25/7/97

The ecology of *Melangyna viridiceps* and *Simosyrphus grandicornis* (Diptera: Syrphidae) and their impact on populations of the rose aphid, *Macrosiphum rosae*

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A thesis submitted for the Degree of Doctor of Philosophy in the Faculty of Agricultural and Natural Resource Science at the University of Adelaide

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The University of Adelaide
July 1996

Declaration

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Ebrahim Soleyman-Nezhadiyan, July 1996

Acknowledgement

The long and tedious task of preparing a thesis cannot see the light of the day without appreciable help from supervisors, colleagues, and friends, and to all of them I extend my sincerest gratitude. There are a few, however, who deserve special appreciation.

It is due to Dr. Derek Maelzer that this project ever started. His experience in insect ecology and experimental designs was an invaluable source of knowledge before and after his retirement. Dr. Peter Bailey deserves a very special appreciation for sound supervision, patience and criticism. Special thanks to Dr. Roger Laughlin who spent a lot of time reading and criticising this thesis, even though he had retired. Roger's contribution in setting and repairing of incubators, and in consultation in temperature-dependent experiments was priceless. Thanks also due to Prof. Otto Schmidt for his encouragement during my study.

Thanks are due to Dr. Mike Keller for consultation and encouragement and to Dr. Andrew Austin for helpful advice and contributions to identifying syrphids and their parasitoids; to Dr. Peter Cranston for identification of syrphid species; to Dr. Mary Carver for identification of aphids and her generosity in giving me valuable information. The identification of plant species by Mr. David Cooke from Animal and Plant Control Commission and Dr Jenifer Gardner is also appreciated.

Also appreciated are the dear fellows of the lab. discussion group who always inspired useful conversations; Jörg Kitt, Dr. Brigitte Tenhumberg, Bijan Hatami, Latif Salehi, Lynne Grbin, Steven Ball, Scott Field, Bill Frost, Hermin Herminanto, and Dwi Iswari. Thanks to Dr. Paul Dangerfield for his useful assistance and friendship, to Ms. Margaret Cargill for English comments and to Dr. Estan Eckert for providing the weather data for the project.

I am thankful to Anke Johnsen (secretary), Terry Feckner and Dr. Gary Taylor and other members of the Department of Crop Protection for making my stay here pleasant.

I am thankful to The Islamic Republic of Iran which provided me with financial assistance to carry out this project.

Most of all I would like to thank my wife, Mina, my daughter, Nazia, and my sons, Nima and Pejman, for their patience, and for creating a nice environment at home during my study.

Melangyna viridiceps

Simosyrphus grandicornis

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Summary

Some syrphid flies are regarded as important control agents of aphids. Their larvae feed mainly on aphids and other Sternorrhyncha and the adults feed on pollen and nectar of flowers and honeydew of Steynorrhyncha. Some of these species have been utilised to suppress aphids in some cropping systems in Europe and New Zealand by planting attractive flowers near to crops on which aphid pests occur. The work reported in this thesis aims to describe sufficient of the biology of two common species of Australian syrphids, *Melangyna viridiceps (Macquart)* and *Simosyrphus grandicornis* (Macquart) to evaluate their potential as biological agents og aphids in the Mediterranean climate of South Australia. To test the hypothesis that the impact of these syrphids in suppressing aphids could be enhanced by providing supplementary pollen plants, a model system of the two syrphid species and rose aphids, *Macrosiphum rosae* (Linnaeus.) was studied in Adelaide during 1993-1995.

To test the effects of pollen supplementation, rose aphids were used because they are evidently present during nine months of the year in South Australia. The rose flowers are not attractive to syrphid flies so any effects of pollen supplementation by other plants could be easily detected. A number of native and introduced plants were tested as pollen sources for syrphids in one rose garden. Then, the numbers of syrphids and rose aphids at this rose garden were compared with other rose gardens without such plants. *M. viridiceps and S. grandicornis* adults laid more eggs on rose aphid colonies near to pollen sources than those not provided with pollen (chapter 9). However, any reduction in rose aphid numbers could not be attributed to providing suppplementary pollen.

At least several factors may have contributed to the failure of pollen supplementation to reduce aphid numbers: 1) the seasonal cycles of syrphids (especially that of *M. viridiceps*) were not synchronised with those of the rose aphids, and neither syrphid species was most abundant when the aphids were most abundant, 2) both aphid species can utilise prey other than rose aphids and 3) parasitoids of these syrphids may reduce their effectiveness.

Pollen preferences of adults of both syrphid species were measured by comparing species of pollen in dissected adults with the availability of flowers in a 1.5ha study area (chapter 6). Both species use flower resources selectively from the three strata of herbs, shrubs and trees. *M. viridiceps* preferred pollen from herbs to that of the other two strata. Although *S. grandicornis* is highly attracted to wild radish (*Raphanus raphanistrum*), most of the flowers which attracted this species were from trees. *S. grandicornis* appeared to eat mainly nectar and honeydew.

S. grandicornis and *M. viridiceps* differ in their seasonal occurrence; adults of *S. grandicornis* were active during August to May and *M. viridiceps* during April-May to November (with the peak in July-September) in the two years 1993-1995, while rose aphids were numerous during October (spring peak) and April-May (Autumn peak). *S. grandicornis* was the more important predator of rose aphids as the density of its immature stages on rose aphid colonies was greater than that of *M. viridiceps*. However, the number of immature stages of *S. grandicornis* declined prior to the peak of rose aphids in autumn.

In the field, female *S. grandicornis* laid eggs equally on buds with aphid densities above and below the mean number of aphid per infested bud (MNAI) for any particular site and sampling occasion. However, once eggs were found on buds, total number of eggs was significantly higher on these buds which were infested with numbers of aphids higher than the MNAI. In laboratory experiments, females of *S. grandicornis* showed a functional response to increasing rose aphid density up to an optimum of 71-100 aphids per bud. The response to high density of aphids by *S. grandicornis* minimises the risk of starvation for the offspring. The first instar larvae of *M. viridiceps* consumed green plant materials when deprived of aphids.

Parasitization of *S. grandicornis* eggs and larvae by *Diplazon laetatorius* (Fabricius.) (Hymenoptera: Ichneumonidae) may have limited the ability of *S. grandicornis* to prevent the increase in rose aphids numbers in summer and autumn when parasitism increased to

80%. This parasitoid did not appear to affect *M. viridiceps* perhaps because of different seasonal activity. Other natural enemies recorded were not important during the study; the larval parasitoid *Syrphophagus nigricornis* (Girault) (Hymenoptera: Encyrtidae) parasitised 0.65% of larvae and the nematode *Syrphonema* sp. (Syrphonematidae) parasitised 1.9% of adults.

Suction trap catches of adults in winter indicate that *S. grandicornis* probably overwinters as adults, but its main periods of activity are during the warm months of the year. *M. viridiceps* was captured by water trap in summer, indicating that this species oversummers as adult, but the peak activity is during cool months (winter-spring). *M. viridiceps* started activity at 0900-1000 with the estimated flight threshold of 12.8°C and peaked mostly around noon. In spring, when both species occurred together, *M. viridiceps* was active earlier in the day than *S. grandicornis*. During hot days, *M. viridiceps* peaked and left the sunny sites earlier than *S. grandicornis*. Some individuals of both species were then observed in the shade of *Acacia* trees located close to the rose garden. This confirms the importance of shelters for protecting natural enemies. The recapture rate of less than 10% of marked *M. viridiceps* indicated that the adult populations of these syrphids were very mobile with respect to the 1.5ha. study area.

The number of generations of *S. grandicornis* and *M. viridiceps* was estimated as 10 and 11-13 per year, respectively, during this study. The pre-oviposition period of females was 6.8±0.66 SE days for *M. viridiceps* and 5.6± 0.64SE for *S. grandicornis* after which an average of 288±34SE and 307.9±23.2SE eggs were laid during the total adult life span of 19.5±1.65 and 13.8±1.3 days respectively. The total duration of the three larval instars at 20°C was 10.8 and 12.3 days for *M. viridiceps* and *S. grandicornis*.
and for the pupa was 8.3 and 7.7 days, respectively.
These results suggest that manipulation of syrphid numbers to control pest aphids in crops may be difficult in habitats similar to those described in this study. Although the results refer specifically to rose aphids, other pest aphids on crops in South Australia occur at similar times to rose aphids.

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Chapter 1

Introduction

Some members of the family Syrphidae (Diptera) with common names of "flower flies", "hover flies" and "syrphid flies" are important predatory insects (Schneider 1969). The larvae of a number of species feed on aphids, and other groups of insects, including psyllids, coccids, cicadas, aleurodids, chrysomelids, and lepidopterous larvae (Schneider 1969; Rank and Smiley 1994; Wratten *et al.* 1995). The adult hoverflies feed on pollen, nectar and honeydew. Pollen is rich in protein and essential during yolk deposition whereas nectar consists mainly of carbohydrate and essential for energy production in both males and females (Haslett 1989b).

By comparison with Europe, in Australia Syrphidae "seem to be rather poor in species and may be a relatively recent element of the fauna of this continent" (Colless and McAlpine 1991).

Two of the three common aphidophagous species of syrphids in South-eastern Australia are *Melangyna viridiceps* (Macquart), which is indigenous to Australia and probably occurs Australia-wide, and *Simosyrphus grandicornis* (Macquart) which is widespread in Australia and Oceania (Carver personal comm. 1996). *M. viridiceps* and *S. grandicornis* are common in Adelaide.

The rose aphid, *Macrosiphum rosae* (Linnaeus.), is an exotic species which occurs on rose buds in Australia (Maelzer 1977). *M. rosae* feeds mainly on rose buds until the stage at which sepals start to fold back (Maelzer 1976, 1977). The aphid is the most serious insect pest of roses in South Australia; nurseries, and home gardeners use insecticides to control this aphid (Kitt 1996).

Habitat management of a number of aphid species by provision of flowers around or across fields may increase the number of syrphids (Putman and Wratten 1984; von Klinger 1987; Felki 1988; Cowgill *et al.* 1993 a,b; Harwood *et al.* 1994; White *et al.* 1994, and 1995; Wratten and van Emden 1995). In this context, some flowers have been found to be especially attractive to adult syrphids; e. g. those of *Phacelia tanacetifolia* Benth., *Sinapis arvensis* L., *Coriandrum sativum* L. and *Fagopyrum esculentum* Moench. (Buckwheat). Some attractive plants are either weeds or are difficult to manipulate agronomically (Cowgill *et al.* 1993a).

The importance of syrphid flies in suppressing populations of aphids was recorded in some crops in different parts of the world (e.g. Tamaki 1978, on peaches in US; Chambers and Adams 1986, on cereals in UK). In Australia, the only significant study of syrphid biology was done by Clark (1963) who studied the effect of *Syrphus sp.* on populations of the psyllid, *Cardiaspina albitextura* Taylor. Some data on syrphids are given in studies on the ecology and population dynamics of aphids or other insects (e.g. Ward 1934; Minko 1961; Gutierrez *et al.* 1971; Gutierrez *et al* 1974; Hales 1976; Hales and Carver 1976; Maelzer 1977; Ridland and Berg 1978; Mohammad 1979; Richards 1980; Hussein 1982; Crawford 1983; Allen 1984; Carver and Woolcock 1986; Stechmann and Völkl 1990) but the effect of Australian syrphids on aphids by habitat manipulation and the provision of attractive flowers has not been reported.

The present study was undertaken to determine (1) the influence of the two common syrphid species on populations of rose aphids in rose gardens in Adelaide, (2) whether the provision of attractive flowers increased the suppressive effect of syrphids on rose aphids, and (3) to observe some ecological and biological aspects of the two syrphid species in a Mediterranean climate to obtain a better understanding of their biological control potential.

Overview:

In Chapter 2, the relevant literature on some syrphid species is reviewed. The studies are mainly of European species from temperate climates; the literature on Australian species is sparse as is the literature on syrphids in Mediterranean climate. Chapter 3 describes general materials, methods, rearing procedures and sites of sampling at different rose gardens. Chapter 4 describes the monitoring of seasonal changes of adult syrphids by a census-walk method, suction traps and water traps. Chapter 5 deals with diurnal activity patterns and the movement of the two species. In Chapter 6, selection of flowers by syrphids is measured by comparing pollen in the guts of hoverflies with the availability of resource flowers. Oviposition behaviour of adults in the field and in cages is described in Chapter 7. Capture efficiency of larvae is also described in this chapter. The voracity of both species is described in Chapter 8 and a day-degree model of temperature-dependent development is used to estimate the number of generations in Adelaide during 1993-95. In Chapter 9 the seasonal occurrence of immature stages of the two species has been investigated. The natural enemies and the seasonal changes in parasitism is described in Chapter 10.

Chapter 2

Review of literature

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2. 1 Taxonomy of Syrphids

The members of the family Syrphidae (Diptera) are commonly known as "Hover-flies" and "Flower-flies" because they are hoverers and attracted to flowers (Coe 1953). The aphidophagous Syrphidae belong in the subfamily Syrphinae (Rotheray and Gilbert, 1989) within two tribes, the Syrphini and Melanostomini . There are more than 4700 species of Syrphidae known around the world, of which about 300 species occur in Central Europe (Chambers 1988). Australia has a poor fauna of syrphids (Colless and McAlpine, 1991) which includes 13 genera and 23 species (Thompson and Vockeroth, 1989)

Thompson and Vockeroth (1989) catologued Australian Diptera including the Syrphidae. The taxonomy of immature stages of Syrphidae has been studied by Dixon (1960), Chandler (1968e), Rotheray and Gilbert (1989), and Chu (1992), but the taxonomy of immature Australian species has not been studied.

In Australia, Hardy (1933) provided some useful notes on, and keys to, Australian syrphinae, including the species under study. Ferguson (1926) grouped the Syrphidae of Australia into 6 subfamilies, Microdontinae, Syrphinae, Volucellinae, Cerioidinae, Eristalinae and Milesinae. Curran and Bryan (1926) described new Australian Syrphidae housed in the Bernice Bishop Museum in Honolulu.

According to Vockeroth's classification (1969), the family Syrphidae is divided into two subfamilies, Milesiinae and Syrphinae. The subfamily Syrphinae is divided into 6 tribes, Paragini, Chrysotoxini, Bacchini, Melanostomini, Toxomerini and Syrphini with the two presently studied genera, *Melangyna* and *Simosyrphus,* included in the latter tribe.

2. 1. 1 *Melangyna* Verrall species

The genus *Melangyna* was first described by Verrall (1901) with the type-species, *Melanostoma quadrimaculatum* (Verrall, 1837). The only synonym of this genus is *Stenosyrphus* (Matsuma and Adachi, 1917) with the type species *Scaeva lasiophthalma* (Zetterstedt, 1843).

2. 1. 2 Distribution and origin of Australian *Melangyna (Austrosyrphus)*

The genus *Melangyna* includes four subgenera; *Melangyna* (*Melangyna* and *Melangyna* (*Meligramma*) distributed in the Holarctic region, *Melangyna* (*Austrosyrphus*) distributed in Australia and New Zealand, and *Melangyna* (*Melanosyrphus*) distributed in New Guinea. Vockeroth (1969) states that the presence of two subgenera of a genus in Australia, New Zealand and New Guinea is unusual unless it extended its range south of Japan in eastern Asia. He suggests that the early entry of a *Melangyna*-form into Australia may have occurred across an island bridge from Asia, and subsequently a small group of species has been evolved from this ancestor. The subgenus *Melanosyrphus*s, which occurs in the high altitudes of New Guinea, may have established from this Australian group (Vockeroth 1969).

Melangyna (*Austrosyrphus*) in Australia and New Zealand includes the species *collatus* (Walker.), *jacksoni* (Bigot.) and *viridiceps* (Macquart.) recorded from New South Wales, and *novaezealandiae* (Macquart) recorded from New Zealand (Thompson and Vockeroth 1989).

2. 1. 3 *Simosyrphus* Bigot: synonymy, origin and distribution

The genus *Simosyrphus* was first described by Bigot in 1881, and Hull (1949) designated *Syrphus grandicornis* Macquart (1842) as the type species. Synonyms for the species are *Metasyrphus fasciatus* Shiraki (1963) *and* *Syrphus vitiensis* Bezzi (1928) (see Thompson and Vockeroth, 1989). This genus includes the single species, *Simosyrphus grandicornis,* which is distributed over Australia and the Pacific Islands. However there is a variation in the pattern of microtrichia on the wing veins of specimens from different Pacific Islands. Since a similar pattern of microtrichia is only observed in Hawaiian and

Australian specimens, it can be concluded that the Hawaiian specimens are of Australian origin (Vockeroth 1969).

2. 2 Importance of Syrphidae as bio-control agents

The voracity of aphid predators, the multiplication rate of the aphid and synchronisation between predators and aphids are the main contributions determining the effectiveness of predators (van Emden 1966). Syrphids can be a major factor in controlling aphids in crops. Tamaki *et al.* 1967, for example, reported that four species of hoverflies were the only biological agent that effectively controlled the autumn generation of green peach aphid, *Myzus persicae* (Sulzer.) on peach trees in the United States. The syrphid, *Episyrphus balteatus* (De Geer.) was the most important predator of *Sitobion avenae* (Fabricus.) in the United Kingdom cereal crops with the density of the predator larvae as low as 0.1 m^{-2} (Winder *et al.* 1994). The larvae of hoverflies, mainly *Episyrphus balteatus* (De Geer), prevented the increase of the aphid species *Sitobion avenae* and *Metopolophium dirhodum* (Walker.) in four of the six cereal fields analysed in the UK (Chambers and Adams 1986). However, in some crop situations, syrphids do not effectively control aphids; e.g., in Czechoslovakia, syrphids ovipositing on sugar beet carrying large colonies of *Aphis fabae* (Scopoli.) (Hodek *et al*. 1966).

Some predatory syrphid larvae feed on prey other than aphids; e. g. the early instar larvae of the cabbage white butterfly and diamondback moth, whiteflies, and potato tuber moth (Resendiz-Ruz 1993; Kroschel & Koch 1994; see also Wratten *et al*.1995). *Xanthandrus comtus* (Harris.) eats larvae of Lepidoptera; *Parasyrphus tricinctus* (Fallén.) feeds on Lepidoptera and Hymenoptera (sawfly larvae); *Parasyrphus nigritarsis* (Zetterstedt.) feeds on eggs and larvae of chrysomelids of the genus *Melasoma* (authority.). *Sphaerophoria* species feed on aphids, but also on psyllids, coccids, cicadas, and aleurodids (for overview: see Schneider 1969). *Parasyrphus melanderi* (Curran.), a specialist predator, feeds on the eggs and larvae of *Chrysomela spp*. (Coleoptera: Chrysomelidae) and can overcome their host-defensive secretions of salicyl aldehyde (Rank 1994; Rank & Smiley 1994).

Australia has a rich fauna of Psylloidea and Coccoidea. *Melangyna viridiceps* and *Simosyrphus grandicornis* are two syrphid species which feed on these groups of insects (Carver 1989). Similarly, Clark (1963) reported that a syrphid sp. closely related to *Melangyna viridiceps* attacks the psyllid *Cardiaspiana albitextura* (Taylor.) (Psyllidae) in New South Wales.

An important measure of the effectiveness of syrphids in controlling aphids is predation per unit time (Schneider 1969). The main factors which influence the effectiveness of hoverflies are: 1) Relative density of predatory stages compared with that of prey; 2) Voracity of hoverfly larvae in response to increasing numbers of prey; 3) Degree of contact between voracious stages and prey (Schneider 1969).

The ability of hoverflies to control aphid populations depends on the distribution and abundance of the aphid. In a wood or in a small plantation surrounded by mixed natural forest, the aphid *Cinara todocola* (Inouye.) on thuja saplings suffered heavily by syrphids when the aphid population was increased artificially. In contrast, high populations of *Cinara bogdanovi ezanoa* (Inouye.) which infested ten thousand young plants suffered little from natural enemies including syrphids (Furuta 1988).

The effectiveness of aphidophagous insects in controling populations of aphids depends on the threshold number of aphids for the particular crop (Bonnemaison 1965, Schneider 1969) and their status as virus vectors (van Emden 1965). Since natural enemies generally have higher temperature thresholds of activity and reproduction than aphid populations (Bonnemaison 1965), the voracity and synchronisation with the aphid's reproduction are also important factors which quantitatively determine the impact of aphidophagous insects (Hodek *et al.* 1965b). In Germany, when aphids and syrphids were well synchronised, aphid infestation was slight (Groeger 1993).

