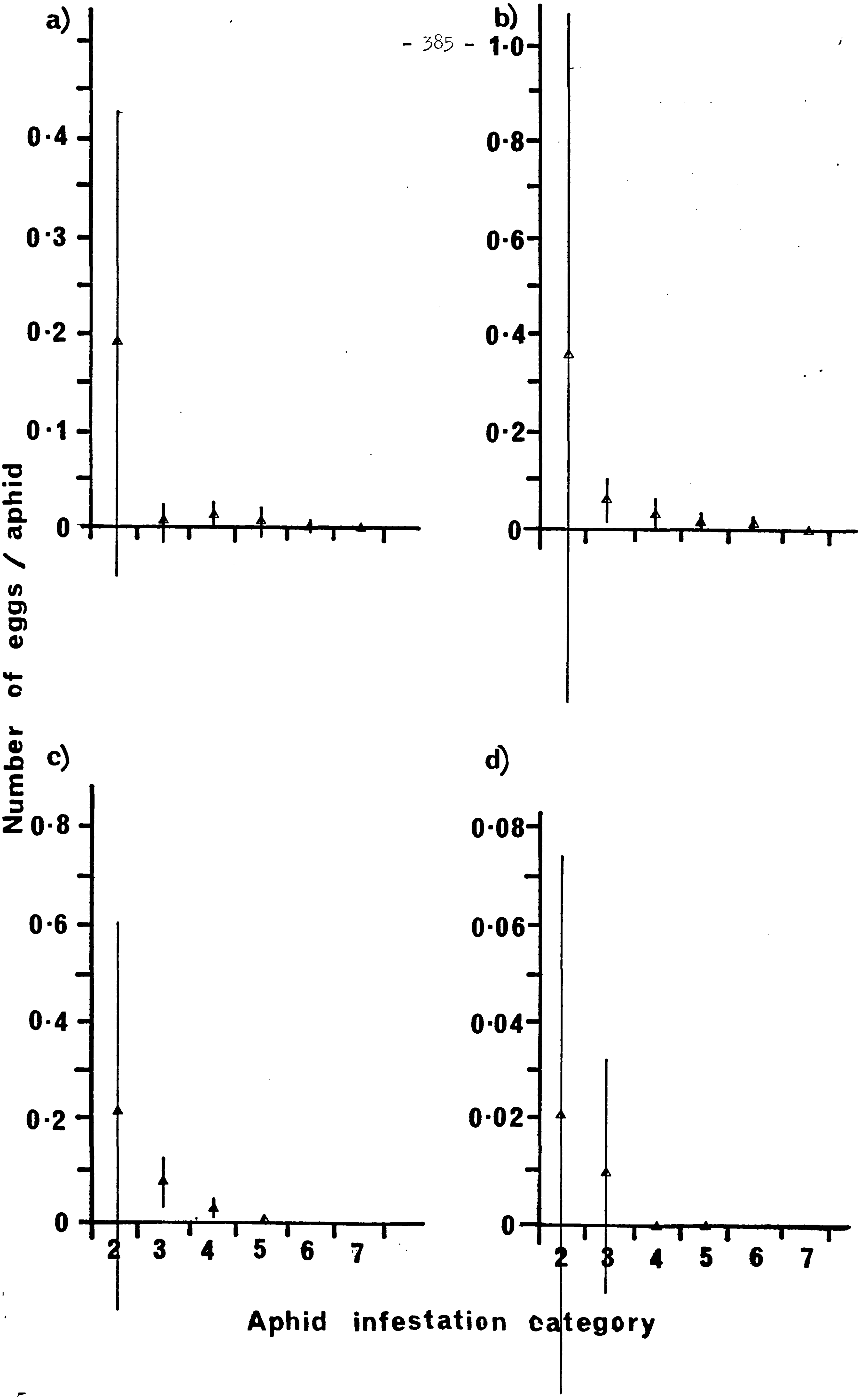


Figure C8 a-g: The relationship between aphid population size and the number of batched syrphid eggs laid per aphid in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
0·4
0·3
0·2
0·1
0
b)
1·0
0·8
0·6
0·4
0·2
0
c)
0·8
0·6
0·4
0·2
0
2
3
4
5
6
7
d)
0·08
0·06
0·04
0·02
0
2
3
4
5
6
7
Number of eggs / aphid
Aphid infestation category

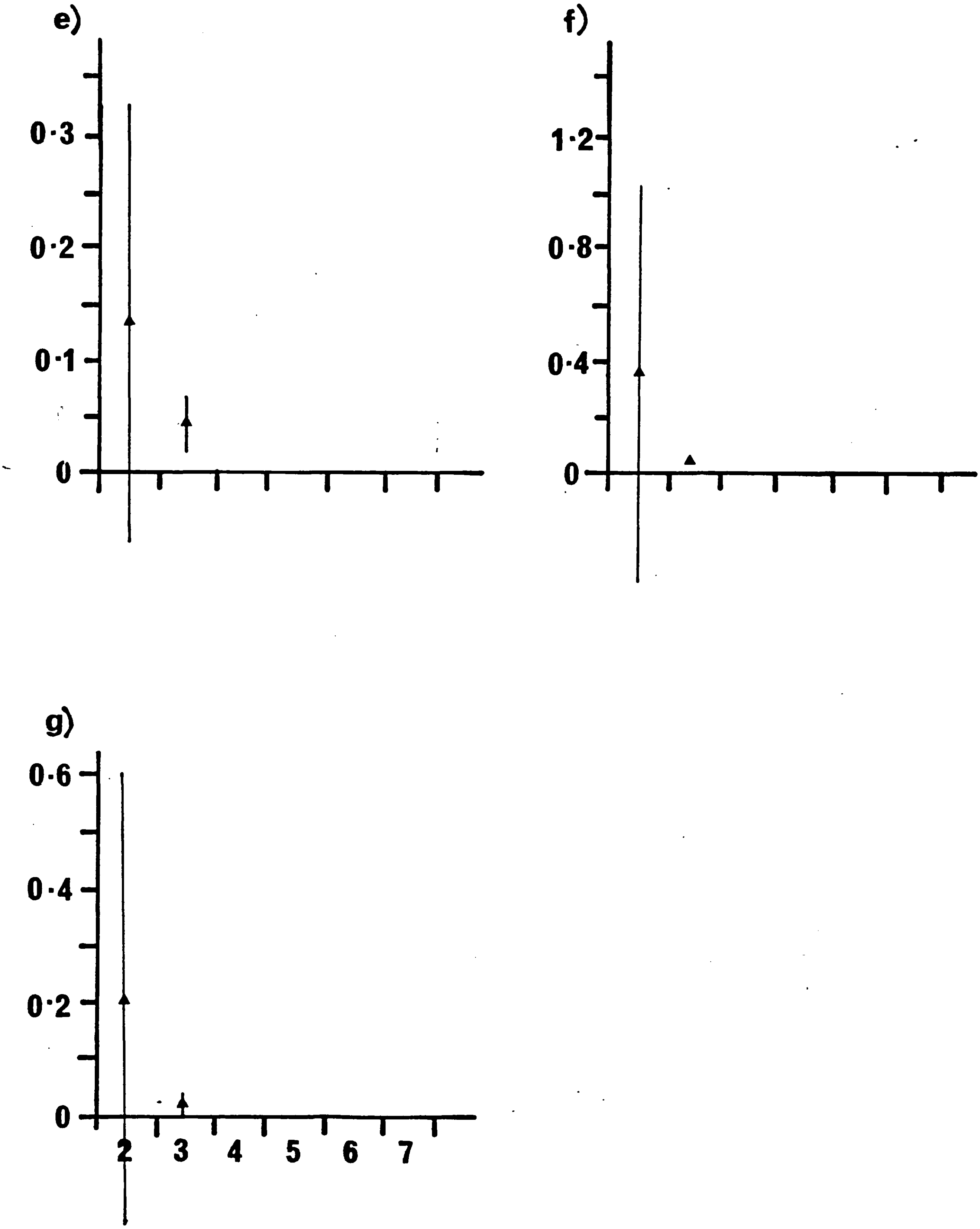