Although the importance of hoverflies in controlling aphids has not been studied extensively in Australia, changes in populations of some species of aphids and their complex of predators, including syrphids, have been analysed; for example, Khan (1979) studying the ecology of black citrus aphid, *Toxoptera citricidus* (Kirkaldy.), during three years, mentioned the two species of syrphids, *Melangyna viridiceps* and *Simosyrphus grandicornis* as predators in spring. However, he did not discuss their importance in controlling the populations of black citrus aphid. Hussein (1982) studying the natural enemies of *Myzus persicae* (Sulzer.) on potato in South Australia mentioned that *Melangyna viridiceps* was the only syrphid species on potato, but its numbers were relatively low and it was unimportant in control. In New South Wales, Clark (1963) observed that the syrphid, *Syrphus* sp. killed up to about 35% of third to fifth instar nymphs of *Cardiaspina albitextura* (Psyllidae) living on *Eucalyptus blaketis* but this mortality played a minor part in determination of the psyllid's abundance.

There were few attempts to use exotic syrphid species in controlling aphids in Australia and New Zealand. The Western Australian Department of Agriculture introduced some unidentified syrphid predators from Philippine Islands in 1907 for the control of rose aphids but none became established (Wilson 1960). In 1969-71, 1119 pupae of *Eupeodes Macroconfrater* (Wiedemann), *Episyrphus balteatus*, *Scaeva pyrastri* (L.) were imported from Pakistan to New Zealand. Parasitism was high in the field and it was not possible to obtain high rates of mating success with these species in quarantine (Cameron *et al.* 1989). During the period 1968 to 1976, *Syrphus sp., E. confrater* and *Scaeva pyrastri* were cultured for release at the Lincoln Research Centre, Canterbury, but they did not establish under New Zealand conditions.

2. 3 Biology and ecology of Syrphidae

<u>2. 3. 1 life cycle</u>

While the life cycle of most species of aphidophagous hoverflies is little known (Dusek and Láska, 1986), those that were investigated and have been described show a variety of life cycle strategies. The number of generations varies in some species, which may be as many as five or six generations a year depending on temperatures (Hagen and van den

Bosch 1967). Most investigations on the life cycles of hoverflies have been done in Europe. There is not much literature on the life cycle of Australian species. However, in chapter 4, the overwintering and oversumming of the two species, *Melangyna viridiceps* and *Simosyrphus grandicornis* will be discussed. In Chapter 8 the number of generations of the two species is estimated.

Based on the overwintering stages, seven main types of annual life cycle of European syrphid species have been described (Table 1) (Dusek and Láska 1986). One type overwinters as an imago, four types as larvae and two in the pupal stage. Type 2 which overwinter as larvae and have an obligatory diapause in spring and summer are most abundant in Czechoslovakian species (86%) (Dusek and Láska 1986). European species of *Melangyna* probably overwinter as pupae (Ssysmak and Gilbert 1993).

Scaeva pyrastri, S. selenitica (Meigen.) and possibly S. *dignota* (Rondani.) *Eupeodes lapponicus* (Zetterstedt.) and *Episyrphus balteatus* overwinter as fertilised females in European climates. As a rule, these species hibernate only as females which copulate in autumn (for overview: see Schneider 1969) or occasionally as males (Johnson 1969). The hibernating females have expanded abdomens, well developed fat bodies and their guts are full of concentrated nectar and honeydew (Schneider 1969). They select cavities in trees and ground as refuges for hibernating (Schneider 1969).

Those syrphid species with one generation per year survive by entering diapause at the end of larval growth during summer and autumn when food is scarce. In Europe, the activities of univoltine species are concentrated in spring with the heaviest aphid infestation on trees and shrubs and at the peak of the flowering period. Multivoltine species of hoverflies have no diapause during the larval stage, and most of them hibernate as adults. The larvae of these species frequently pupate on plants in the vicinity of aphid colonies (Schneider 1969). Between the first and second groups, there are some transitional types with oligovoltine development. These transitional groups have relatively short obligatory or facultative larval diapause (Schneider 1969).

Table 2. 1:various life cycle types in aphidophagous syrphids (Dusek and Láska 1986)

Cycle type	Generation per year	overwintering stage	diapausing stage	kind of diapause	notes
1	>2	Imago	Imago	F-partial diapause	
2	1	Larvae	Larvae	O-total diapause	spring & summer
		Larvae	Larvae	O-partial diapause	spring & summer
3	1	Larvae	Larvae	O-total diapause	short term
4	2	Larvae	Larvae	O-total diapause	summer, 1st generation winter, 2nd generation
5	>2	Larvae	Larvae	F-total diapause	short term
6	more than 1	Pupae	Pupae	F-total diapause	
7	1	Pupae	Larvae	O-total diapause	short term

F=facultative, O=obligatory

There are some contradictions about overwintering of some European species of hoverflies. For example, Gauss (1961) observed females of *Eupeodes luniger* (Meigen.) overwintering in warm places close to buildings, while Dusek and Laska (1986) found the early spring occurrence of larvae which means that this species overwinters as pupae.

In Central Europe, the distribution of syrphid species with different life cycle strategies is related to aphid occurrence during the year (Dusek & Láska 1986). Generally, two peaks of aphids occur in central Europe: one in spring to early summer and another smaller peak in autumn with low aphid abundance in mid-summer. Depending on the life cycle strategies (Table 2. 1) , different species of syrphids exploit one or both peaks of aphid abundance (Dusek & Láska 1986).

2. 3. 2 Development period

The development periods of egg, larva and pupa, depend on the temperature. Barlow (1961) showed that the embryonic development in *Syrphus corollae* (Fabricus.)was relatively constant and all viable eggs hatched after 3 days at 22-24°C.

The development time for the larvae of *Syrphus corollae*, one of the commonest aphidophagous species in summer in Czechoslovakia is 31 days at 10°C, 12.6 days at 15°C (Adam *et al*. 1987), 7.3 and 7.7 days (Dusek & Láska 1986) at 22-24°C (40-80% R.H. and 17 hours light) for males and females respectively (Barlow 1961). Larvae of the aphidophagous species *Syrphus luniger* complete the 3 larval instars (Clark 1963; Hägvar 1974; Schneider 1969) in 8-10 days at 22°C (for overview see: Schneider; 1969). However, the developmental period for larvae depends on the number of aphids eaten. For example, the larval stage duration of *Syrphus corollae* Fab decreased from 9.2 days to 7.9 days with an increase in the number of consumed aphids (Cornelius and Barlow 1980).

In the laboratory, pupae of *Syrphus luniger* develop in 16 or 17 days at 25°C (Schneider, 1969), while the pupae of *Syrphus corollae* develop in 7.9 and 8.1 days at 22-24°C (40-80% RH. and 17 hours light) in males and females respectively (Barlow 1961).

The total development time from egg to adult emergence for six syrphid species feeding on tea aphids at 26±2°C and 80% RH varied from 18 to 22 days (Radharishnan and Muraleedharan 1993).

The development time for Australian syrphid species has not been investigated and is discussed in Chapter 8.

2. 3. 3 Voracity

A suitable predator for use in biological control should be able to consume large numbers of prey when they are abundant and to survive on few during times of prey scarcity (Ng 1991). The number of aphids eaten by predators or parasites depend on the potential voracity, abundance, specificity, rate of multiplication, activity and searching behaviour of the aphidophagous insect (van Emden 1965). The voracity depends also on the density (Scott and Barlow 1986) and defence strategy of aphids (van Emden 1965). While some aphidophagous insects are polyphagous they may prefer one or some aphid species to others (Yakhontov 1965a).

Searching efficiency and prey handling time are two of the basic characteristics of success in food acquisition. The characteristics of the prey, including size, speed and density; characteristics of predator including speed and technique, and also abiotic factors affect the searching efficiency of syrphid larvae (Leir and Barlow 1982). The hunger of a predator may affect searching efficiency and handling time. Although an animal might be expected to eat faster when it is hungry, starved *Eupeodes corollae* larvae had a longer handling time than unstarved larvae but consumed more of the contents (Leir & Barlow 1982).

Third instar hoverfly larvae consume the largest number of prey compared to other stages (Schneider 1969). Starvation at the beginning of the third instar larvae of *E. corollae* affected development (Bombosch 1962). Although the voracity depends on temperature, an increase in temperature from 15 to 25° C has no uniform effect on the total quantity of food consumed by some syrphid larvae (reviewed by Schneider 1969). Bombosch (1962) showed that the number of aphids eaten by *Syrphus corollae* depended on the relative humidity and less so on temperature.

The voracity of some syrphid species are given in Table 2. 2. *Macrosyrphus confrater* consumed the maximum number (886.8) of aphids feeding on *Aphis gossypii* (Glover.), and *Syrphus corollae* ate the minimum number (86) feeding on *Myzus persicae* and *Aphis fabae*. However, except for *Scaeva pyrastri* which feeds on fourth instar *Aphis gossypii*, the stages of the prey have not been mentioned. Moreover, the voracity of different species of syrphids cannot be simply compared by the number of unequal sizes of aphid species .

As a comparison with some other predators, Agarwala and Saha (1986) showed that *Ischiodon scutellaris* (Fabricus.) and *Eupeodes confrater* (table 2. 2) were more voracious than three species of coccinellids, *Coccinella septempunctata* (Linnaeus.), C. *transversalis* (Fabricus.) and *Menochilus sexmaculatus* (Fabricus.). In this experiment, *C. septempunctata*, *C. transversalis* and *M. sexmaculatus* consumed 761, 519.6 and 217.4 *Aphis gossypii*, respectively, during the larval period at room temperature. *Leis conformis* (Boisduval.) larvae consumed 176 third instar *M. rosae* in 131.4 day degrees greater than 10°C during larval development (Maelzer 1978).

2. 3. 4 Larval behaviour

Larvae of hoverflies are active at night (Clark 1963; Hamrum 1966; Vickerman & Sunderland 1975; Holms 1985) and only starved larvae or those which were taken from small colonies of aphids, were active during the day (Rotheray 1986a). The majority of *Syrphus* sp. larvae remain motionless beneath psyllid tests on *Eucalyptus* leaves during the day (Clark 1963). Larvae of many syrphid species rest in leaf folds and curls, while the larvae of some species rest underneath open leaves (Rotheray 1986a) either because their prey are mostly present underneath the leaves, or because they are negatively heliotropic (Bhatia 1939).

Table 2. 2: the mean number of aphids eaten by different species of hoverflies

syrphids	aphids	Author	No. eaten
Scaeva pyrastri	*Aphis fabae* IV inst.	Schneider 1969	162
Syrphus ribesii (Linnaeus.)	"	"	234
S. vitripennis (Meigen.)	"	"	134
Scaeva albomaculata (Macquart)	*Aphis craccivora* (Koch.)	Yakhontov 1965b	580-600
""	*Aphis gossypii*	"	610-666
Eupeodes corollae	*Aphis craccivora*	"	380-410
Eupeodes corollae	*Aphis gossypii*	"	420-480
Eupeodes corollae	*A. fabae* & *M. persicae*	"	867
Eupeodes corollae	*Aphis fabae*	Bombosch 1964	844
Syrphus ribesii	*M. persicae*	Sundby 1966	609
Sphaerophoriascripta (Linnaeus)	*Aphis craccivora*	Yakhontov 1965b	350-375
" "	*Aphis gossypii*	" "	380-400
Syrphus sp	*Cardiaspina albitextura* (Psyllids)	Clark 1963	100-160
Ischiodon scutellari	*Aphis gossypii*	Agarwala & Saha 1986	618.4
Eupeodes confrater	*Aphis gossypii*	Agarwala & Saha 1986	886.8

In response to aggregation of the prey, syrphid larvae show an increased turning rate just after contact with an aphid, which tends to keep them in an area with a high density of prey (Hughes *et al*. 1984). Although some third instar larvae of syrphids do not remain close to aphids after feeding, the larvae of *Syrphus ribesii, Epistrophe eligans* (Harris.) and *Platycheirus scutatus* (Meigen.) in the colonies of *Aphis sambuci* L. on *Sambucus nigra* L. usually rest amongst the aphids (Rotheray 1986a). Therefore, the dispersion of syrphid larvae is more likely to reflect plant topography and aphid colony characteristics rather than the mechanism for defence against visually hunting predators (Rotheray 1986a).

Syrphid larvae are slow moving, soft, and blind and, as such, are vulnerable to predators (Rotheray 1986a). In addition, droplets of a pheremone released from cornicles of aphids may promptly fix them and prevent moulting of syrphid larvae (Edwards 1966). Larvae of hoverflies defend against predators in two ways; primary defences which are mechanisms that are initiated before encountering predators and secondary defences which are responses resulting from a direct predator encounter (Rotheray 1986).

The primary defences include the pattern on the body and hiding mechanisms. Stamp *et al.* (1993) used the word "crypsis" for characteristics that make an organism less apparent to its enemies. In comparison with other Diptera, the larvae of specialist syrphids are patterned to match their backgrounds while the colour of larvae of generalist predatory syrphids tend to be translucent green or brown (Rotheray 1986). It is possible that the third instar larvae hide in leaf rolls for thermoregulation rather than for escape from predators, but since the first, second and the third instar larvae of many syrphids are exposed on leaves, stems and bark, neither explanation is sufficient (Rotheray 1986; Holms 1985).

The secondary defences include frozen posture with the head contracted, raising the head and emitting sticky saliva at the attacker, rolling over repeatedly and falling from the substrate (Rotheray 1986a). For instance, syrphid larvae defend themselves against ants with a slimy exudation (Schneider 1969).

Quality of plants, the degree of starvation and the ability to move around the place on which prey feed (prey substrate) influence the searching behaviour of larvae. The ability of syrphid larvae to manoeuvre over the prey substrate is also an important factor affecting larval searching efficiency (Rotheray 1986a). Locomotive ability of syrphid larvae is largely determined by the morphology of larvae and the substrate (Rotheray 1986 b). On horizontal surfaces, the hungry larvae of *Scaeva pyrastri* behave in a positive phototactic manner, but in vertical substrates they behave in a negative geotactic way. After a time, the larvae crawl downward and become positively geotactic and, if no prey is found, the larvae search the other branches (Schneider 1969). In addition to the qualities of plant substrate (Shah 1982), the degree of starvation influences the intensity of searching (Rotheray & Martinat 1984). The larvae of *Syrphus ribesii* after 24 hours starvation spent longer time on leaves than 48-hour starved larvae. Satiated larvae remained close to aphids when not feeding probably to be close to the aphids for the next meal. Although the third instar larvae reduced their casting and speed of locomotion after feeding, they nevertheless tended to move away from aphids. The distance of moving away depended upon the availability of thigmokinesis or contact; the first instar larvae which contact aphids stay within aphid colonies. If the third instar larvae do not contact aphids they move away (Rotheray & Martinat 1984). The risk of losing contact with prey between two subsequent meals is probably reduced by thigmokinesis and low activity levels of satiated larvae (Rotheray & Martinat 1984).

2. 3. 5 Fertility, fecundity and longevity

The age at which females lay eggs varies between several days to many weeks, depending on the species. Oviposition by *S. corollae* probably occurred in the second day of adult life Barlow (1961). Longer pre-oviposition periods are recorded for females of *Episyrphus balteatus* and *Platycheirus albimanus* (Fabricus.) which became gravid in rearing cages after being fed bee pollen for about two weeks (Budenberg and Powell 1992). Mated *Syrphus luniger* developed ovaries three weeks after emergence from puparia and laid eggs from about the sixth week after the emergence of adults (Dixon 1959).

Fertilisation of syrphid eggs may be controlled by the female presumably by controlling the release of sperm from the spermathecae (Barlow 1961). Fertilisation seems to be related to suitable conditions for oviposition; for example, *Scaeva seleniticus* alternatively laid fertilised eggs among potato aphids on shoots and unfertilised eggs beside it on a piece of cellophane with no aphids (Schneider 1969).

Fertility of eggs can be judged by their colour on the day before they hatch in *Syrphus corollae* ; fertilised eggs are grey whereas unfertilised eggs remain white, distended or collapsed. In addition, some fertilised eggs do not hatch and the proportion of fertilised eggs which hatch is called "viability". Barlow (1961) showed that there was no relationship between the age of *Syrphus corollae* females and fertility or viability of eggs; or between pupal weight and fecundity of the subsequent adult female. Scott and Barlow (1984) showed that when more aphids were offered to the larvae of *Metasyrphus corollae*, they consumed more aphids and produced heavier pupae. However, the lifetime fecundity of *Metasyrphus corollae* was correlated with the longevity of adults, not the weight of pupae (Scott and Barlow 1984).

The number of eggs laid by syrphids (fecundity) varies according to species and rearing condition. *S. corollae* females produced an average of 419 and a maximum of 1694 eggs (Schneider 1969); and they laid 400 eggs during an 18 day oviposition period at about 23°C (Barlow 1961). *Scaeva albomaculata*, *Syrphus corollae* and *Sphaerophoria scripta* laid 250-400, 250-300, and 150-320 eggs respectively (Yakhontov 1965 b). The maximum fecundity was seen in the first 15 days of adult life of *Eupeodes corollae* (Scott and Barlow 1984) (=*Syrphus corollae*, Barlow 1961).

Under laboratory conditions, the average longevity of adult *E. corollae* was 18.2 days for males and 18.8 days for females. The median longevity of males and females was 24 and 20 days respectively (Barlow 1961). However, Scott and Barlow (1984) showed that the size of cage in which adults were kept influenced the longevity of *Metasyrphus corollae*.

2. 3. 6 Oviposition behaviour

Certain species of predators are attracted to the species of host plant(s) of their prey, whereas in others the presence of prey is a signal for attraction (Hagen *et al.*1976). However, for some predators in which the larvae are predacious and the adults are not, prey searching is not the only process affected by allelochemicals (Hagen *et al.* 1986).
Chandler (1968a,b) suggested that the aphidophagous syrphids may conveniently be divided into two categories according to oviposition behaviour; aphid-seeking

(aphidozetic) hoverflies such as *Syrphus* species which tend to lay single eggs close to aphids; and plant-seeking (phytozetic), such as *Melanostoma* and *Platycheirus* species, which lay eggs in small batches, often on uninfested plants. On sugar beet, aphidozetic species were attracted when the level of aphid infestation became high and then, when the aphids disappeared, the phytozetic species alone were attracted.

Syrphids may lay eggs on different strata depending on the presence or absence of aphids. After long periods in the absence of aphids, *Syrphus corollae* lays more eggs when aphids are present, but in the absence of aphids they will also lay on clean leaves or other surfaces such as dirty breeding vials, in honeydew, and in dead *S. corollae* (Bombosch 1966; Bombosch & Völk 1966). The latter authors concluded that oviposition by *S. corollae* is directed to the presence of the aphid.

Gravid females are attracted to honeydew as a cue for finding a suitable site for oviposition. Volatile olfactory cues from honeydew-treated plants attract more syrphids than non-treated plants or honeydew (Budenberg and Powell 1992), and liquid exudations of aphids are an important source of chemical stimuli (Schneider 1969). *Episyrphus balteatus* laid eggs in response to artificially applied honeydew and the numbers of eggs laid by this insect increased as the concentration of applied honeydew increased (Budenberg and Powell 1992). Similar responses to honeydew have been observed in other predators. For example, *Chrysopa carnea* is attracted to the kairomone in the honeydew, possibly due to acidification of tryptophan (Hagen *et al.* 1976).

Investigations on the relationship between the density of aphids and the number of eggs laid by syrphids on different host plants have produced differing results. Most aphidophagous hoverflies lay eggs on heavily infested plants and among the largest aphid colonies to supply ample food for their larvae (Dixon 1959; Peschken 1965; Bänsch 1965; Chandler 1968b; Tamaki and Long 1978; Budenberg 1992) but such a strategy results in a delay of syrphid larvae in controlling aphid density (Hughes 1963). The optimum size of aphid populations for oviposition are different according to the syrphid species; density-dependent oviposition of syrphids may only occur when the number of *Brevicoryne brassicae* (L.) exceeds more than several hundreds per plant on brussels sprout (Chandler 1968).

Some species of syrphids respond to a specific number of aphids. Tamaki *et al.* (1967) showed that 30 or more peach aphids, *Myzus persicae* , was the optimum for laying eggs on leaves of peaches in autumn. He also demonstrated a positive relationship between the number of syrphid eggs and the number of aphids up to 30-40/leaf. However, there was no relationship between the number of syrphid eggs and the number of aphid when densities exceeded 40 aphids per leaf. Tamaki *et al.* (1967) showed that the number of aphids per unit area of leaf rather than the number of aphid per leaf is a factor which strongly affects syrphid oviposition. A similar response to aphid density was observed in *Syrphus* sp. which did not lay eggs on *Eucalyptus* trees until more than 10% of the psyllid nymphs present on a test area reached the fifth instar, and heavy oviposition occurred only when over 50% of the psyllid test area contained nymphs (Clark 1963). On 23 to 56 cm high thuja trees in a nursery, syrphids laid few eggs when aphid numbers were low and increased in response to higher numbers of the aphid *Cinara tujafilina* (del Guercio.) (Furuta 1988). Dixon's investigations (1959) on broom, *Sarothamnus scoparius* (L.) have shown that the syrphids laid eggs at low aphid densities but more eggs were laid on the larger colonies of the aphid *Acyrthosiphon spartii* (Koch.).

For some species of syrphids, no significant correlation may exist between the number of syrphid eggs and the number of prey. *Parasyrphus melandri* feeds on chrysomelid larvae, but no relationship between the number of eggs and the number of chrysomelid larvae was observed (Rank & Smiley 1994). Similarly, no relationship was detected between the number of syrphid eggs and the number of *Brevicoryne brassicae*. on brussels sprout plants (van Emden 1963). However, Chandler (1968b) suggested that the reason for the results of van Emden was the low population of *Brevicoryne brassicae* .

The background of a crop often influences the number of aphid colonies on a plant. Thus, *Brevicoryne brassicae* are more attracted to sprout plants in bare soil than amongst weeds (Smith 1976b). Although it is convenient for the natural enemies of insects to be attracted by the same optomotor and colour stimuli as their prey, this has not been shown in many species (Smith 1976b). For example, *Episyrphus balteatus* is attracted onto the sprout plants among weeds and lays more eggs on sprout plants between weeds than those on bare ground, providing the aphids are scarce. Otherwise, high populations of aphids override the plant factors as ovipositor stimuli and the syrphid is then attracted to the sprout plants in bare soil (Smith 1976 b).

Quality of aphid colonies and strata that aphids live on are factors which stimulate oviposition in syrphids. In the laboratory, when a suitable chemical stimulus is present, crinkled surfaces, crevices and corners in the plant surfaces were preferred as oviposition sites (Bombosch 1966). Aphidophagous hoverflies visually select between suitable aphid colonies by the number of alates or young colonies (Kan 1988a, b & 1989; Hemtinne *et al.* 1993; Kindlmann & Dixon 1993). Bombosch (1966) reported aphids' colour as a stimulating factor for syrphids to lay eggs.

The height of plants may influence the number of eggs laid by syrphids. Chandler (1968d) studied the height preferences for oviposition of aphidophagous Syrphidae in the cage and in the field on bare and weedy soil. He found that each syrphid species laid most of their eggs in a certain height. In general, he concluded that the height preferences for oviposition depends on the habitat that the species naturally prefers.

The synchrony of life stages of the predator and aphid may also influence the population size and effectiveness of a predator (van Emden 1965). Chandler (1967) states that a predator which lay eggs in advance of infestation, or in the presence of low population of aphids, is likely to be more effective in biological control. For example, two spotted ladybirds laid eggs well before the peak of aphid population (Hemptinne *et al.* 1992). Similarly, the egg laying of syrphids in maize stands starts slowly but the majority of eggs

(50% of total eggs) are laid when the number of aphids are at the peak (Racz 1986). Syrphids and hemerobiids were more closely synchronised with aphids than coccinellids on maize in Canada. However their numbers were too low to control *Rhopalosiphum padi* (L.) and R. *maidis* (Fitch.) on maize (Coderre and Tourneur 1986). Maximising the fitness with regard to biological control, aphidophagous ladybirds need to synchronise their reproduction with the early stage of aphid population (Hemptine *et al*. 1992)

Visual, chemical and mechanical stimuli create a complex pattern of oviposition stimuli but chemical stimuli are the most effective factors in selecting oviposition sites (Dixon 1959). Aphidophagous hoverflies select their oviposition habitats and plants by optical and olfactory responses through the size, density, colour, form and odour of plants. Then, the aphid colonies are selected by gustatory and optical response to honeydew and aphid form. After that, the actual sites of oviposition are selected by tactile response through the movement of aphid appendages (Chandler 1966, 1968 c).

2. .3. 7 Food resource selectivity of adults

Pollen and nectar of flowers are food of adult hoverflies. Pollen is used as a source of protein for the development of ovaries in females. Pollen, which is rich in amino-acids, increases adult longevity and oviposition time, shortens larval development and reduces larval exposure to predation (Schneider 1969). Males also feed on pollen but consume less than females. Nectar provides carbohydrates for energy-consuming activities (Haslett 1983). The males of the syrphid *Rhingia campestris* (Meigen.) ingest a significantly greater proportion of nectar to protein than females (Haslett 1989b). Females feed on nectar only at the beginning and at the end of ovarian development. The first peak of nectar consumption is associated with finding a male and the second is related to oviposition efforts (Haslett 1989b).

Gut dissection is used to identify pollen spp. consumed by hoverflies. Haslett (1983) using a photographic method, observed pollen digestion in hoverflies and concluded that *Cheilosia albitarsis* (Meigen.) and *Rhingia compestris* (and probably all other pollen eating syrphids) obtain nutrients from pollen by causing the grains to exude their contents into the gut by rupturing from the pollen tube. The exact conditions which cause the pollen grains to exude the content are not clear, but Haslett (1983) suggested that nectar sugar in the gut may provide the stimulus. A small proportion of the pollen remained intact and passed out of the fly undigested.

Some species of hoverflies are highly selective in feeding on pollen, whereas others feed on pollen from a number of plant species (Haslett 1989b). In the literature, the terms 'specialist' and 'generalist' are used to distinguish between two types of food resource exploitation (Jervis & Kidd 1996). In New Zealand, Wratten (1995) indicated that *Melanostoma fasciatum* (Macquart.) and *Melangyna novaezelandiae* fed on 13 types of pollen and *Taraxacum*-type pollen was the most frequent in the guts. In Europe, *Scaeva pyrastri* consumed 14 different pollen species in early spring (Schneider 1969). Holloway (1976) investigated pollen feeding in 11 species of New Zealand syrphids from 6 genera. He classified the hoverflies into 2 groups: (i) large and very hairy species which ingested a wide variety of pollen, almost all from entomophilous species of plants: (ii) small and relatively hairless species, including *M. novaezelandiae* which ingested 1-6 kinds of pollen mostly from anemophilous plants.

Pollen in the gut can not always be used as an indicator of hoverflies' selectivity. Pollen may be trapped in nectar, honeydew or dew, or collected from the surface of leaves (Gilbert 1986; Gilbert 1991; Ssymank & Gilbert 1993; see also Jervis & Kidd 1996). Some species feed on nectar more than pollen, and high-nectar flowers are visitied more frequently by these syrphid species; analysis of gut contents of these species may yield only pollen, and therefore be a poor indication of diet. Therefore, flower species visited by syrphids may sometimes be a better measure of selectivity of hoverflies. In New Zealand, Primack (1983) showed that *Melangyna novaezelandiae* (Walker) visited 6 native and 2 non-native plants whereas *M. novaezelandiae* visited 23 native and 5 non-native species of plants in New Zealand.

There is a close relationship between the morphology of mouthparts and the diet of hoverflies, namely between the depth of corollae and the frequency of syrphids visiting flowers. Handling time in adult syrphids is usually measured from the time of inserting the proboscis to sucking up nectar and withdrawing the proboscis. Hoverflies with a longer and thinner proboscis ingest a greater proportion of nectar, compared to those with a short proboscis which ingest more pollen (Gilbert 1981). However, Haslett (1989b) showed that *Rhingia campestris* which is a specifically long-tongued species and is associated with flowers that have deep corrallae, widely utilised shallow flowers from all the wavelengths of the 'blue' group (Haslett 1989b). He concludes that colour and availability of food are more important than the effects of depth of corolla for this species (Haslett 1989b). Gilbert (1991), considered that colour and odour probably influenced flower selection by hoverflies.

Flower species are not necessarily visited by hoverflies in proportion to their abundance in a given habitat (Cowgill 1989). Selectivity of hoverflies is quantified by comparing pollen of the gut with relative abundance of food resources available (Haslett 1989a). Haslett (1989a) quantified the variation in pollen feeding between 6 species of UK hoverflies by using a 'selectivity' index He calculated the index by the formulae $S(A)=\frac{\sum p/f}{n}$ or $S(B)=\frac{\sum (f-p)2}{n}$ where p is the mean proportion of each pollen types eaten by a fly species, f is the proportion of the equivalent flower species in the habitat and n is the total number of the pollen types eaten. Cowgill *et al*. (1993) used Murdoch's index (Murdoch 1969) to compare the ratio of the number of flower type in the diet of the flies with the ratio in the environment by the formula $C=\frac{Ne/N'e}{N/N'}$, where Ne and N'e are the number of visits to species I and II, respectively; N and N' the abundance of plant species I and II respectively. Values of 0-1 and more than 1 to infinitive indicate selecting and non-selecting behaviours respectively .

2. 3. 8 Diurnal activities of adults

Light intensity, temperature, humidity and wind velocity are the main exogenous factors which influence diurnal activities of insects (Corbet 1966). However, it is not possible to separate the influence of all weather variables on the activity patterns of insects. The main determinants of syrphid diurnal activities are probably the thermal economy and the size of the species (Gilbert 1985; Wilmer 1983). A negative correlation was observed between thoracic width and percentage of time spent flying, and the largest species appeared first in the morning (Gilbert 1985). The properties of cuticle for reflecting sunlight is an important factor in the early-morning thermal balance (Wilmer & Unwin 1981; Wilmer 1983). This is a particular advantage in the cool days of spring for larger species to access floral resources earlier than smaller species (Gilbert 1985). Although hoverflies have more activities on sunny days, in general with little exception, some species avoid direct sunlight near the middle of the day (Maier and Waldbauer1979), while others are inactive during a cloudy period (Kevan & Baker 1984).

Gilbert (1981) classified hoverfly activities in different categories: pollen feeding, nectar feeding, simultaneous pollen- and nectar-feeding, aphid honeydew-feeding, imbibing water, resting, cleaning, hovering, mate searching, mating, and oviposition. However, he later simplified the behaviour to feeding, flying and resting (Gilbert 1985). Cowgill *et al* (1993b) followed Gilbert's first classification but in the final analysis of results they pooled categories of grooming, ovipositing, imbibing water, hovering and copulating to form the category "others". Pollen, nectar and water are taken at different times of the day by adult syrphids. The adults of all the species studied so far, always feed on pollen in early morning; nectar feeding increases to a peak near midday; and water feeding near midday in some other species (Gilbert 1985) . However, nectar and pollen are often available together and when foraging one, the other will be obtained (Haslett 1989). Feeding from flowers occurred significantly more in the sun than in the shade, especially for nectar feeding hoverflies (Gilbert 1985).

The peak activity of hoverflies may occur at different times of the day depending on plant and hoverfly species and season. In the UK, Wilmer (1983) showed that the peak number of all hoverflies on the plant *Heracleum sphondylium* (L.) occurred around mid morning, declined rapidly in the early afternoon and few were seen by 14:00 hours GMT, whereas no clear peak was observed on the plant *Tilia platyphyllos* Scop. In the United States, Lewis and Taylor (1964) found the peak activities of 13 species of hoverflies to be between 1100 and 1400 hours GMT. In addition, males of all species flew both in the sun and shade, but females flew mostly in shadedy spaces (Gilbert 1985c).

2. 3. 9 Adults and colours

Colour is an important floral attribute and a long distance signal which attracts actively flying diurnal anthophiles, eg. Diptera and Hymenoptera. Yellow flowers are highly attractive to most diurnal anthophiles. Ultra violet reflection, which provides blue colour for flowers, is usually not attractive to insects (Kevan 1978). Kevan (1978) named the colours for insects equivalent to man. Based on this nomenclature system, colours at the same analogous positions on insect trichromatic diagrams receive the same name, but with a prefix such as 'bee' or 'insect'. For example, human yellow and blue are "insect-red" and "insect-green" respectively (Kevan 1978). Visual cues for the initial detection and learned discrimination provided by the colour patterns of flowers, are two signalling systems which orient bees and hoverflies towards flowers (Lunau 1993).

A clear colour preference is observed in some species of hoverflies. *Cheilosia* spp. prefers the blue and low UV, *Rhingia* spp. blue and violet, *Volucella* spp. white and *Eristalis pertinax* (Scopoli.) yellow, and to a lesser extent white (Haslett 1989). *Episyrphus balteatus* and *Metasyrphus corollae* prefer many food plants with white flowers, however, colour choice experiments show that preferences are not absolute and it is necessary to compare the availability of different flower colours in the habitat at the time of the syrphid species' activity (Haslett 1989b).

2. 3. 10 Mobility and migration

In a diverse environment, dispersion of an animal is an important factor for the long-term development of a population (Andrewartha & Birch 1954). Insect movement may be restricted to the habitat normally occupied (trivial movements) or take the insect away from its original habitat (migratory movements) (Southwood 1962).

Migratory behaviour is typical of generalist predators such as *M. corollae* (Kennedy 1961; Svensson 1984), and usually occurs early in the adult stage (Svensson 1984). Syrphid adults can easily escape from non-suitable environments (Schneider 1969). Then, the energy invested in flight reduces fertility (Roff 1977).

The migration patterns have been observed in some species of hoverflies; for example, *Episyrphus balteatus*, *Eupeodes corollae*, *Syrphus vitripennis*, *Eupeodes latifasciatus* (Macquart.) *Melanostoma mellinum* (Linnaeus.), *Sphaerophoria scripta* and *Didea fasciata* (Maquart.). Hundreds of thousands of *Episyrphus balteatus*, which is a generalist predator, were caught during migration in the Valais Alps in Switzerland (for overview see Schneider 1969). Migration of *M. corollae* was followed along the south-east coast of Sweden by the use of water traps. The migration occurred within 1-2 days against the wind; the origin of this migration was not clear but analysis of the migrants' guts showed that they had consumed pollen from plants which did not grow in the area of study (Svensson 1984). During investigation of the migration of *M.corollae*, Svensson (1984) showed that more females than males were captured by water traps. Svenson stated that females of *M.corollae* tend to migrate when the aphid density is low in the area in which they emerge. However, the males may not response to this stimulus. This and differential losses might be explanations why more females were captured during migration (Svensson 1984).

Most investigations on the migration of hoverflies have been performed in cool-temperature zones in northern Europe, where food for adults and larvae is scarce during autumn and winter. Autumn migration may be related to the search for winter habitats (Schneider 1969). In contrast, in the Mediterranean climate of South Australia, food is more abundant in winter, but scarce in summer which, by analogy with Europe, suggests that migration, if it occurs, may be in spring.

In addition to migratory behaviour, syrphid flies may sometimes move long distances from feeding place to egg-laying sites but prefer areas where food sources are near to oviposition sites (Schneider 1969). By dissecting hoverflies and detecting the presence of *Phacelia* pollen grains it was indicated that hoverflies which had fed in a *Phaceilia* strip moved up to 250 metres to lay eggs on cereal plants (reviewed by Wratten and van Emden 1995).

2. 3. 11 Natural enemies

Syrphid fly populations suffer from mortalities caused by different types of predators, parasitoids and diseases.

Kristin (1991) studied the diet of nestlings of 13 species of insectivorous songbirds in beech-oak forest in May-June during two years. He found that Syrphidae were consumed by 11 species (84%) of birds. Of those eaten, 76% were larvae, 3.8% were pupae and 19.9% were imagos.

In India, life table studies of the syrphid *Metasyrphus corollae* showed that it suffered high mortality from a number of sources including bacteria such as *Bacillus* spp. (Sharma & Bhalla 1992), and parasitization, mainly by *Diplazon multicolor* (Gravenhorst.) and *Diplazon laetatorius* (Fabricus.) (Hymenoptera: Ichneumonidae; Diplazontinae).

Nakata (1994) reported that *Orius sauteri* (Poppius) (Heteroptera: Anthocoridae) preyed on syrphid larvae in a potato field in Japan.

In Australia, Clark (1963) stated that the low survival rate of *Syrphus* sp. larvae on *Eucalyptus* trees was due to parasitism by pteromalid and ichneumonid wasps and also by mortality from birds, lizards, the ant, *Iridomyrmex purpureus* (Smith.) and a (Bacterial/fungal) disease. In the diseased larvae, a discolouration occurred and they soon died and adhered to leaves. Other factors that cause mortality in syrphid larvae are cannibalism, dislodgement from foliage by wind, and shedding leaves (Clark 1963).

The following families of Hymenoptera contain species which are parasites of syrphid larvae: Braconidae, Ichneumonidae, Encyrtidae, Eupelmidae, Pteromalidae, Chalcididae, Figitidae, Ceraphronidae, and Diapriidae (Schneider 1969). The subfamily Diplazontinae (Ichneumonidae) is the commonest recorded source of parasitoids of aphidophagous Syrphidae (Rotheray 1981). *Diplazon laetatorius* is one of the most common and detrimental species of Syrphidae, but the defence reaction of blood cells in the larvae of some Syrphidae may eliminate the egg of *Diplazon* species (Rotheray 1981; Beckage 1985). Rotheray has also studied *Callaspidia defonscolombei* Dahlbom and *Melanips opacus* (Hartig.) Figitidae, and *Bothriothorax clavicornis* (Dalman) and *Syrphophagus* sp. Encyrtidae (Rotheray 1979, 1981).

Adult *D. laetatorius* and *D. tibiatorius* consume syrphid eggs and first instar larvae usually after oviposition. Syrphid eggs are also eaten by *Enizeum ornatum* (Gravenhorst.) and *Homotropus pictus* (Gravenhorst.) without initial attempts at oviposition (Rotheray 1981). Females of *E. ornatum* eat or kill larvae of all instars of syrphids, especially when they are old or deprived of hosts for a few days (Rotheray 1981).

Parasitoids are attracted to their hosts by different cues. The parasitoid of hoverfly larvae responds to contact chemicals present on the larval integument but the texture of the integument is not important, and since the parasitoids of syrphid larvae do not use visual cues for searching, it is doubtful that larval cuticular pattern attracts the parasitoid (Rotheray 1979, 1981). On the other hand, movement is a necessary cue to stimulate oviposition behaviour in *E. ornatum* (Rotheray 1981). The host haemolymph stimulates the parasitoids to release eggs, and differentiation of this cue is the reason for specificity in host relations (Rotheray 1984).

Syrphid parasitoids, depending on species, oviposit in specific parts of larva; *Bothriothorax clavicornis* (Encyrtidae) and *Syrphophagus* sp. (Encyrtidae) lay eggs just behind the head and at the posterior end of larvae, respectively (Rotheray 1981), while *Callaspidia defonscolombei* (Figitidae) lays egg in the lobes of the cerebral ganglia of the host (Rotheray 1979).

Rotheray (1981) has calculated the oviposition rate for each of the six species of hoverfly parasitoid by dividing the mean handling times (during which a parasitoid attacks, subdues a host, oviposits and prepares for further search, Waage 1983) by the number of eggs usually oviposited per host. He suggested that *D. laetatorius* and *D. tibiatorius* with fast oviposition rates are potentially able to spend longer periods of time searching for hosts and are at advantage over competitors.

2. 4 Prospects for increasing syrphid numbers in crops

2. 4. 1 Feeding habits and abundance

There are four factors which limit natural syrphid populations: (1) access to pollen for oogenesis in females, (2) presence of aphids for stimulating oviposition and providing food for larvae, (3) parasites and predators, and (4) weather conditions. In addition, chemical insecticides is an "unnatural" factor which limits syrphid abundance. These factors affect the natural rate of increase of syrphid population and make it more complicated than the rate of increase measured in the laboratory (Barlow 1961).

In comparison with adults which feed on pollen and nectar, syrphid larvae use diverse food resources. The diversity, distribution, abundance, and stability of syrphid species are related to the larval feeding habits. Those species whose larvae live in leaf litter and feed on arthropods, or aphidophagous larvae, are more abundant than monophagous species restricted to herbs, trees, galls, subterranean aphids and those living in specialised habitats such as tree rot holes and social-insect nests. In general, amongst predatory syrphids, those with restricted prey are least abundant (Owen and Gilbert 1989).