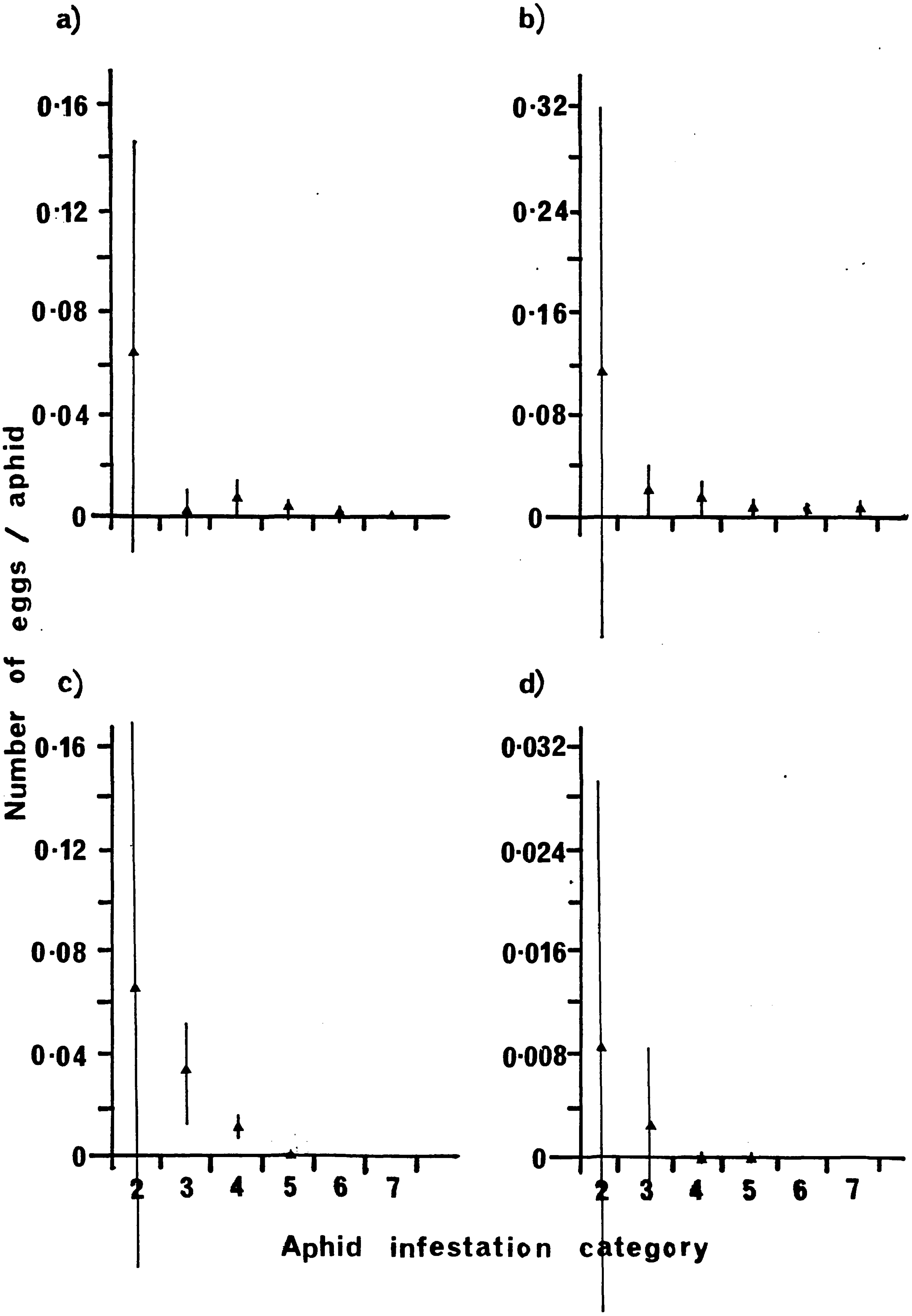