Owen and Gilbert (1989) in their 15 years of weekly sampling by Malaise-traps in the UK showed that: (i) when syrphid were categorised into saprophagous, predatory and phytophagous, they showed the same average abundance; but saprophages are more widely distributed and phytophages were most restricted, (ii) when syrphids were grouped on the degree of feeding specialization, polyphagous species such as *Syrphus ribesii* were more abundant, less stable and more widely distributed than moderately specialised species such as *Platycheirus scutatus* The highly specialised predators had a stability of population numbers as low as polyphagous predators whereas the moderately specialised ones, such as *Platycheirus ambiguus* (Fallén.), showed the least fluctuation in their populations.

2. 4. 2 Plant diversity and abundance

Diverse communities are more stable than simple ones (Elton 1958; MacArthur 1955; Watt 1965) because natural enemies are more efficient in diverse systems than in simple ones whereas in simple systems specialist herbivores easily find, stay and reproduce (Root 1973, Wratten & van Emden 1994).

Many indigenous biocontrol agents may be eliminated by replacement of natural vegetation by monocultural crop systems (Waage & Barlow 1986) which do not provide adequate food for them (Powell 1986). Habitat management through the following methods are used to boost the number of natural enemies and decrease the number of pests (van Emden 1990; Wratten & van Emden 1994):

1- Replacing crop species, which are attacked by larger pest numbers, with less vulnerable species or introducing resistance crop cultivars

2- Crop arrangement in space; mixed and row intercropping,

3- Plant ground cover in crops; like intercropping, undersowing or the presence of weeds,

4- Providing plant diversity outside the crop

5- Planting flowers attractive to natural enemies in or near the crop

The effects of weeds on increasing the number of predators and parasitoids are accounted for in the literature. Intercropping or the presence of weeds frequently decreases the number of pests on crops (Ryan, *et al.* 1980; Smith 1969). Fewer immigrant aphids and higher numbers of anthocorid predators were observed on the weedy plots of brussel sprout plants (Smith 1976 a,b) while aphidophagous syrphids from the genus *Melanostoma* laid 1.5 times as many eggs on sprout plants in weedy plots.

The creation of a grass-sown raised earth bank within farmlands increased the number of predators, mainly species of Araneae, Carabidae and Staphylinidae, from 150 m^{-2} in the first year to 1500 m^{-2} in the second year (Thomas *et al.* 1991). Greater mortality from predation was observed in a population of *Brevicoryne brassicae* at the edges than at the centre of a *Brassica* crop because of the presence of flowers nearby (van Emden 1965b).

Plants outside the crop provided sources of food for adults, alternative prey at times of prey scarcity within the crop, and a place for overwintering and oversummering (Wratten & van Emden 1995). The prey living on plants outside the crop may provide a reservoir of natural enemies when the beneficial insects on the crop are killed by insecticide or during the removal of the crop after harvesting (van Emden 1990). Harwood *et al.* (1992) monitored hoverfly activity using fluorescent yellow water traps in transects at right angles to the field margins provided with and without native wild flowers. They indicated that wild-flower strips around the margins influenced the local abundance of syrphids. Similar results were obtained in a replicated within-field experiment conducted in cereal crops by Cowgill *et al.* (1993b). They recorded the highest number of *Episyrphus balteatus* in the untreated headland strips.

The importance of field boundaries in providing an overwintering habitat for many polyphagous predators in farmlands was demonstrated by Sotherton (1984, 1985). Demonstration of the impact of highly mobile beneficial insects such as syrphids (van Emden 1990) on their hosts with and without-crop diversity is difficult. However, Pollard

(1971) showed that the number of eggs laid on sprout plants at two sites that were 5 km. apart were significantly higher in diverse sites than in arable sites.

There is little work published on the effects of field-boundaries on pest control programs in Australia. However, a joint research project between Lincoln University, New Zealand and Orange College (University of Sydney) will investigate the influence of field-boundaries on biocontrol agents (Wratten & van Emden 1995).

In conclusion, to make decisions on retaining the wild plants in relation to the pest problems is difficult (van Emden 1981) because weeds can act as a reservoir of pests (van Emden 1981). In addition, weeds may be the alternative hosts for pests in cold climates. Thirdly, insects feeding on weeds may also be 'forced' off the plants by early maturation, by lack of weed food caused by the insects own attack or by the use of herbicedes (for overview: see van Emden 1981). Therefore, the diversity *per se* is not important, but the important point is that the changes in habitat diversity should be purposely designed to obtain specific effects within the relevant socio-economic constraints of the crop (Powell 1986).

2. 4. 3 Plants attractive to syrphids

Adult syrphids feed on pollen and nectar (Schneider 1969). The aim of providing attractive floral resources for hoverflies in croplands is to boost their potential for bio-control (MacLeod 1992). However, the consequences of increasing some of these plants near or in crops are unknown (Wratten & Powell 1991), and many native flowers that attract beneficial species of hoverflies are weeds and their encouragement would not be agronomically acceptable (Cowgill 1989).

Different plants and flowers have various levels of attraction to hoverflies. Therefore, adult syrphids may be selective or generalist in feeding on pollen (Haslett 1989b; Cowgill 1989). For example, In Yugoslavia, the flowers of *Paliurus spina christi*, *Chrysanthemum cineraraefolium* and *Castanea sativa* attract hoverflies in large numbers in the middle of

June (Schneider 1969). *Melangyna viridiceps, Melangyna* sp. and *Simosyrphus grandicornis* were each less than 1% of visitors to macadamia flowers in eastern Australia (Heard & Exley 1994).

A study in the UK of the foraging activities of hoverflies on 5 different plant food sources: borage *Echium lycopis* (Boraginaceae), buckwheat *Fagopyrum esculentum* (Polygonaceae), coriander *Coriandrum sativum*: (Apiaceae), marigold *Calendula officinalis* and sunflower *Helianthus annuus* (Asteraceae) showed that colour, depth of corolla tube and nutritional value of pollen were the most important factors in determining food preference by syrphids (MacLeod 1992). Of these, buckwheat and coriander were the two most attractive to the syrphids *Episyrphus balteatus* and *Metasyrphus corollae*. However, when coriander was sown around a field of winter wheat, it failed to significantly increase syrphid diversity when assessed as species numbers within that field (MacLeod 1992).

Tansy leaf, *Phacelia tanacetifolia* (Benth.) (Hydrophyllaceae), and buckwheat are two species of plants which have been shown to provide pollen and/or nectar for hoverflies (Wratten & Powell 1991). *Phacelia* is grown in West Germany to provide nectar for honeybees, and is sown in the U.K as a cover crop in areas low in nitrogen (Wratten & Powell 1991).

The 'habitat island' of strips of flowering coriander and tansy leaf was used to study field penetration of hoverflies. The pollen types of the two plant species were used as a marker to determine how far adults of *Melanostoma fasciatum* penetrated into the field. The results indicated that this hoverfly species penetrated at least 15m in each direction from central strips (Lövei *et. al.* 1993a). Hickman and Wratten (1994) indicated that more syrphids *Episyrphus balteatus* and *Metasyrphus corollae* were attracted to the field with *Phacelia* than that without *Phacelia*. In contrast, more aphids were found in the field without *Phacelia* than in fields with this plant species. Similarly, the number of adults of *M. fasciatum* on cabbages was approximately seven times as many in plots with *Phacelia* than in those without. Although no significant differences in numbers of syrphid eggs were observed fewer aphids were found in plots with *Phacelia.*

The attractiveness of some novel crops for hoverflies was compared in New Zealand and the UK (Lövei *et. al.* 1993b). In New Zealand, buckwheat, *Phacelia*, coriander and quinoa Chenopodium quinoa (Chenopodiaceae); and in the UK, buckwheat, coriander, sunflower, borage and marigold were compared for the number of attracted hoverflies. The authors concluded that coriander was the best candidate as an attractant crop for syrphids, and that buckwheat and *Phacelia* should be tested further. However, Hickman *et al.* (1995) observed that gravid females of *M. fasciatum* consumed twice as many *Phacelia* pollen grains as coriander in New Zealand.

Wratten and van Emden (1995) concluded from recent field studies that syrphid numbers could be increased by increasing the flora of field margins and within crops, and choosing the right type of plant diversity. They recommended drilling *Phacelia* seeds around the UK cereal fields in spring to provide a cheap (one UK penny/metre) ground cover in place of weeds, increase foraging by honeybees and bumble bees and provide a focus of interest for the farmer. Most investigations on *Phacelia* and other attractive flowers have been concentrated in UK and New Zealand around cereal fields. The usefulness of *Phacelia* under Australian conditions, where the species of hoverflies are different from those in the UK and New Zealand, remains to be tested. *Phacelia,* which was planted in South Australia to enhance the efficacy of parasites of red scale of citrus, did not survive the hot late spring and summer and it was also unsuccessful as a fodder crop (Maelzer 1994, personal comm.).

2. 5 Techniques for estimating syrphid abundance and activity

2. 5. 1 Standard walk-recording

Hoverflies are swift fliers and it is not easy to assess their incidence in place and time (Schneider 1969). However, a standard walk-recording method has been used in many investigations to estimate the relative population size of syrphids in a certain place at specific times. Maier and Waldbauer (1979) used a standard walk to measure diurnal activities of syrphids by capturing resting syrphid flies or those which were feeding or flying within one meter of the plants during the first half of each hours between 0700 and 1800. MacLeod (1992) also used 24 standard census walks, lasting 15 min each, along a 200 m strip of coriander between 06:30 and 12:30 BST to estimate the effect of coriander flowers on the numbers of attracted syrphids. However, he could not show a significant difference between the treated and control plots. Gilbert (1981 & 1985) also used a standard census walk method at constant speed, three times a day usually beginning 30-60 minutes before sunrise and ending between 16.00 and 16.30 to investigate the pattern of feeding of syrphids on nectar and pollen and test the relationship between the length of tongue and the proportion of pollen or the number of visits on different depth of corollae. Cowgill (1993a,b) similarly investigated the numbers and behaviour of syrphid flies during standard walks in fixed time intervals .

2. 5. 2 Water traps

When cone traps, single rebel sticky traps, double rebel sticky traps and Canadian traps, were compared with water traps, the latter were found to be the most efficient in catching hoverflies (Finch 1990, 1991).

Yellow water traps were developed for catching alate aphids (Evans & Medler 1966) but they have also been used to trap syrphids (Finch 1990, 1991, Dixon 1959, Smith 1976). The attraction of hoverflies to different colours of water traps is based on their visual attraction to flowers as pollen and nectar resources (Powell *et al.* 1996). Water traps with different colours have been used to estimate the relative numbers of syrphid populations in colour preference experiments. However, the attractiveness of the traps depends on the abundance of syrphid-attracting plants, not the population size of..? (Ssymank and Godesberg 1991). For example, a greater number of syrphids were captured at the flowering time of broom plants and the numbers decreased by the end of flowering period (Dixon 1959).

Yellow is not the most appropriate trap colour to use for every purpose because it is not ecologically selective (Kirk 1984). Each trap colour catches more than one ecological group. Therefore, by careful choice of colours, it should be possible to catch particular group(s) of insects; e. g. non-grass foliage insects and their predators and parasites; grass foliage insects; flower dwelling insects; predators and parasites associated with foliage; wood-borers (Kirk 1984). Finch (1995) suggested that changing the background of water traps provides insects with additional choices which is sufficient to reduce the numbers that land in the trap.

Site, colour of outer surface, and the height of a water trap are important in capturing syrphids. To ensure that natural populations of predators are not depleted by trapping, water traps are placed well into the crops, and the numbers of captured beneficial insects can be reduced. Painting the outer surface of bowls black, further reduced the number of syrphids captured, in comparison with the standard yellow trap (Finch 1990, 1991). The height of water traps is an important factor for catching males and females; the traps with 30 cm height caught more males, whereas those at soil level caught more females (Finch & Skinner 1974).

An experiment with sticky traps with different colours, orange, white, lemon yellow, golden yellow, black and green has shown that the white traps were most effective to attracting aphidophagous syrphids, *Episyrphus balteatus*, *Metasyrphus corollae*, *Sphaerophoria scripta*, *Chrysotoxum intermedium* (Meigen.) and *Syrphus sp.* (Ortu and Floris 1990). However, in another study, the attractiveness to hoverflies of 3 colours, white, blue and yellow was measured and it was shown that blue was most attractive, followed by white and yellow (Sol 1966).

The attractiveness of water traps depends also on the physiological condition of insects. For example, adult hoverflies are most trappable when they are newly emerged and hungry and when food sources are scarce (Schneider 1969; Sol 1966). Males and females may be caught in water traps differentially. Except for one female specimen of *Platycheirus* *manicatus* (Meigen.), all syrphids caught in water traps used by Dixon were males and she concluded that white traps only catch males (1959).

The movement of hoverflies into the field and the preferenced food resources can be measured by water traps. In an experiment, the traps were installed in transects from the field margin to the centre drilled with *Phacelia* strip. Then, the flies caught in traps were dissected to find *Phacelia* pollen. It was shown that flies moved up to 250 metres into the crop (Harwood *et al.* 1994). Similarly, fluorescent yellow water traps at right angles to wheat and coriander strips at distances of 1m, 5m, 15m, 25m, and 50m were used to investigate the number of hoverflies attracted to wheat and coriander (MacLeod 1992).

2. 5. 3 Suction traps

Johnson and Taylor developed and standardised suction traps to measure densities of flying insects (reviewed by Southwood 1978). These traps are now used for accurately estimating aerial populations of insects with more accuracy than in most other habitats. Wind speed, density of insects and periodicity behaviour of insects are factors which influence the choice of the type of suction traps (Southwood 1978). Unlike light traps operating at night, suction traps do not attract insects from a distance and capture only those flying over the traps (Banks 1959).

Banks (1959) investigated the abundance of syrphids by the use of 5 suction traps from April to November during 5 successive years in a study of the predator complex of *Aphis fabae*. Banks caught 32 species of a total of 54 common and frequent species of British syrphids. The total numbers captured per five years for 22 species were less than 10 and a maximum of 532 *Melanostoma mellinus*. Banks (1959) indicates that the strong flyers such as *Scaeva* spp and *Syrphus ribesii* may escape in small suction traps, while Schneider (1969) mentions that suction traps are effective in capturing the strong and lively species.

2. 5. 4 Sampling for immature stages

Population densities of aphid-specific natural enemies are usually underestimated because they are often overlooked. For example, the recorded numbers of syrphid larvae are very variable, especially the smaller ones, because they resemble the cast wheat in wheat fields (Chambers *et al* 1983).

In a study reported by Lapchin *et al.* (1987), three methods were used and compared for sampling coccinellids and syrphids in a winter wheat field. In the first, an observer walked within each sub plot and recorded the number of coccinellid and syrphid adults, pupae and larvae for 2 minutes. In the second, two observers walked successively within each sub plot and collected coccinellid and syrphid larvae and pupae. In the third method, wheat plants were collected from each sub-plot to examine the number of coccinellid and syrphid larvae and pupae in the laboratory (Lapchin *etal.* 1987). The population density of syrphid larvae estimated by the detailed visual method was less than 1% of that from plant sampling (Lapchin *etal.* 1987). Because of the low capture efficiency due to cryptic coloration, relative immobility, and resting in leaf axes, the visual methods were not suitable for counting the number of syrphid larvae (Lapchin *etal.* 1987). The plant sampling method was also found to be most suitable for larvae and pupae of the main species of syrphid, *Episyrphus balteatus* and *Sphaerophora scripta.* However, syrphid eggs are easily seen at the beginning of the season when the foliage area is small (Lapchin *etal.*1987) and may be counted with greater accuracy.

In most investigations, the number of immature stages of syrphids were recorded with the number of prey on the same sampling unit. For example, Tamaki (1974), studied the autumn population of *Myzus persicae* on peach trees, and numbered the first 10 leaves, five twigs per tree, with a felt pen. Then, the leaves were checked periodically for all life stages of aphids and natural enemies.

In winter wheat fields, Cowgill *et al.* (1993) used randomly selected 1sqm. quadrats to record, at weekly intervals, the number of wheat stems and the number of eggs and larvae of syrphids on the ear and upper leaves of each stem.

Chambers and Adams (1986) took samples at approximately weekly intervals in winter wheat, and examined between 100 and 400 shoots for aphids and syrphids. Ten plants of sugarbeet, broccoli and radish per each plot were randomly selected and the insect population on the same plant was counted 2-3 times per week (Tamaki *et al.* 1981).

Tenhumberg and Poehling (1991) studying the efficiency of syrphid larvae as predators of aphids on winter wheat, recorded the abundance of natural enemies by counting of 10 x 10 ears and flag leaves in the first year and whole plants (12 x 10) in the second year.

2. 6 The rose aphid, *Macrosiphum rosae* (Linnaeus.)

2. 6. 1 Taxonomy, origin, and distribution

M. rosae belongs to the tribe Macrosiphini in the sub-family Aphidinae (Hemiptera: Aphididae). This species is distributed throughout most of the world on wild and cultivated roses except eastern Asia (Blackman & Eastop 1985). *M. rosae* may have been introduced to Australia by European settlers (Maelzer 1977; Carver 1989).

2. 6. 2 Biology

2. 6. 2. 1 Life cycle

In regions with mild winter, e. g. Adelaide, *M. rosae* reproduces anholocyclically on rose (Maelzer 1977; Kitt 1996) but is occasionally found on *Centranthus ruber* (Valerianaceae), *Scabiosa* spp (Dipsacaceae (Dr M. Carver, personal communication). In the Palearctic region, its presumed area of origin, *M. rosae* may be concurrently and synoptically both anholocyclic on rose and holocyclic and heteroecious between rose and members of the families Valerianaceae and Dipsocaceae (Börner & Heinze 1957).

2. 6. 2. 2 Host plants

Rose aphids feed on all cultivars of *Rosa* spp. even though their suitability may be different (Kitt 1996). In addition to roses and the plant families Dipsacaceae and Valerianaceae, rose aphids can be found occasionally on other species of Rosaceae: *Fragaria*, *Geum*, *Pyrus*, *Malus*, *Rubus* and Onagraceae: *Chamaenerion*, *Epilobium* during summer (Blackman & Eastop 1985). In Australia, small numbers of rose aphids might be found on *Centranthus ruber* (L.) (Valenanaceae) and *Scabiosa spp*. (Dipsacaceae) (Maelzer 1977; Wöhrmann *et al*. 1991).

2. 6. 2. 3 Damage by *M. rosae*

In addition to direct damage by sucking sap from vascular system, *M. rosae* is able to transmit at least 12 virus diseases (Blackman & Eastop 1985). The economic injury threshold for *M. rosae* is 50 aphids per infested bud (Maelzer personal communication).

Chapter 3

General Materials and Methods

3. 1 Sites of study

This study was mainly conducted at four rose gardens in Adelaide, South Australia: Claremont, Urrbrae, Mercedes College and Centennial Park. Three other rose gardens were also used for occasional sampling.

3. 1. 1 The Claremont rose garden planting

The Claremont plot of 74 roses with an area of 611.5 m^2 (38.7m x 15.8 m) was located at the Waite Campus and provided with attractive flowers (Fig 3. 1 and 3. 2a). The roses were planted 1.5m x 1.5m apart on a southern slope. Twenty Hybrid tea rose bushes, were planted in November 1992, and the remainder of three varieties, Bettina, Zolta rose and Luis De Fumes were planted on 8 July 1993. All roses were numbered from one to 74.

Native plants recorded as being attractive to insects and birds (Anon. 1980; Eliot 1990; Dashorst & Jessop 1990) were planted around the Claremont rose garden. The following characteristics were considered for selection of the native flowers:

-fast growing and flowering for a long period.

-absence of prickles to allow easy sweep-net sampling.

-grow well in clay soil; the same soil in which the roses were planted.

-have yellow or white flowers which are reported to attract hoverflies.

-small to medium size shrubs suitable for counting adult syrphids.

The selected plants with these characteristics were: *Olearia axillaris* (D.C.), (Asteraceae); *Callistemon* sp. (Myrtaceae); *Grevillea crithmifolia* (R. Br.) (Proteaceae); *G. glabrata* (Lindl.), *Goodenia varia* (R. Br.) (Goodeniaceae); *Go. ovata* (Sm.), *Helichrysum* (Asteraceae). They were obtained from commercial nurseries in Adelaide and planted on 6 July 1993.

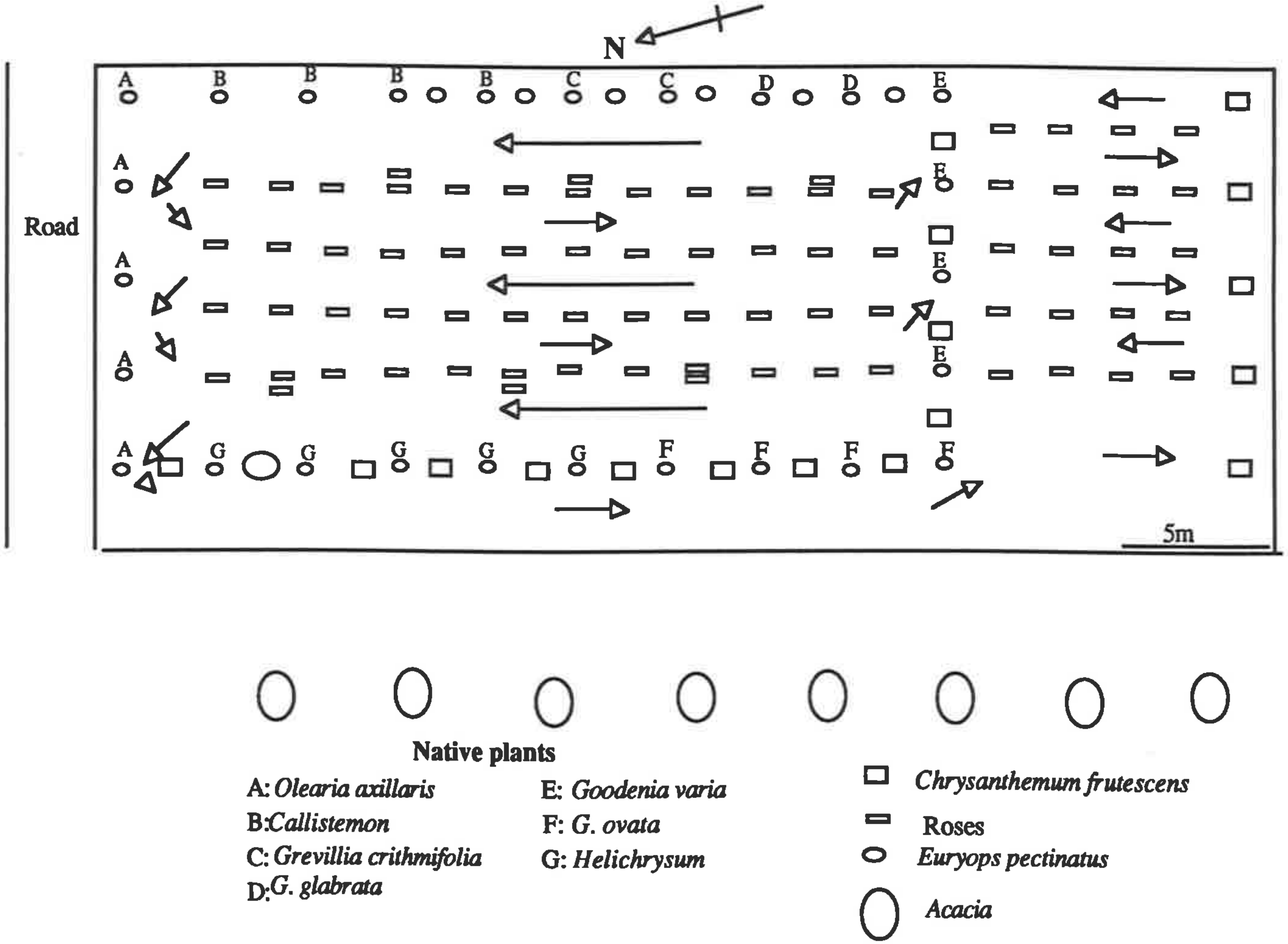

Figure: 3. 1: Census-walk direction. The Claremont rose garden and sites of attractive plants. Direction of census-walk is also shown (Chapter 4).

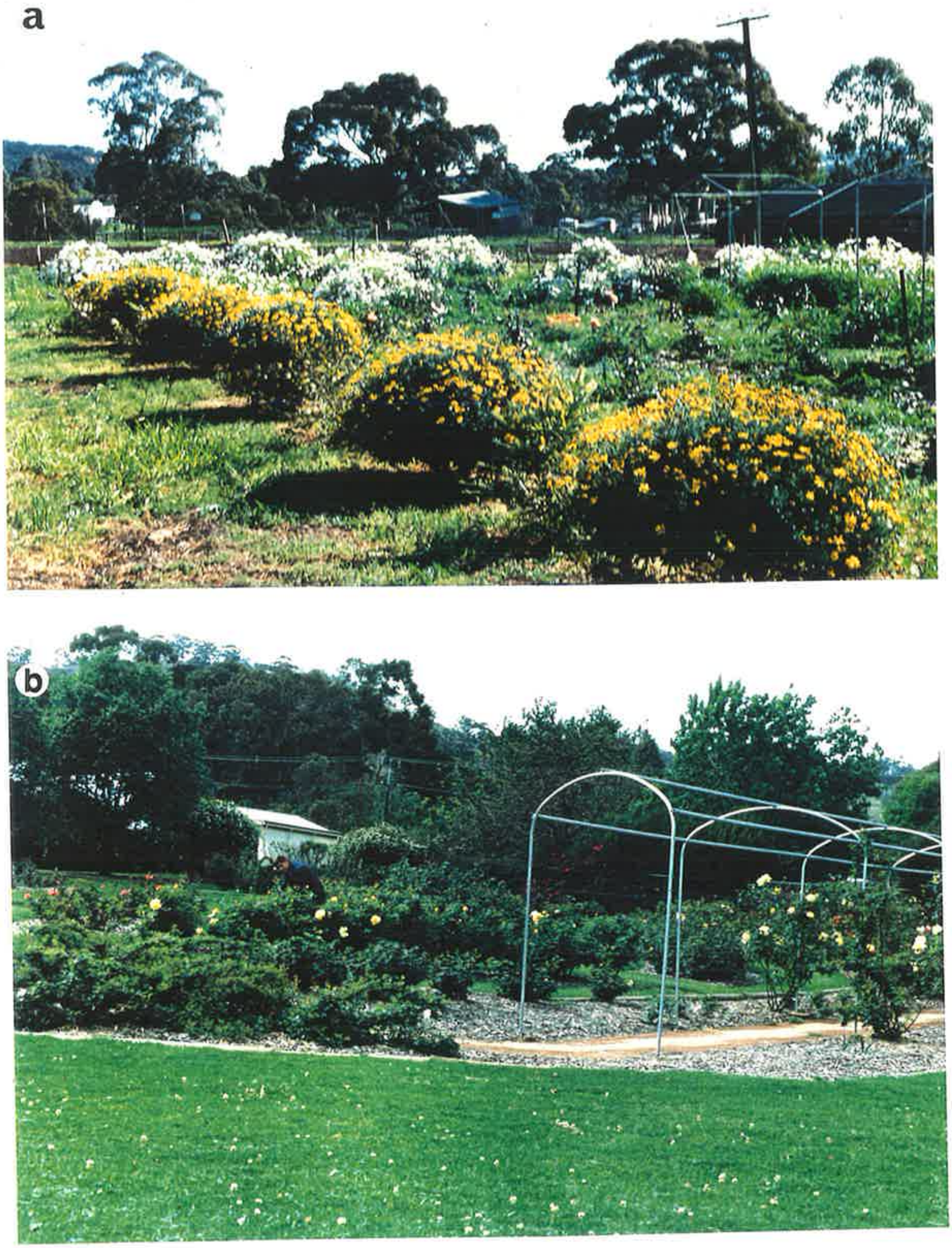

Figure 3. 2: Sites of study, a: Claremont rose garden, b: Urrbrae rose garden.

Figure 3. 2: Sites of study (continue), c: Mercedes College rose garden, d: Centennial Park rose garden.

In addition to native plant species, preliminary observations showed that some introduced plant species of daisy (Asteraceae) are attractive to syrphids. Therefore, 18 pots of the marguerite daisy, *Chrysanthemum frutescens* (L.) (Asteraceae) were propagated in the glasshouse at the Waite Campus and transplanted with 1.5m between plants on the southern and eastern sides of the Claremont rose garden, where they grew to a height of 30cm. One extra row was also planted 10m away inside the rose garden from the east side This plant species has white petals and a yellowish centre.

Another non-native "attractive" daisy was an African daisy, *Euryops pectinatus* (Cass.) (Asteraceae) of which 6 were obtained from a commercial plant nursery in Adelaide and planted at the north side of the Claremont rose garden. All the six daisy pots were transplanted on 8 July 1993.

Thirty six trees of 8 *Acacia* species in two rows had been planted 20m away from southern side of the rose garden in 1990. These species were *A. meisneri* (Lehm.) *A, podalyriifolia* (A. Cunn.), *A. decora* (Reichb.) *A. baileyana,*(F. Muell.) *A. drummondii* (Lindley) *A. microcarpa* (F. Muell.) *A. dealbata* (A. Cunn.), and *A. buxifolia* (A. Cunn.) (Mimosaceae); their heights ranged from 1.5-3m.

Maintenance of the Claremont rose garden

The roses and the attractive shrubs were irrigated according to temperature and rainfall by a drip system with 4 litres per hour with turbo keys. Therefore, the watering had no direct effect on the aphids. The rose flowers at stages 8-10 were pruned back fairly hard to induce further growth after weekly recording. All roses were annually pruned during winter in July. Copper based fungicides were applied against black spot twice during 1994. The weeds were cut 2-3 times a year in spring and autumn.

3. 1. 2 Other rose gardens

In addition to the Claremont rose garden, three pre-established rose gardens were also used for regular sampling. The Urrbrae rose garden (Fig. 3. 2b) was also located at the Waite campus but about 100m away to the north of the Claremont rose garden and just beside an arboretum with many different species of trees. This rose garden consisted of about 1000 bushes from different varieties of roses. No insecticides were used during the sampling program until the last week of February 1994. Thereafter, sampling was stopped and this rose garden was not used in the second year (94-95).

The Mercedes College rose garden consisted of 344 rose bushes located about 1 km to the south west of the Waite campus. The roses were more closely-planted than other rose gardens and surrounded by densely planted trees (Fig. 3. 2 c).

The Centennial Park rose garden had approximately 6000 rose bushes of different varieties and was located about 5 km to the south-west of the Waite Campus (Fig. 3. 2 d) with the central $1000m^2$ being sampled. No insecticides were used in this rose garden.

3. 2 Climate of South Australia

Adelaide is the driest Australian capital city and has a Mediterranean-type climate with cool wet winters and hot dry summers. Monthly rainfall averages over 50 millimetres from May (Autumn) to September (Spring) (Fig.3.3a) and is fairly reliable. Summer rainfall is light (Fig.3. 2A) and unreliable, and months with no rain are not uncommon. A high evaporation rate during the summer months limits plant growth, and the length of the agricultural season is approximately 10 April to 8 November (Trumble 1937). Outside this period, plant growth is possible, in most years, only with supplementary irrigation. The first significant rains generally arrive during late April or May, and winter (June to August) is usually the wettest period (South Australian Year Book 1996). The annual average rainfall is about 528mm in the city centre but the average at the Waite Campus, which is closer to the Adelaide hills, is 611mm.

Mean monthly minimum and maximum temperatures are also given in Fig. 3.3b The warmest months are January and February with the mean maximum temperature around 29°C. On average, temperatures in excess of 40°C are recorded on about three days each year. July is the coldest month with a mean maximum of 15°C.

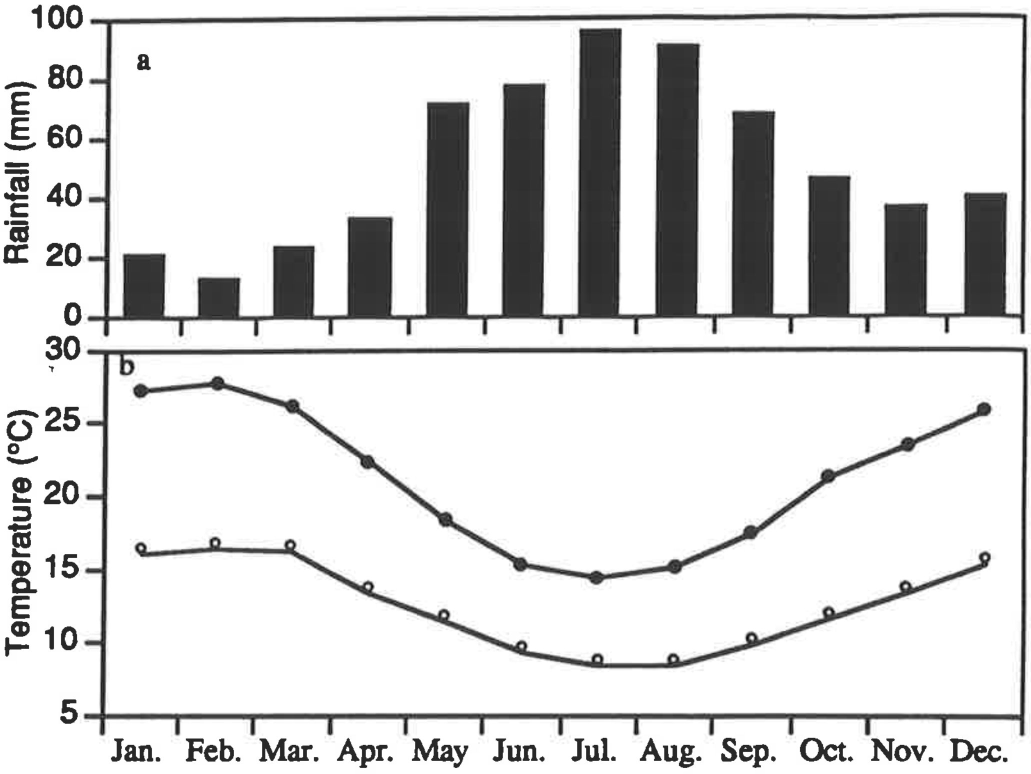

Figure 3. 3: Weather data for Adelaide, 1984-1994 (data from the Waite Meteorological Station, University of Adelaide). (a) the average monthly rainfall (mm), and (b) mean daily maximum and minimum temperatures for each month

3. 3 Culture

3. 3. 1 Culture of *Acyrthosiphon pisum* (Harris.)

A stock culture of *Acyrthosiphun pisum* (Harris), as food for syrphids, was maintained in the insectary throughout this study. The aphids were grown on broad bean plants (*Vicia faba*) grown in 15cm (in diameter) plastic pots containing a recycled University of California soil mixture. Pots with the plants were transferred to 40cm x 56cm x 66cm rearing cages which contained broad bean plants previously infested by aphids. Light was provided through a window and also from a bank of three white 40 watt and one violet 36 watt fluorescent tubes one metre in length. The temperature inside the insectary was maintained at 21±2°C. Three to five pots of broad bean were placed in each rearing cage (Fig. 3. 4 a).

3. 3. 2 Culture of Syrphids

Plants infested with aphids were transferred to the rearing cages (Fig. 3. 4 b) 2.30m x 2.30m x 2.90m growth chamber with 30000 lux on the top of the cages and a 16: 8 light to dark photoperiod, 20±1°C and 60-70% relative humidity. Light was provided by four 40 watt fluorescent tubes, one incadescent bulb (Lucalux, LU 400/40), and one fluorescent lamp (True Light) providing all essential wavelengths for the plant growth.

Gravid females of *M. viridiceps* and *S. grandicornis* captured from the field were released in to the rearing cages.

3. 3. 3 Oviposition unit

When needing to conduct experiments with a single female; e.g. for longevity or fecundity "oviposition" units (Fig 3. 4 d) were used. Each of these consisted of a cylindrical clear plastic cage 15.5cm diameter x 15cm high. Ventilation of the unit was provided by a 8 cm gauze-covered hole at the top and two similar 4cm holes on the wall of the cage covered by gauze.

3. 3. 4 Release cages

For most experiments, adults captured from the field were transported in wooden frame sleeve cages (30cm x 30cm x 30cm) then released in glasshouse compartment or field cages. The top and three sides of these cages were covered by perspex and the floor was wooden (Fig. 3. 4 c).

3. 3. 5 Field cages

Field cages were used to provide semi-natural conditions in some experiments; for example for measuring the longevity of adults after marking, or studying oviposition behaviour. These 2m x 2m x 2m cages were made from a metal frame and covered by gauze (Fig. 3. 5). Each cage was fastened to the ground by ropes and wooden pegs.

3. 3. 6 Rotatable table

A rotatable round table was used for adult choice experiments. The table was constructed from 20mm thick timber (100cm diameter) and a 24cm high metallic stand. Two rows

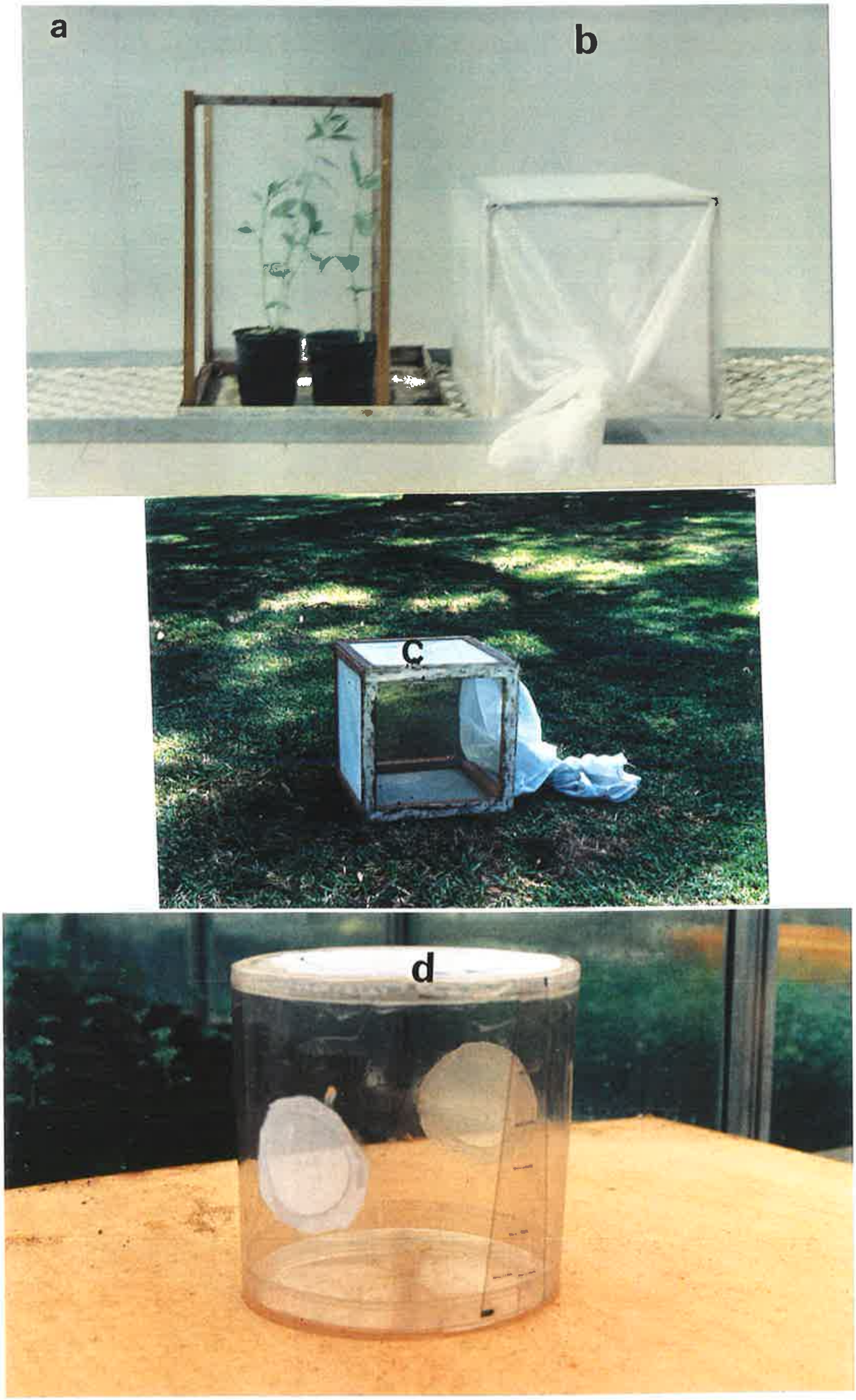

Figure 3. 4: The cages used in study, a: Aphid rearing cage, b: Syrphid rearing cage, c: Release cage, d: Oviposition cage.