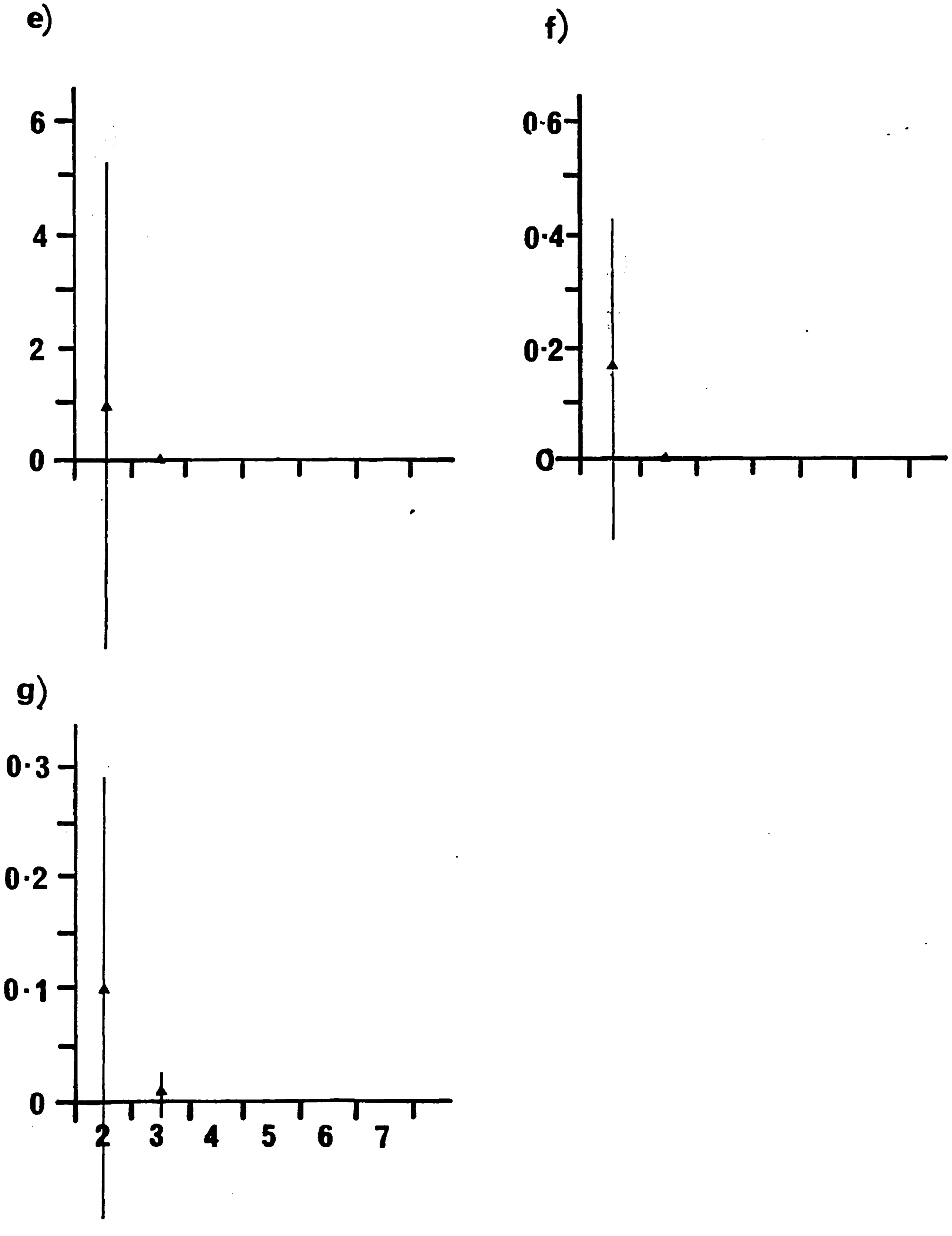

e)
0·3
0·2
0·1
0
f)
1·2
0·8
0·4
0
g)
0·6
0·4
0·2
0
2
3
4
5
6
7

Figure C9 a-g: The relationship between aphid population size and the number of egg batches laid per aphid in

a) cauliflower
b) Brussels sprout
c) white cabbage
d) red cabbage
e) Chinese cabbage
f) swede
g) radish


a)
0·16
0·12
0·08
0·04
0
b)
0·32
0·24
0·16
0·08
0
c)
0·16
0·12
0·08
0·04
0
d)
0·032
0·024
0·016
0·008
0
2
3
4
5
6
7
2
3
4
5
6
7
Number of eggs / aphid
Aphid infestation category


e)
6
4
2
0
f)
0·6
0·4
0·2
0
g)
0·3
0·2
0·1
0
2
3
4
5
6
7

APPENDIX D

Table D1: Fecundity, fertility and longevity of ten laboratory-reared Episyrphus balteatus flies

Replicate Number	Longevity (days)	Total number of eggs laid	% of eggs that hatched	Pre-oviposition period (days)	Oviposition period (days)	Post-oviposition period (days)
1	33	1026	79	15	17	1
2	45	1521	64	8	32	5
3	24	674	67	8	15	1
4	11	168	46	5	6	-
5	17	924	45	7	20	-
6	34	1280	66	9	24	1
7	26	956	64	6	20	-
8	32	767	64	8	24	-
9	31	921	69	13	18	-
10	24	386	62	9	14	1

Table D2: <u>One-way analysis of variance on the number of observations of sucrose-feeding by male and female flies of different ages</u>

Fly age (days)	Source of variation	df	SS	MS	F-ratio
2	Among sexes	1	0.05	0.05	0.24 ns
	Within sexes	18	3.70	0.21	
	Total	19	3.75		
4	Among sexes	1	0.05	0.05	0.36 ns
	Within sexes	18	2.50	0.14	
	Total	19	2.55		
6	Among sexes	1	0.45	0.45	1.00 ns
	Within sexes	18	8.10	0.45	
	Total	19	8.55		
8	Among sexes	1	0.45	0.45	0.50 ns
	Within sexes	18	16.10	0.89	
	Total	19	16.55		
10	Among sexes	1	2.45	2.45	2.67 ns
	Within sexes	18	16.50	0.92	
	Total	19	18.95		
12	Among sexes	1	3.11	3.11	3.11 ns
	Within sexes	17	17.00	1.00	
	Total	18	20.11		
14	Among sexes	1	0.03	0.03	0.11 ns
	Within sexes	17	4.70	0.28	
	Total	18	4.73		
16	Among sexes	1	0.89	0.89	1.49 ns
	Within sexes	16	9.56	0.60	
	Total	17	10.44		
18	Among sexes	1	2.72	2.72	0.97 ns
	Within sexes	16	44.89	2.81	
	Total	17	47.61		

Table D2: continued

Fly age (days)	Source of variation	df	SS	MS	F-ratio
20	Among sexes	1	0.50	0.50	1.00 ns
	Within sexes	16	8.00	0.50	
	Total	17	8.50		
22	Among sexes	1	0.06	0.06	0.11 ns
	Within sexes	16	8.44	0.53	
	Total	17	8.50		
24	Among sexes	1	0.15	0.15	0.37 ns
	Within sexes	15	6.09	0.41	
	Total	16	6.24		
26	Among sexes	1	0.10	0.10	0.38 ns
	Within sexes	14	3.65	0.26	
	Total	15	3.75		
28	Among sexes	1	0.15	0.15	1.15 ns
	Within sexes	12	1.56	0.13	
	Total	13	1.71		

Table D3: One-way analysis of variance on the number of observations of pollen-feeding by male and female flies of different ages

Fly age (days)	Source of variation	df	SS	MS	F-ratio	
2	Among sexes	1	6.05	6.05	2.25	ns
	Within sexes	18	48.50	2.69		
	Total	19	54.55			
4	Among sexes	1	8.45	8.45	2.29	ns
	Within sexes	18	66.50	3.69		
	Total	19	74.95			
6	Among sexes	1	5.00	5.00	2.24	ns
	Within sexes	18	40.20	2.23		
	Total	19	45.20			
8	Among sexes	1	0.45	0.45	0.25	ns
	Within sexes	18	32.10	1.78		
	Total	19	32.55			
10	Among sexes	1	0.05	0.05	0.05	ns
	Within sexes	18	17.70	0.98		
	Total	19	17.75			
12	Among sexes	1	0.10	0.10	0.26	ns
	Within sexes	17	6.32	0.38		
	Total	18	6.42			
14	Among sexes	1	33.96	33.96	130.62	***
	Within sexes	17	4.46	0.26		
	Total	18	38.42			
16	Among sexes	1	43.56	43.56	12.11	**
	Within sexes	16	57.56	3.60		
	Total	17	101.11			
18	Among sexes	1	56.89	56.89	19.32	***
	Within sexes	16	47.11	2.94		
	Total	17	104.00			