Figure 3. 5: The field cage

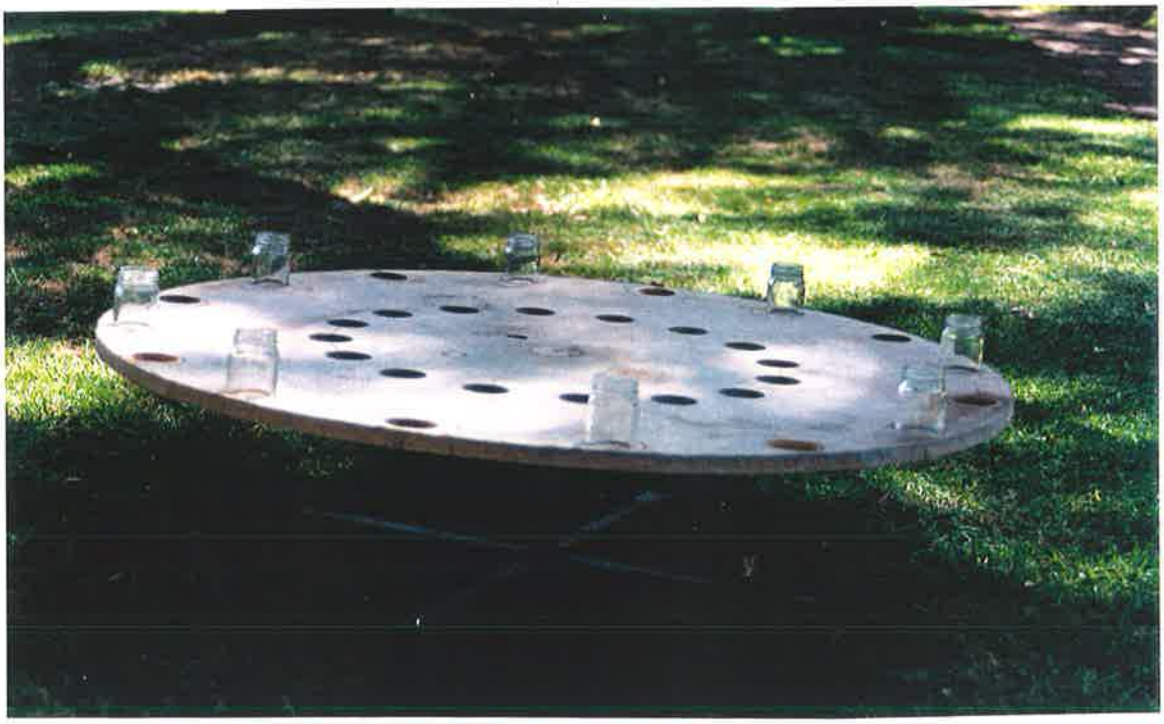

Figure 3. 6: The rotatable table used for choice experiments

each with 16 holes were made on the surface of the table to hold glass jars in which various flowers and plants were placed. The distances between two holes on outer and inner circle were 18cm and 10cm respectively, and the distance between two circles was 21cm (Fig. 3. 6).

3. 4 Optimum elevation of food in cages

3. 4. 1 Introduction

The position of resting and feeding sites in the rearing cages was found to be important to optimise feeding of adults and reduce mortality. The following experiment was conducted to determine the optimum elevation at which food should be offered in a rearing cage.

3. 4. 2 Materials and Methods

An experiment with a completely randomised design with four treatments and three replications was conducted to test the null hypothesis that different elevations of food in the cage had the same effect on attraction of adults. The experiment was conducted at 20±1°C with 10000 lux at the bottom of the cage and 16: 8 light to dark photoperiod. Food (same amounts of pollen, cubed sugar and water) was placed within each cage at four elevations (0, 15, 35, 40cm) on adjustable tables (Fig. 3. 7).

Forty five adult *M. viridiceps* were captured from the field and released into the cage. Then the numbers of syrphids on each food platform were recorded each hour on 24 occasions, and the means of the treatments were compared with an ANOVA.

3. 4. 3 Results

The highest number of *M. viridiceps* was attracted to the food located at the highest elevation (45cm). No differences were found between 0, 15 and 30cm elevations (α=0.05, F=57.17, p=0.0001, LSD=9.92) (Fig. 3. 8).

As a result of these observations, food was presented to syrphids in culture on a platform 40cm high (10cm lower than the cage height)

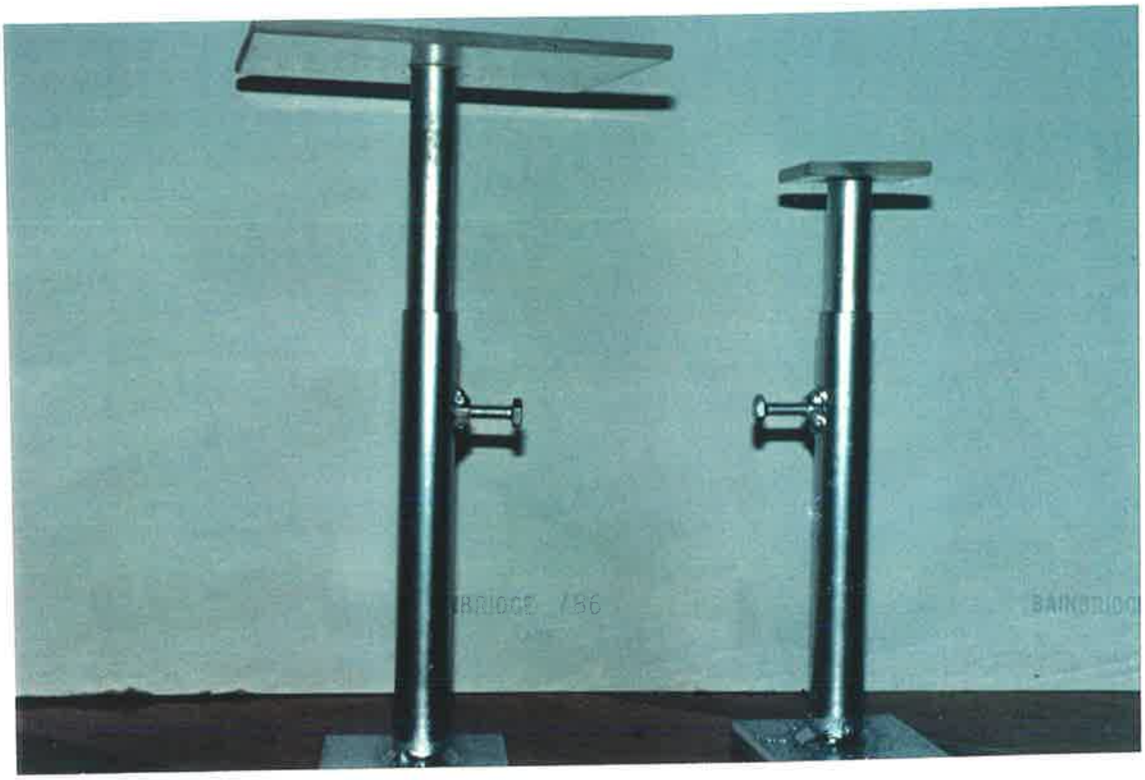

Figure 3. 7: The adjustable tables used in the food elevation experiment.

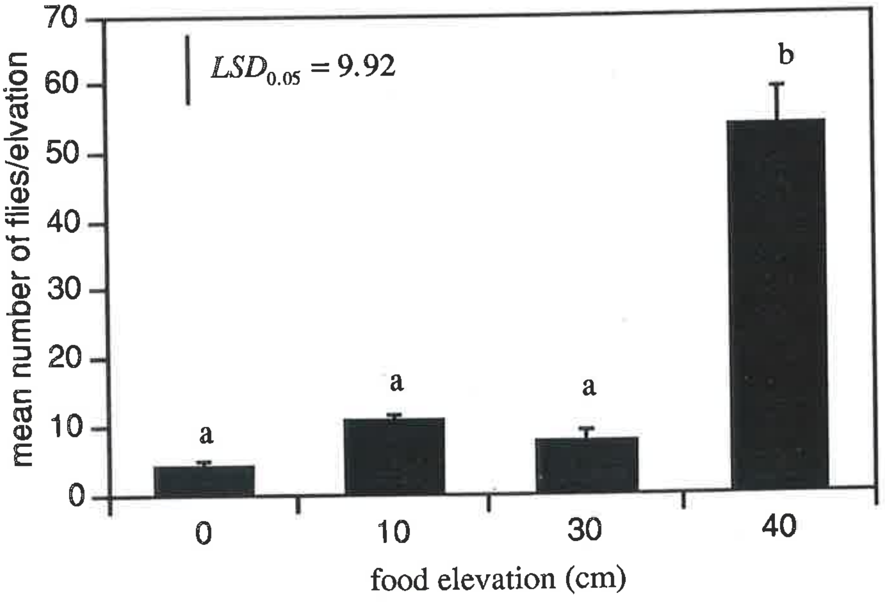

Figure 3. 8: Mean numbers of *M. viridiceps* attracted to different food elevations within a rearing cage. Vertical lines show standard errors of mean. Elevations with no significant differences are shown with the same letters.

Chapter 4

Seasonal occurrence of adult hoverflies

4.1 Introduction

Measurements of adult hoverfly populations have usually been made using a census walk (Frazer and Gilbert 1976; MacLeod 1992; Cowgill 1993), or using different types of traps at places where they are most likely to be caught (Dixon 1959; Sole 1966; Ortu 1990; Wratten 1995) including places preferred by males for their ambushing flights, watering places particularly after long dry periods, plants infested with aphids and psyllids, and flowering plants (Schneider 1969). For example, in Yugoslavia, flowers of *Paliurus spina -chrysti*, *Chrysanthemum curerariaefolium* and *Castanea sativa* are most attractive to syrphids in the middle of June. In August, *Ferulago gabonifera* is favourable for collection of syrphids and at the beginning of October, *Aster tripolium*, *Inula viscosa* and *Asparagus maritimus* are favourite sites (Glumac 1966).

The vegetation and attractive places within an area of study change seasonally, so the study of changes in numbers of adult hoverflies during the year using only one sampling method is difficult. Thus, different methods of adult recording at different places have been used in this study to estimate the populations of these insects; suction traps, and census-walk were used during the period of flowering time of daisy plants (autumn, winter and spring) while water traps were used throughout the year.

Capture-recapture method was also used to estimate the number of hoverflies in the area of study (Lincoln 1930; Seber 1965; Jolly 1965; Southwood 1978; Pollock *et al.* 1990). The method of estimation depends on the assumption that the population is closed or open; open population changes with additions and deletions, but a closed population has no additions and deletions in the area of study (Pollock *et al.* 1990).

The sizes of populations of phytophagous and saprophagous hoverflies have been estimated by capture-recapture method by using cellulose paint applied with a fine blade of grass for marking the tibiae (Neilsen 1969, Conn 1976). Even with a 30-50% rate of recapture, there was a large error in estimating population size because samples were small. In this experiment to estimate the population of *M. viridiceps* by Lincoln Peterson method (Seber 1982; Pollock *et al.* 1990), the following assumptions were made:

The population was closed to emigration and immigration.

All individuals in the population had the same probability of being captured.

The probablity that individuals were recaptured not affected by marking.

All possible samples after marking had equal chance of being selected.

The marks were not lost between any two samples.

The frequency of the catches of the marked individuals did not affect the probablity that those individuals were recaptured on further occasions.

The aims of the experiments were to:

study seasonal fluctuations of adult hoverfly numbers

estimate the population size of *M. viridiceps*.

4. 2 Materials and Methods

Three methods of recording were used to estimate the relative numbers of hoverflies in the field. Two suction traps were placed near daisy flowers and were used during March to May 1994 and 1995 to measure the numbers of syrphids attracted to daisy flowers, and hence to estimate their relative numbers in the area of study. During this period, five water traps were also placed in the Claremont rose garden close to daisy flowers to capture adult syrphids alighting on daisies planted at the rose garden. Attempts were also made to estimate the number of *M. viridiceps* in the field by a capture-recapture method. Since syrphid flies are attracted to flowers, so the numbers of flowers were also recorded on six African daisy plants and 17 marguerite daisies. The method of counting is described in Chapter 6.

4. 2. 1 Seasonal occurrence of adult syrphids

4. 2. 1. 1 Catches in suction traps.

Each suction trap was of the exposed cone type with a 22.5cm fan unit and a maximum height of 55cm off the ground. In 1994, when there were many syrphid adults on the African daisy plants in the Claremont rose garden, one trap was set up in the vicinity of, and on the sunny side of, an African daisy plant and run from 1/4/1994. Later, another trap was set up on the shady side (noon shade) of the same plant and run from 11/8/94 to 11/11/94. The traps were emptied weekly during March to June and daily from June to October.

In 1995, two suction traps were used again but one was set up near an African daisy plant and the other near a marguerite daisy plant. These traps were run from March to November 1995 and were emptied at 2-4 days intervals. The position of suction traps next to daisy plants are shown in Fig. 4. 1.

Sexes and the development stages of females' reproductive organs were recorded on each occasion. Based on the development of reproductive organs, the females were classified into A (no evidence of the growth in ovaries), B (at the beginning of oogenesis) , C (with small and non-mature eggs), and D (with mature eggs). The different stages of female's reproductive organs were identified by dissecting under stereo-microscope or by the use of hand lens with x3 magnification through the clear abdomen of insect, especially in stages C and D. Total numbers in the classes C and D were classed as "gravids" in calculations. The gravid females were also recognisable by the whitened underside of their abdomens due to the presence of eggs (Chambers 1988).

Values of wind speed (at 2 meters height), solar radiation and temperature were obtained from the weather station located at the Waite Campus and were used in multiple regression analysis. The mean wind speed and total solar radiation of the 5 hours from 9 am to 2 pm, when *M. viridiceps* were active on the African daisy, were also used in regression analysis.

Figure 4. 1: Position of suction traps next to marguerite daisy (Top) and African daisy (Bottom).

4. 2. 1. 2 Water traps

To test for the best colour to use in water traps, two groups of water traps each with three different colours, yellow, white and blue, were organised during summer 1993. The first group was set up in the Claremont rose garden (Chapter 3) between rose plants from 19/12/92 to 18/2/93 (summer). The traps were placed on the ground in a randomised block design with three replicates. The second group of traps were located between citrus trees in an experimental orchard about 100 meters from the Claremont rose garden at the same period as the previous group.

For seasonal monitoring five yellow water traps were placed at the Claremont rose garden between March and November 1995.

Each water trap was a 29cm x 39.5cm x 12cm plastic container with a 2.5cm diameter gauze-covered hole as the overflow outlet. Each container was filled with nine litres of water mixed with nine ml. formalin (0.1%) as a preservative (Dixon 1959; DeBarro1991) and a small quantity of detergent. The flies were collected weekly, and the sexes and the gravidity of females were recorded. The containers were washed and their water changed every week.

4. 2. 1. 3 Census walk

A census-walk method lasting 5-10 minutes was used 1-4 times a week on one row of African daisy (6 plants) and three rows of marguerite daisy (17 plants) at the Claremont rose garden between 1200 -1300 during March to November, 1995. The mean number of flies recorded by census walk per plant species per occasion for each week was regressed on the total number of flies caught in the suction trap placed near each plant species. However, It should be noted that, for ease of plotting the data, the data have been designated as being taken in the 1st, 2nd, 3rd, or 4th week of each months. The actual sampling dates and designated sampling days, denoted as weeks within months, are given in Appendix 4. 1. The same adjustment for ease of plotting was made to the sampling data of the numbers of flowers and numbers of flies caught in traps.

4. 2. 2 capture-recapture method

4. 2. 2. 1 Preliminary experiments

Comparison between holding methods

Two methods of holding were used for marking *M. viridiceps*. In the first method, an electric vacuum-cleaner (Electolux 700 Watts) was connected to a PVC three way joint (Fig. 4. 2) (Morris 1965) and the pressure of the vacuum was adjusted by a valve. In the second technique, a 10cm x 10cm nylon pouch with a mesh width of 0.25mm was used for holding the syrphid. An experiment was conducted to compare the two holding methods. A control was included as a third treatment.

days old flies that had been reared in the laboratory (Chapter 3) were used in this experiment. In the vacuum method, a fly was released from a vial and the vacuum cleaner was turned on immediately and the fly sucked on to the gauze. In the "pouch method", the insect was allowed to walk out of the vial to the pouch which was closed by hand and the insect was held in an appropriate position for marking through the holes of the pouch.

The individuals of each treatment were released into a 30cm x 30cm x 30cm sleeved cage in the field. The cages were made from wooden frame and covered by gauze and fastened to the ground (Chapter 3). The insects were fed with cubed sugar, bee pollen, and cut fresh flowers of African daisy (*Senecio pterophorus*) and marguerite daisy (*C. frutescens*) in pots in water which were changed every two days. Water was offered in 100 ml vials with floating cork pieces to prevent the insects being drowned.

The experiment was run for 8 days from 23 June 1993, with a minimum temperature of 5.4 and a maximum of 17.8° C with 5.4 mm rainfall on 30 June. The number of survivors per treatment were counted at the end of the experiment and analysed by ANOVA.

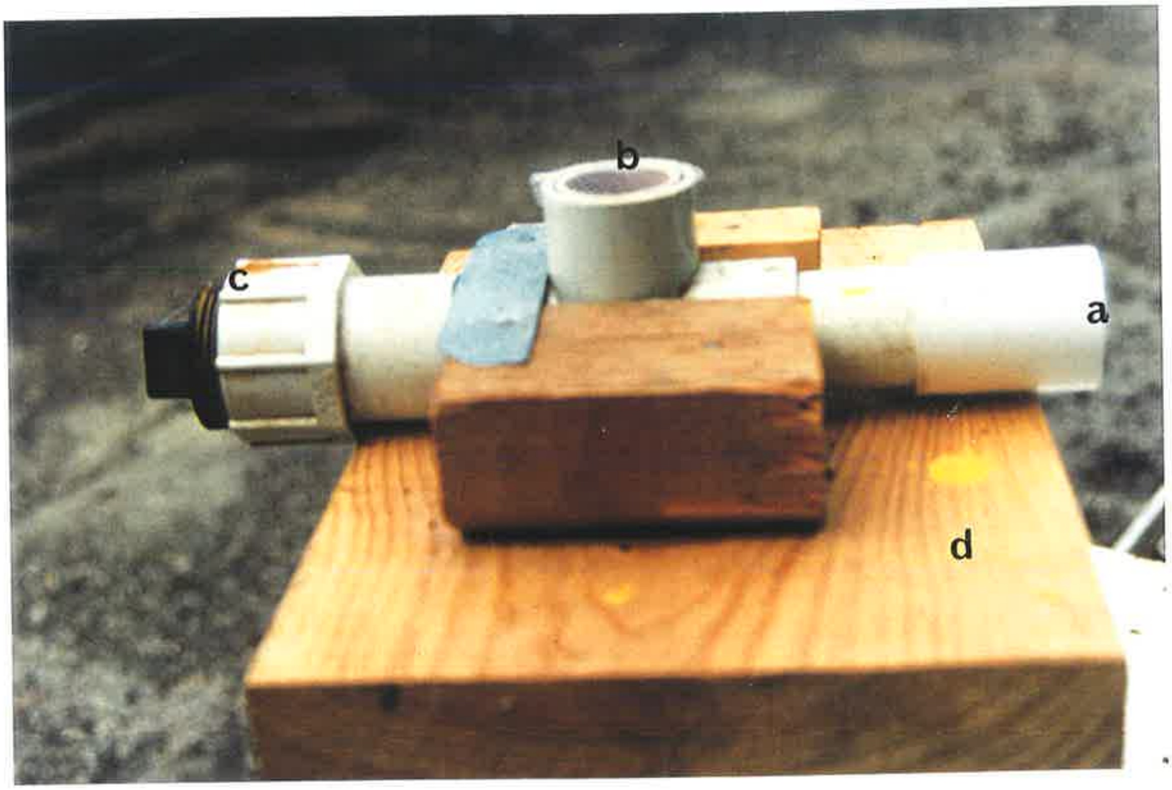

Figure 4. 2: PVC three ways joints used for holding the insect for marking; a, connection to vacuum cleaner; b, Gauze net; c, adjustable valve; d, base.