Table D3: continued

Fly age (days)	Source of variation	df	SS	MS	F-ratio	
20	Among sexes	1	88.89	88.89	51.61	***
	Within sexes	16	27.56	1.72		
	Total	17	116.44			
22	Among sexes	1	20.06	20.06	2.95	ns
	Within sexes	16	108.89	6.81		
	Total	17	128.95			
24	Among sexes	1	16.02	16.02	10.82	**
	Within sexes	15	22.22	1.48		
	Total	16	38.24			
26	Among sexes	1	7.17	7.17	5.20	*
	Within sexes	14	19.27	1.38		
	Total	15	26.44			
28	Among sexes	1	1.16	1.16	4.30	ns
	Within sexes	12	3.20	0.27		
	Total	13	4.36			

*** $p < 0.001$

** $p < 0.01$

* $p < 0.05$

Table D4: The number of observations for resting behaviour recorded during each hour of the experiment

a) Males

Rep No	Number of observations during each hour										Total
	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	4	3	4	4	2	4	6	5	6	4	42
2	6	5	3	2	2	3	6	6	6	3	42
3	4	6	5	5	3	6	3	5	5	6	48
4	4	1	5	4	5	4	4	5	6	6	44
5	6	5	5	4	2	4	3	3	5	-	37
6	4	4	4	4	2	4	4	6	4	4	40
7	5	6	5	1	4	4	6	5	5	6	47
8	5	6	2	3	4	5	5	6	5	6	47
9	4	3	1	5	2	5	6	5	6	4	41
10	5	4	5	4	3	5	4	5	4	3	42

b) Females

Rep No	Number of observations during each hour										Total
	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	7	7	4	5	7	6	1	6	6	7	56
2	2	3	3	2	2	3	1	4	3	3	26
3	3	4	4	2	1	3	3	1	3	4	27
4	*	*	*	*	*	*	*	*	*	*	*
5	4	2	3	1	2	5	5	4	5	6	37
6	8	3	3	8	3	4	2	5	9	9	54
7	2	4	3	3	2	2	1	2	3	4	26
8	3	4	1	3	2	1	2	2	3	4	25
9	3	4	4	2	4	2	3	4	4	4	34
10	3	3	3	3	2	3	3	3	4	3	30

* Fly dead

Table D5: The number of observations of flying behaviour recorded during each hour of the experiment

a) Males

Rep	Number of observations during each hour										Total
No	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	3	2	3	3	3	-	-	-	1	15
2	-	-	2	3	3	2	-	1	-	-	11
3	1	-	-	-	-	-	-	1	-	-	2
4	-	1	-	-	-	1	-	1	-	-	3
5	-	1	1	3	3	1	2	2	-	2	15
6	-	-	2	5	4	-	-	-	-	-	11
7	-	-	1	1	-	-	-	-	-	-	2
8	-	-	-	1	1	-	-	-	1	-	3
9	1	1	2	1	1	1	-	1	-	-	8
10	-	3	-	-	-	-	-	-	-	5	8

b) Females

Rep	Number of observations during each hour										Total
No	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	-	-	1	-	-	1	-	-	-	2
2	2	-	-	5	2	-	5	2	1	-	17
3	1	1	3	1	2	3	-	3	1	-	15
4	*	*	*	*	*	*	*	*	*	*	*
5	1	1	1	-	1	-	2	3	2	-	11
6	-	1	-	-	2	-	1	2	-	-	6
7	2	1	3	2	1	4	2	3	-	-	18
8	-	-	3	1	2	3	3	2	1	-	15
9	1	-	1	3	1	3	1	3	1	-	14
10	4	-	2	-	-	-	-	5	-	-	11