The effect of the site of marks on the body of *M. viridiceps*

The aim of this experiment was to compare the survival rate of 1-3 day old *M. viridiceps* reared in the laboratory and to test the durability of a mark either on the notum or on the wing.

Humbrol enamel (Hull, England) was applied to an insect by a headless insect pin which was inserted in a match. To hold the insect, the nylon pouch technique, as described in the previous experiment was used. In the first treatment the paint was applied to the notum, and in the second treatment the costal margin of the wing was marked. The third treatment was a 'control' in which no paint was used.

The experiment was conducted as a complete randomised block design with three treatments and three replications in the Claremont rose garden between 1 to 9 July 1993, with a minimum temperature of 6.6°C, a maximum of 16.9°C and with 5 rainy days of 2, 4.2, 4, 40.8 and 2.8mm rain. Each replicate consisted of 30 flies which were released in a 2m x 2m x 2m cage (Chapter 3) which were placed on the ground over black polythene to suppress weed growth. Pollen, sugar and water were offered as the previous experiment. The number of survivors and the presence of the marks were recorded at the end of the 9th day.

4. 2. 2. 2 Estimating populations at Claremont

Four capture-recapture experiments were conducted on flies caught on African daisy plants in June and on bean plants in October 1993 when *M. viridiceps* were abundant on both plant species at the Waite Campus. The bean plants were cultivated around the Claremont rose garden in an area of approximately 1500 m^2. The height of the bean plant at the time of the experiment was about one meter with 20 cm space between plants.

All the experiments were run independently (two days apart in June and five days apart in October) and a single-mark release method with multiple recaptures was used in each experiment. The approximate number of marked-released and recaptured were obtained by the chart given by Robson and Regier (see Seber 1982) based on the rough estimate of population and the accuracy of 0.5 and the level of 95% (Seber 1982). However, these numbers also depended on the availability of the syrphid flies in the area of the study.

Two different colours of enamel were used in two successive experiments. The number of marked individuals recaptured on each occasion was recorded and the flies were then released in the field.

Flies were initially captured on African daisy or bean plants (depending on the experiment) by sweep net between 1100-1500 hours and held in a 30cm x 30cm x 30cm sleeved cage and fed with flowers, cubed-sugar and water (Chapter 3). The cage was taken to the laboratory, the insects were removed and held with the nylon pouch technique and marked on the notum (see materials and methods in preliminary experiments). All marked insects were collected in a sleeved cage. The cage of marked insects was opened in the same place whence they had been captured at night of the same day or on the next day at dawn. The number of insects which were injured or not able to fly from the cage were subtracted from the number of marked insects to find the actual number of released insects. After at least 24 hours (usually from 11.00 am), flies were recaptured by a sweep net. The number of recaptured flies were recorded per day during each set of experiment and released in the same day during each set of experiment.

4. 3 Results

4. 3.. 1 The numbers of daisy flowers

Since the numbers of flies seen in the census-walks and the numbers caught in the suction traps were both likely to be dependent on the numbers of flowers of the 2 daisy species, it is useful to describe first the pattern of flowering of the 2 daisy species and the results of the census-walks of flies on them.

The numbers of flowers were not counted in 1994, but the changes in the numbers of flowers of both the African and marguerite daisy in 1995 in the Claremont garden are given in Fig. 4.3b; and the numbers of adult syrphids recorded by a census-walk around both species of daisy are given in Fig. 4.3a. Both daisy species flowered from the first observations in March until early November, but clearly the African daisy had two peaks of flowering, one in late June-early July and another in late September-early October. The marguerite daisy, however, had only one peak in September-October, and the numbers of flowers gradually increased up to this peak from March. The numbers of *M.viridiceps* also show 2 peaks, one in July-August and another in September, with the latter being somewhat earlier than the peak of spring flowering of the 2 daisy species. *S.grandicornis* had a small peak in October.

A comparison of the numbers of flowers and of flies in Figs. 4. 3a,b do not suggest any obvious dependence of the numbers of flies on the numbers of flowers. From June to October, the numbers of flowers of each daisy species were obviously much larger than the numbers of flies on them. But it is instructive to look at the numbers of flowers outside these months reduced to about the same scale as the numbers of flies. So in Fig. 4.4a is plotted the numbers/ 50 of yellow daisy flowers and the numbers of *M.viridiceps* (in census-walks) per 1000 African daisy flowers; and in Fig. 4.4b is plotted the numbers/200 of white daisy flowers and the numbers of *M.viridiceps* per 1000 white daisy flowers. Fig. 4.4a now suggests, perhaps, that the numbers of *M.viridiceps* per 1000 yellow daisy flowers "crashed" after a peak in November and that this reduction was due to a shortage of daisy flowers rather than a shortage of flies. Certainly, after November, there were no daisy flowers and no syrphids were seen alighting on the daisy plants.

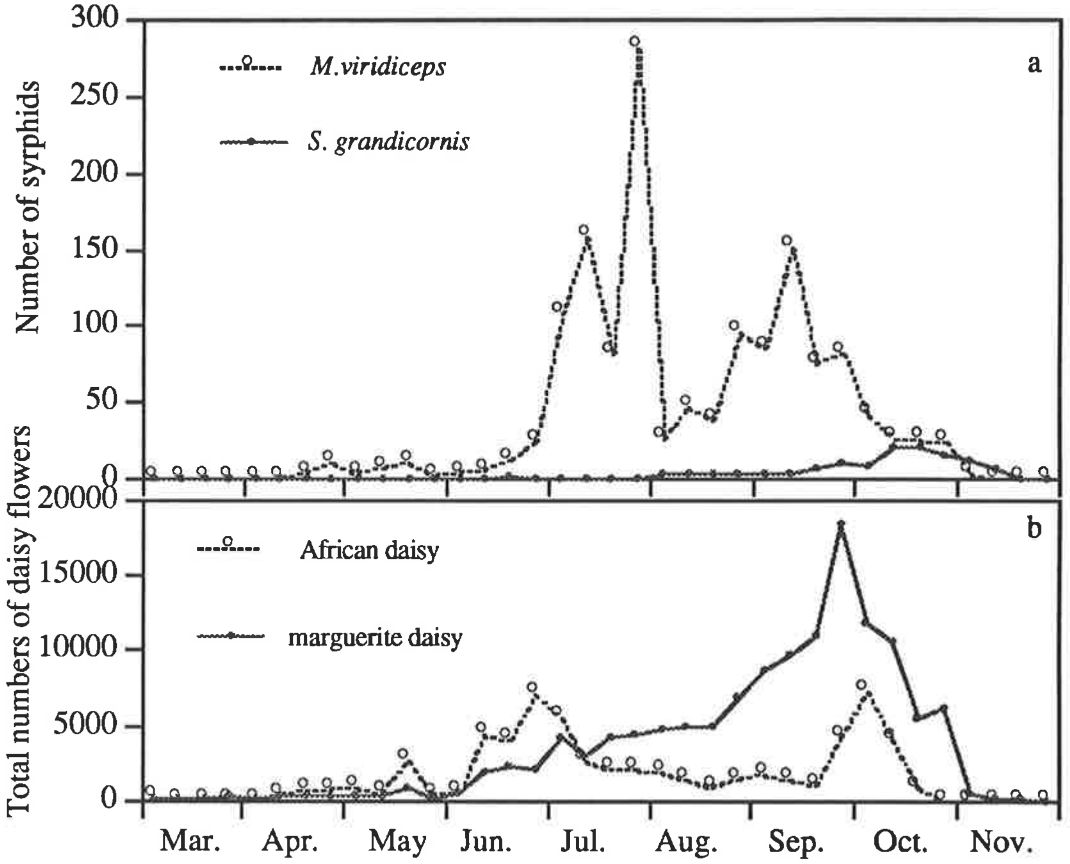

Figure 4. 3: (a), Total number of adult syrphids recorded by census walk around African and marguerite daisies at the Claremont rose garden in 1995; (b), changes in numbers of African and marguerite daisy flowers at the Claremont rose garden in 1995.

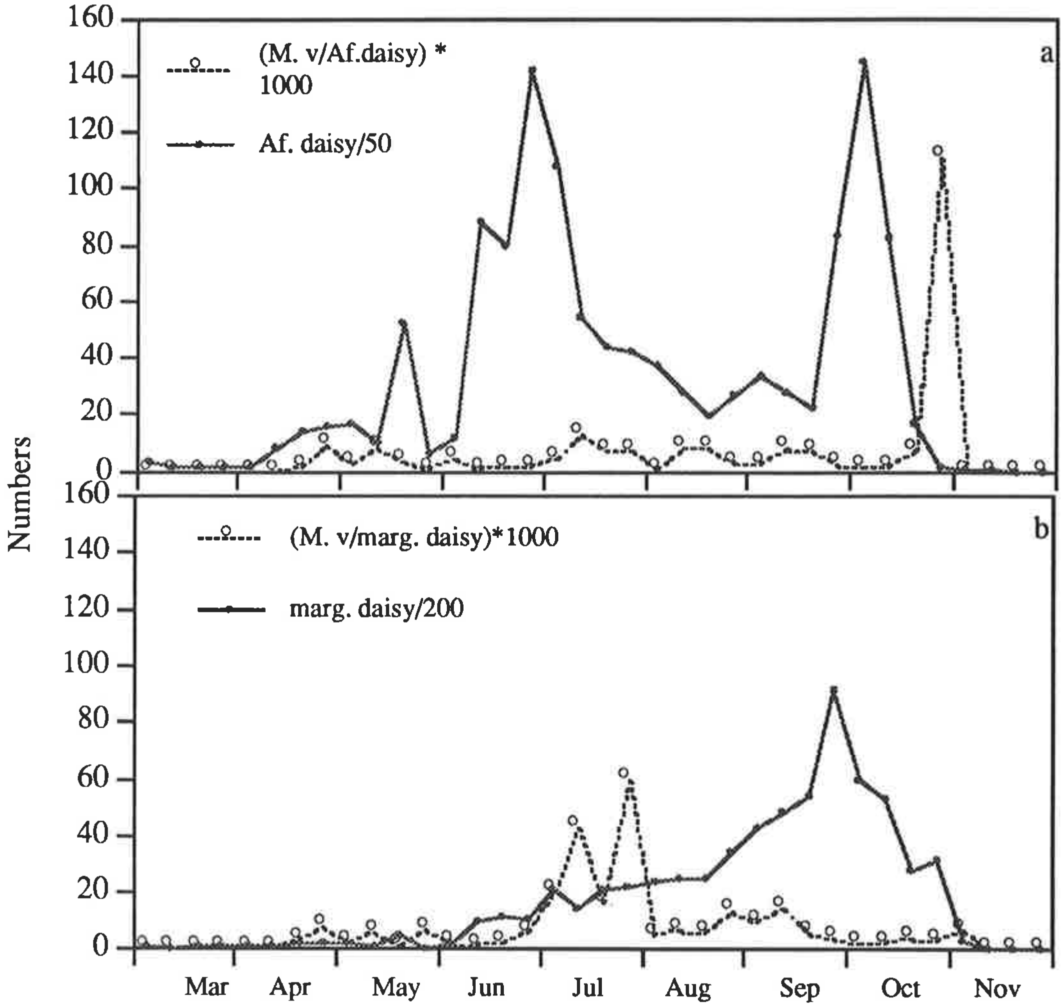

Figure 4. 4: Changes in number of *M. viridiceps* recorded by the cenus-walk on African and marguerite daisy plants (per 1000 flowers) and numbers of daisy flowers. Numbers of flowers scaled down for comparison (see text).

4. 3. 2 Suction trap

The activity of *M. viridiceps* started in autumn (April) when the weather changed, but the main period of activity was during winter. *M. viridiceps* was not caught in suction traps in November with the increase in temperature and ending of the flowering period of African daisy (Fig. 4. 5a). However, the flight activity of this species could be observed until December. No gravid females of *M. viridiceps* were captured at the beginning of the activity in April-May, but they were caught between July and October (Fig. 4. 5b).

Although *S. grandicornis* were active in the field all the year in Adelaide except June and July (Chapter 9), low numbers of this species were caught in the trap located adjacent to African daisy during March to May. However, numbers caught increased from August and peaked in spring (October-November) on African daisy. One and two *S. grandicornis* were caught in July 1994 and 1995 respectively even though no apparent activity of this species was observed in the field (Fig. 4. 5c).

Daisies flower during all the activity period of *M. viridiceps* but only during spring and autumn for *S. grandicornis*. The two daisy species flower from March to November in Adelaide. So in summer when *S. grandicornis* is yet active, daisies are not on flower. The flowers peaked in late September (Fig. 4. 3b) and decline in the late October when maximum temperature increased to about 30°C or higher.

4. 3.. 2. 1 Comparison between numbers of catches in shade and sun

The number of males, females, gravid females and total number of *M. viridiceps* captured in suction traps installed in the shade and sun were compared by t-test. The analysis of data obtained in 1994 showed that (i): the number of males are significantly more in the sun (mean/day=1.63) than in the shade(mean/day=0.684) (p=0.0001, df=112, t=9.46), (ii): the number of females are significantly more in the sun (mean/day=1.35) than in the shade

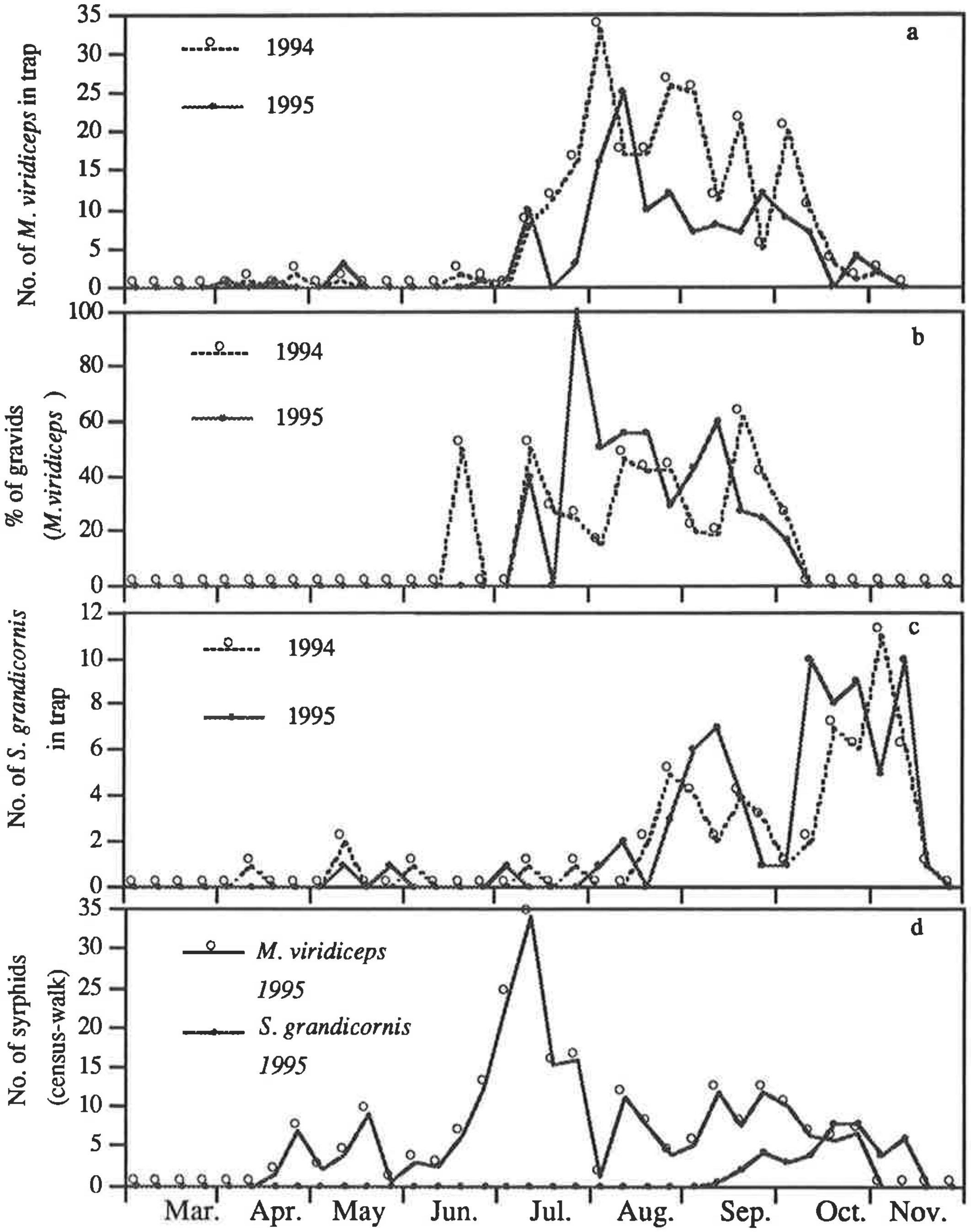

Figure 4. 5: Changes in numbers of adults of *M. viridiceps* and *S. grandicornis* in the Claremont rose garden in 1994 and 1995: (a) total numbers of *M. viridiceps* caught in suction trap per week; (b) percentages of gravid *M. viridiceps* in the trap;(c) total numbers of *S. grandicornis* caught per week; (d) mean numbers of both species recorded on six African daisy plants per counting occasion during 1995.

(mean/day=0.74) (p=0.002, df=113, t=3.23), (iii) more gravids were captured in the sun (mean/day=0.55) than the shade (mean/day=0.32) (p=0.0001, df=111, t=10.70).

4. 3. 2. 2 Relationship between weather variables and number of adults caught in suction traps

Multiple regression was used in an attempt to analyse the relationship between the number of flies caught per day and weather.

Initially, the number of flies caught was regressed on each corresponding weather variable by simple regression. The most significant variable was taken as the first variable in multiple regression, and other variables were added to it singly first and then in pairs, to get the best combination of significant variables.

When the daily catches from 11 July to 3 September 1994 were regressed on weather variables, the only significant variable was temperature (p=0.003, R=0.4 and n=55) ($y=0.454x+12.44$). A significant relationship between the number of gravid females (classes C+D) and the daily mean temperature (R=0.56, n=55 and p=0.0001) was also detected ($y=1.74x+12.85$).

There was no relationship between the number of catches and mean wind speed between 0900 and 1400 hours (2.3-7.7km/h). No significant relationship was found between the number of *M. viridiceps* caught in the traps and the number of sunny hours per day or total solar radiation from 09:00 to 14:00 hours (0.32-13.6 meg. j./m^2) in simple and multiple regressions.

The mean number of catches on rainy days and on days without rain were compared by t-test, and no significant differences were detected (2.83±0.4 SE, and 2.52±0.5 SE *M. viridiceps* for non rainy and rainy days respectively).

4. 3. 3 water traps

3. 3.1 Numbers caught in summer

Nine *M. viridiceps* and four *S. grandicornis* were caught in water traps (18 traps, six of each white, blue and yellow) installed at the Claremont rose garden and citrus orchard. Two of nine *M.viridiceps* and two of four S. *grandicornis* captured during summer were females. Although the total number of catches was low, these data indicate, at least, that the both species and sexes of *M. viridiceps* and *S. grandicornis* were present in the study area during summer.

Data obtained for the number of catches during summer was not enough to be analysed for the attractiveness of syrphid flies to different trap colours. However, 11 syrphids of both species were captured in yellow traps, and one S. *grandicornis* and one *M. viridiceps* were recorded in white and blue traps respectively.

The traps installed at Claremont and the orchard caught 2 gravid females of *M. viridiceps* on 30 December 92 and 18 February 93 when the mean daily maximum temperature during seven days between December 30 and the previous traps-collection date was 31.4°C and during seven days between February 18 and the previous collection date was 32 °C. These catches indiate that at least some females of *M. viridiceps* retain reproductive activity in hot weather in summer. Although no gravid female *S. grandicornis* were captured in the traps during summer, all stages of this species could be observed during summer on rose aphids.

3. 3. 2 Numbers caught in other seasons

Five yellow traps were placed at the Claremont rose garden close to suction traps from March to November 1995. Lower numbers of syrphids were caught in comparison with numbers in suction traps (Fig. 4. 6; Table 4. 1).