* Fly dead

Table D6: <u>The number of observations of feeding behaviour recorded during each hour of the experiment</u>

a) Males

Rep No	Number of observations during each hour 9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	Total
1	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	1	-	-	-	1	1
3	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	1	-	-	-	1
5	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	1	-	-	-	-	1
7	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	1	-	-	1
9	-	-	-	-	-	-	1	-	-	-	1
10	-	-	-	-	-	-	-	1	-	-	1

b) Females

Rep No	Number of observations during each hour 9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	Total
1	-	-	-	-	-	-	-	-	-	-	-
2	-	1	-	1	1	1	-	-	-	1	5
3	-	-	-	-	-	-	-	-	-	-	-
4	*	*	*	*	*	*	*	*	*	*	*
5	-	-	-	1	-	1	-	-	-	-	2
6	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	2	-	-	1	1	-	-	4
8	-	-	1	-	-	-	-	-	-	-	1
9	-	-	-	1	1	-	-	-	-	-	2
10	-	-	-	-	-	-	-	-	-	-	-

* Fly dead

Table D7: The number of observations of sucrose feeding recorded during each hour of the experiment

a) Males

Rep No	Number of observations during each hour										Total
	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	1	-	-	-	-	1
3	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	1	-	-	-	1
5	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	1	-	-	1

b) Females

Rep No	Number of observations during each hour										Total
	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	-	-	-	-	-	-	-	-	-	-
2	-	1	-	-	-	-	-	-	-	1	2
3	-	-	-	-	-	-	-	-	-	-	-
4	*	*	*	*	*	*	*	*	*	*	*
5	-	-	-	1	-	-	-	-	-	-	1
6	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	2	-	-	-	-	-	-	2
8	-	-	1	-	-	-	-	-	-	-	1
9	-	-	-	1	1	-	-	-	-	-	2
10	-	-	-	-	-	-	-	-	-	-	-

* Fly dead

Table D8: The number of observations of pollen feeding recorded during each hour of the experiment

a) Males

Rep	Number of observations during each hour										
No	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	Total
1	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	1	-	-	-	-	1
7	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	1	-	-	1
9	-	-	-	-	-	-	1	-	-	-	1
10	-	-	-	-	-	-	-	-	-	-	-

b) Females

Rep	Number of observations during each hour										
No	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	Total
1	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	1	1	1	-	-	-	1	4
3	-	-	-	-	-	-	-	-	-	-	-
4	*	*	*	*	*	*	*	*	*	*	*
5	-	-	-	-	-	1	-	-	-	-	1
6	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	1	1	-	-	2
8	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-	-

* Fly dead

Table D9: The number of observations of on-plant activity recorded during each hour of the experiment

a) Males

Rep	Number of observations during each hour										Total
No -1	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	-	-	-	-	-	-	-	-	-	-
2	1	-	1	-	-	-	-	-	-	-	2
3	-	-	-	-	2	7	-	-	-	-	9
4	-	-	-	-	1	3	-	-	-	-	4
5	-	-	-	-	-	-	-	-	-	-	-
6	-	-	1	1	-	-	-	-	-	-	2
7	1	-	-	-	3	3	-	1	1	-	9
8	-	-	1	-	-	2	-	-	1	-	4
9	-	-	-	-	-	1	-	1	2	-	4
10	-	-	-	-	-	-	-	-	3	1	4

b) Females

Rep	Number of observations during each hour										Total
No	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	-	-	-	-	-	-	-	-	-	-
2	-	-	3	2	2	3	1	-	-	-	11
3	-	-	-	-	8	-	-	5	3	-	16
4	*	*	*	*	*	*	*	*	*	*	*
5	-	2	2	1	3	-	-	1	-	-	9
6	-	1	-	1	-	-	1	-	-	-	3
7	-	-	-	-	4	7	-	-	-	-	11
8	-	6	-	-	-	-	-	4	2	-	12
9	-	-	-	-	-	-	-	-	-	-	-
10	3	-	2	-	2	-	-	1	1	-	9

* Fly dead

Table D10: The number of observations of probing and cocking recorded during each hour of the experiment (females only)

Rep No	Number of observations during each hour										Total
	9 -10	10 -11	11 -12	12 -13	13 -14	14 -15	15 -16	16 -17	17 -18	18 -19	
1	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	6	-	-	-	6
3	-	-	-	-	3	-	1	2	-	-	6
4	*	*	*	*	*	*	*	*	*	*	*
5	-	-	2	1	1	-	-	-	-	-	4
6	-	1	-	-	-	-	-	-	-	-	1
7	-	-	1	-	3	-	2	1	-	-	7
8	1	1	-	-	-	1	1	1	1	-	6
9	-	-	1	-	2	2	-	1	-	-	6
10	-	-	4	-	4	-	-	-	-	-	8

* Fly dead

APPENDIX E

Table E1: The number of eggs laid by individual flies on patches of different aphid densities

Rep No	Number of eggs laid on each patch			Total number of eggs
	10	50	250	
1	29	27	20	76
2	3	6	2	11
3	5	-	6	11
4	3	5	7	15
5	2	4	3	9
6	1	5	7	13
7	3	1	2	6
8	7	13	24	44
9	2	5	9	16
10	4	10	14	28

Table E2: The time spent by individual flies inside and outside patches of different aphid densities during a one-hour period

Rep No	Time spent inside patches of different aphid densities (seconds)				Time spent outside patches (seconds)
	10	50	250	Total	
1	777	581	708	2066	1534
2	180	263	18	461	3139
3	1042	-	196	1238	2362
4	491	991	1054	2536	1064
5	152	207	174	533	3067
6	37	198	282	517	3083
7	1209	540	353	2102	1498
8	596	867	1249	2712	888
9	470	881	1586	2937	663
10	392	997	1659	3048	552

APPENDIX F

Table F1: Spray dates for Field Trial 1

Spray No	Spray date	Spray time	Weather conditions at time of spraying
1	27.7.80	1900 h	Cool, dry, still
2	31.7.80	1900 h	Cool, dry, still
3	4.8.80	1900 h	Cool, dry, still

Table F2: Sample dates for Field Trial 1

Sample	Sample date	Sample time	Weather conditions between spray date and sample date
Pre-spray 1	24.7.80	1000 h	
2	26.7.80	1000 h	
Post-spray 1	28.7.80	1000 h	Cool, heavy rain immediately after spray 1
2	1.7.80	1000 h	Cool, heavy rain immediately after spray 2
3	5.8.80	1000 h	Cool, dry

Table F3: Spray dates for Field Trial 2

Spray No	Spray date	Spray time	Weather conditions at time of spraying
1	6.9.81	1900 h	Warm, dry, still

Table F4: Sample dates for Field Trial 2

Sample		Sample date	Sample time	Weather conditions between spray date and sample date
Pre-spray	1	4.9.81	1000 h	
	2	6.9.81	1000 h	
Post-spray	1	8.9.81	1000 h	Short period of rain on 7.9.81
	2	10.9.81	1000 h	Prolonged periods of heavy rain on 9.9 and 10.9.81

Table F5: Spray dates for Field Trial 3

Spray No	Spray date	Spray time	Weather conditions at time of spraying
1	21.8.82	0900 h	Warm, dry, slightly windy
2	25.8.82	0900 h	Cool, dry, still

Table F6: Sample dates for Field Trial 3

Sample	Sample date	Sample time	Weather conditions between spray date and sample date
Pre-spray 1	11.8.82	1000 h	
2	20.8.82	1000 h	
Post-spray 1	22.8.82	1000 h	Prolonged period of heavy rain immediately after spray
2	26.8.82	1000 h	Warm and dry

Table F7: The mean number of aphids per plant in control and treated plots on pre- and post-spray sample occasions during Field Trial 2

Sample occasion	Number of aphids/plant (± SE)	
	Control	Treated
Pre-spray 1	54.5 ± 16.8	46.8 ± 10.2
2	48.6 ± 11.5	47.4 ± 13.3
Post-spray 1	56.0 ± 9.1	47.1 ± 10.0
2	33.1 ± 5.8	36.2 ± 6.7

Table F8: The mean number of aphids per plant in control and treated plots on pre- and post-spray sample occasions during Field Trial 3

Sample occasion	Number of aphids/plant (± SE)	
	Control	Treated
Pre-spray 1	46.5 ± 5.5	56.6 ± 9.5
2	26.6 ± 4.0	18.6 ± 4.1
Post-spray 1	25.9 ± 6.3	24.4 ± 6.9
2	14.8 ± 2.5	25.4 ± 4.5

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