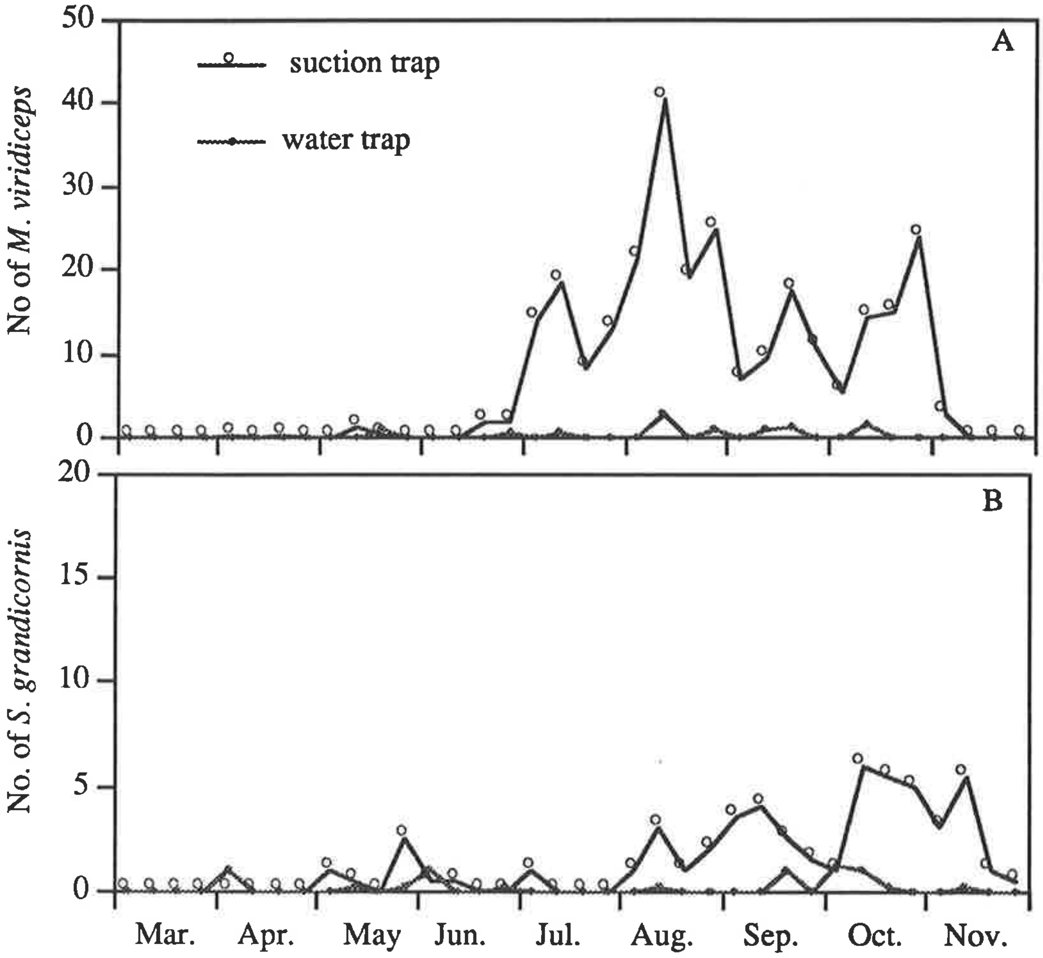

Figure 4. 6: Mean number of *M. viridiceps* (A) and *S. grandicornis* (B) per suction and yellow trap (two suction traps and five water traps) at the Claremont rose garden between March and November 1995.

4. 3. 4 Comparison between traps and census walk

Fewer syrphids were caught in water traps than in suction traps (Fig. 4. 6; Table 4. 1). Although the mean number of *M. viridiceps* caught in water traps was correlated to the numbers caught in suction traps (p=0.01, R=0.41, n=36) and no relationship was found between the number of *S. grandicornis* caught in water traps and suction traps (p=0.27, R=0.19, n=36).

Table 4. 1: Comparison between suction trap and water trap in capturing *M. viridiceps* and *S. grandicornis*..

Syrphid species	suction trap		water trap	
	total catch	mean/trap/week ±SE	total catch	mean/trap/week ±SE
viridiceps	518	7.61±1.65	56	0.31±0.11
grandicornis	104	1.44±0.31	32	0.18±0.06

The mean number of adults *M. viridiceps* per suction trap adjacent to African and marguerite daisies (p=0.009, R=0.43, n=36) showed a significant relationship with the mean number of adults per week recorded by the census walk method in 1995, but no significant relationship was detected for water traps and census walk (p=0.79). Similarly, a significant linear relationship was detected between the mean number of *S. grandicornis* caught in the suction trap and the mean number per week recorded by census walk (p=0.0001, R=0.74, n=36). However, the relationship for *S. grandicornis* caught by water trap was not significant (p=0.06, n=36).

4. 3. 5 Estimating the population of adults *M. viridiceps* by the capture-recapture method

4. 3. 5. 1 Preliminary experiments

The "holding for marking" treatments gave 40.85% survivors for the vacuum technique, 92.6% for the pouch method, and 96.3%for the control. There was no significant difference between the pouch method and the control, but the vacuum technique method differed from the other two at p=0.01. The holding technique with nylon pouch was therefore used in the later experiments.

The analysis of variance showed no significant difference between marks on the notum or wing of surviving individuals (96.3, 92.6 and 92.6% for marking on notum, wing and control respectively) but marking the notum was used in the later experiments because it was easier.

4. 3. 5. 2 Estimating number of populations of *M. viridiceps*

Population sizes were estimated by the modified version of the Lincoln-Petersen method which was originally given by Chapman (1951) as $N^* = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$, where n_1= the number of animals caught, marked and released; n_2=the number of animals captured, of which m_2 have been marked. The total insect number comprised the number of insects lost plus the insect numbers estimated on each day. Seber (1982) estimated of the variance of N* using the formula $V^* = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)2(m_2+2)}$. The 95% confidence limits were calculated by the formula $N^* \pm 1.96\sqrt{v}\,\sqrt{v}$ (Seber 1982).

The estimated numbers of *M. viridiceps* per day (N*) on an African daisy are given in Table 4. 2. In the first experiments which were conducted from 26/6/93 to 29/6/93, the number of *M. viridiceps* (N) were estimated roughly around 200 (the mean number of three counts on one African daisy multiplied by 10 as an arbitrary number) and therefore, the sample sizes should be n_1=40 and n_2=60 (Seber 1982).

5.0 and 5.0% of marked individuals were recaptured on the second, third and fourth day respectively.

Table 4. 2: estimating the population of *M.viridiceps* on African daisy during 26-29 June and 1-5 July 93.

date	temperature min-max C°	n_1	n_2	m	Numbers (N^*) *viridi.ceps*	$\sqrt{v^*}$	95% confidence limits
June 26	3.4-12.9	40	-	-	-	-	
27	5.4-15.6		103	3	1065	441.1	(195, 1935)
28	5.5-14.9		39	2	551	253.1	(55, 1047)
29	11.4-17.2		35	2	492	226.7	(48, 936)
July 1	7.6-15.4	91	-	-	-	-	-
3	10.1-16.2		82	11	635	152.2	(337, 934)
4	7.4-14.6	89	52	3	1197	501.3	(215, 2179)
5	7.4-14.0		43	2	1350	640.5	(127, 2583)

In the second experiment on African daisy plants from 1/7/93 to 5/7/93 (Table 4. 2), the primary estimation of the population size (estimated as described above) was around 400 which, by the use of Robson and Regier's chart (see Seber 1982), estimated both n_1 and n_2 as 90. Except on the day 2 on which 12.1% of marked individuals were recaptured, the number of recaptures were less than 10% of the number of marked-released.

Similarly, in the experiments on bean plants close to the Claremont rose garden, the numbers of *M. viridiceps* were initially estimated roughly as 500 and 700 in the area of study (the number of syrphids were counted in 10m x 10m area and converted to 1500 m^2; Table 4. 3). The number of n_2 were 163, 86, and 132 of which 3.7, 3.6 and 4.5% were recaptured respectively. In the second experiment on bean plants, 9.2, 4.6 and 9.2% of marked individuals (65 flies) were recaptured during 1-3 days after mark-releasing.

Table 4. 3: Estimating the population size of *M. viridiceps* on bean plants (1500m^{2}) during two experiments conducted at the Waite Campus between 18-21 and 26-29 June 1993.

date 1993	temperature min-max C°	n_1	n_2	m	Numbers (N*) *viridiceps*	$\sqrt{V*}$	95% confidence limits
Oct. 18	8.4-15.5	65	-	-	-	-	-
19	8.3-16.9		163	6	1545	505.7	(554, 2537)
20	9.6-16.3		86	3	1443	607.7	(352, 2734)
21	7.6-17.0		132	6	1255	408.0	(455, 2055)
Oct. 26	10.2-21.9	142	-	-	-	-	
27	11.4-28.6		75	6	1552	510.1	552, 2551
28	10.1-16.3	141	112	7	1803	527.3	(567, 3039)
29	9.8-17.3		82	5	1978	704.8	(616, 3360)

During the first two experiments which were conducted in June and July, no eggs and larvae of *M. viridiceps* were found on roses in the Urrbrae and Claremont rose garden. At this time of the year, roses have usually no suitable buds for aphids but even when the number of aphids on infested rose buds increased in October (second two experiments), no eggs and larvae of *M. viridiceps* were observed on roses (Table 4. 4).

Table 4. 4: The mean number of *M. viridiceps* calculated in each capture-recapture experiment, and the mean numbers of rose aphid and syrphids eggs laid per infested shoot present at the area of study during each capture-recapture experiment.

date	*viridiceps* mean no.	aphid/buds Claremont	aphid/buds Urrbrae	*viridiceps* (eggs+larvae)
26-29 Jun.	808	0	0	0
01-05 Jul.	1061	0	0	0
18-21 Oct.	1061	72 (0)	187	0
27-29 Oct.	1778	72.6 (0)	56.9	0

4. 4 Discussion

4. 4. 1 Seasonal changes of *M. viridiceps* and *S. grandicornis*

This study shows that *M. viridiceps* is a cold-loving species and starts activity in autumn and disappears in summer in Adelaide. The numbers of this species peak in July and August when rose aphids are their lowest numbers, and the number of other aphid species are also low in South Australia (Maelzer 1981). The presence of gravid females in suction traps in June and July indicates that this species may prey upon other resources rather than aphids (Carver 1989; Carver, personal communication 1996). In addition, only a low number of eggs of this species on rose aphid colonies in Adelaide from September to October when there are many adults in the field confirms the preference of other prey, at least, to rose aphids (Chapter 9).

grandicornis is a warm-loving species and starts activity when the temperature increases in spring (late August and the beginning of September). While intense flight activity of this species was not observed in autumn at the Claremont rose garden, a relatively high number of eggs was recorded on rose aphids during this season in 1993-1995 (Chapter 9).

4. 4. 2 Oversummering and overwintering

Since low numbers of *M. viridiceps* were captured by water traps during the summer of 1992-93, it can be inferred that at least, some individuals of this species oversummer in the adult stage. South Australia has long hot dry summers and it is probable that adults spend the summer in quiescence which can be interrupted by cold weather. For example, on 30 November 1993, the maximum temperature was 41.2°C, and a few adults of *M. viridiceps* were observed resting in cool places, outside buildings, where the temperature was low because of air conditioning. No *M. viridiceps* adults were captured or observed after 30 November 1993, but some re-appeared on the 1st of January 1994 following a cold period starting on 20th of December, 1993. The daily minimum temperature dropped from 25°C to 9.5°C on 20 December and stayed almost constant until December 30. Individuals of *M. viridiceps* which re-appeared in January were captured by sweep net and the spermathecae of the females were dissected. All individuals captured were females and they were all carrying eggs; no male was captured. All flies captured were carrying sperm. Although no males were captured by net sweeping, the presence of males as well as females in water traps in the summer of 1992-93 indicates that males and females are present in summer in Adelaide. Since this time of the year is not suitable for aphid growth, they probably resorb eggs (Schneider 1969) or lay eggs near other groups of insects.

No *S. grandicornis* were seen flying in June and July (winter) in Adelaide. However, one and two individuals of this species were caught in suction traps adjacent to the African daisy in the winters of 1993 and 1994. This indicates that *S. grandicornis* spends the cold weather, at least, as adults. No evidence of reproductive stage(s) was found to indicate that this species overwinters also as immature stages.

4. 4. 3 Factors influence census-walk method and trap catches

4. 4. 3. 1 Census-walk method

The Census-walk method is vulnerable to the time of recording syrphid adults. The number of hoverflies changes quickly according to time and space. In this study, adults on daisies were counted between 1200-1300 hours. In addition, the activity of hoverflies depends on weather variables and the availability of flower resources. Therefore, the fluctuation in numbers recorded on different days may be due to changes in activity on daisies rather than changes in population size. The effect of this variation on weekly estimates of the numbers of flies was somewhat decreased by taking 1-4 recordings per week.

4. 4. 3. 2 Suction traps

The comparison between data obtained from the traps and the numbers recorded by census-walk indicated that the latter method was probably most reliable and suction traps could be a good indicator to estimate the number of flies alighting on daisy flowers.
However, they are more expensive than water traps and need electric power in the field which mostly is not accessible. Furthermore, the numbers caught in suction traps depends on the number of flowers located at the trap-effective height (Chapter 6). The ecology of

syrphids will be better understood when the flowers which supply pollen and nectar are available for a longer period.

The only weather variable which would seem likely to influence the number of catches of *M. viridiceps* in suction traps was temperature. Observations on African daisy plants showed that *M. viridiceps* appeared when the morning temperature reached 13 C° in July (winter in Australia) (Chapter 5). *M. viridiceps* is more likely to be caught in suction traps in warm days of winter because of the longer activity time during the day on African daisy. Wind speed at the range of this study (maximum 10.9km/h) did not affect the number of flies caught in the suction trap. However, Taylor (1962) indicated that the efficiency of a suction trap decreased gradually with increasing wind speed and, that a 22.5cm trap (the same size trap used in this experiment) was not suitable in winds above 16km/h.

The relationship between daily solar radiation or sunny hours (and also the total solar radiation from 0900 to 1400) singly or in combination with other weather variables and daily number of catches could not be detected in this study. However, within a day, the number of catches in sunny site of African daisy was higher than the site with afternoon shade. This indicates that seasonal foraging activity was not influenced by daily sunny hours but once they start daily foraging, they prefer sunny to shady sites.

No significant effect of the amount of daily rainfall was detected on number of flies caught. However, the activity of syrphids are interrupted by rain in the field. I observed that hoverflies stop activity before rainfall. But the time at which rain falls is not usually mentioned in the weather data and it is probable that the relationship between fly numbers and rainfall would depend on the time of the day at which the rain fell and whether/or not flies were usually active at that time.

4. 4. 3. 3 Water traps

The attractiveness of the yellow trap to *M. viridiceps* and S. *grandicornis* was not statistically detectable because of the low catches in all groups of traps in summer of 1992-

93. However, most individuals were captured in yellow water-traps. This results confirm the investigation conducted in the glasshouse with different painted petri-dishes (Chapter 6), and results obtained by some other investigators (Dixon 1959; Scymank & Godesberg 1991; Wratten *et al.* 1995).

In comparison with the number of syrphids caught in suction traps and numbers recorded by census walk, the numbers in water traps were low. The low catches during the summer of 1992-93 could be explained by no apparent flight activity of *M. viridiceps* and a dispersive flight activity of *S. grandicornis*. However, data of the two years showed that the number of catches was also low when the numbers of flies are relatively high in autumn to spring. It is possible that the traps were overlooked by syrphids because of the presence of high numbers of yellow food resources at the Claremont rose garden (African daisy flowers are completely yellow and the marguerite daisy flowers yellow in the middle with white petals). Colour preference by hoverflies may be influenced by the colour of the most abundant flowers in bloom during the time of sampling (Schneider 1969). Similarly MacLeod (1992) observed that the abundance and activity of *Episyrphus balteatus* on coriander was not reflected in water trap catches. The comparison between data obtained from the traps and the numbers recorded by census-walk indicated that the latter method was probably most reliable and suction traps could be a good indicater to estimate the number of flies alighting on daisy flowers. Physiological conditions also influence the number of hoverflies attracted to yellow colour; for example adult hoverflies are most easily caught when newly emergent puparia are hungry (Schneider 1969). However, because the study has been done over a long period, such physiological aspects can be ignored.

4. 4. 4 Capture-recapture method

In this study, less than 10% of marked-released were captured which indicates that this species has a mobile behaviour, at least, during the 2-5 days of each experiment. The mobility of hoverflies may be attributed to their search for oviposition sites which may be far from pollen or honeydew resources. Pollard (1971) pointed out that considerable mobility of the adult stages meant that adult feeding could take place some distance from oviposition sites, which seems to explain why *M. viridiceps* was found in large numbers around flowers in the study area, but did not often lay eggs on colonies of rose aphids. The cage experiments showed that the low recapture rates are unlikely to be caused by mortality due to the process of marking or by the loss of marks.

Chapter 5

Diurnal flight activity patterns of the syrphid flies, *M. viridiceps* and *S. grandicornis*

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5. 1 Introduction

All sorts of insect movements even within a small suitable habitat are important in successful development, survival and reproduction (Hughes 1979). Insects move during the day in search of resources such as food, mates, oviposition sites and also in response to physical conditions (Cloudsley-Thompson 1975) including light intensity, temperature, humidity and wind velocity.

Different species of syrphid flies may have different times of flight activity (Maier and Waldbauer 1979), but Lewis and Taylor (1964) found most species of syrphids in their study flew at about midday. Although most adult syrphids are active during the day, some have been caught in light traps at night. At least one syrphid species, *Copestylum vesicularium* (Curran.), has been observed visiting flowers of *Cephalanthus occidentalis* L. at sunrise (Gilbert 1985).

The aim of this study was to describe the flight activity of *Melangyna viridiceps* (Macquart) and *Simosyrphus grandicornis* (Macquart) on daisy plants provided as attractive pollen resources at the Claremont rose garden, and to measure the importance of shade in retaining flies in the garden.

5. 2 Materials and methods

5. 2. 1 Winter flight activity

The numbers of *M. viridiceps* on an African daisy (*Euryops pectinatus* : Asteraceae) were counted on a total of 17 days during winter (June and July 1993-94), when adults of this species were abundant. Adults of *S. grandicornis* did not occur in the field at this time of the year.

In 1993, a standard census-walk (Pollard 1977; Maier 1979; Gilbert 1985; Cowgill *et. al* 1993 a,b; MacLeod 1994) lasting two minutes each was made around a large African daisy shrub (2m in diameter of canopy and 2m height) located at the Waite Campus. The mean number of syrphids alighting on the daisy were calculated from at least seven observations between 1200 and 1400 hours per day on nine relatively clear days (at least in the period of counting) in June and July 1993. At each time of observation, temperature was measured by a Minimite D (thermoelectric probe) at 20 cm off the ground in the vicinity of the bush, and light intensity by a Quantum / Radiometer / Photometer in the area of study. Standard temperature, solar radiation, and relative humidity (RH) data were also obtained from a weather station located about 150m away.

away.

In 1994, the changes in numbers of *M. viridiceps* on African daisy were observed over eight days in July. An hourly census-walk method was used between 0800-1600h to record the number of *M. viridiceps* and data obtained between 1200-1300 were used to detect the relationship between the numbers of *M. viridiceps* and the light intensity.

5. 2. 2 Summer flight activity

5. 2. 2. 1 Activity on weeds and the daisy, *C. frutescens*

The time of commencement of the daily activity of both species was observed on a census walk through weeds or along the rows of marguerite daisy, C. *frutescens*, between 0600 and 1800 in November 1993 and 1994. Both studies were carried out at the Claremont rose garden, at the Waite Campus (Chapter 3). Two different census-walks were used; in the first, the number of flies were counted on 17 shrubs of marguerite daisy which were planted in 3 rows between and around the rose plants (Fig. 3. 1). The second census-walk was made at a constant speed lasting approximately 10 minutes, along a set route through the rose garden. The route comprised sections along the rows of roses from the north to the south of the rose garden and the total number of flies which were flying, resting and feeding were counted. Light and temperature were measured hourly at the area of study similar to the previous surveys.

5. 2. 2. 2 Diurnal activity in sunny and shady areas

This survey was conducted on 10, 18 and 19 November 1994 when the maximum standard temperatures were 33.0, 32.5, and 33.8 respectively . Census-walks were carried out at the rose garden on weeds and marguerite daisy (open area, in the sun) with the same method as in pervious survey. At the same time, another census-walk was conducted by another observer in the shade of *Acacia* trees. This area was located about 20m at the northern part of the rose garden and with an equal length to the rose garden's but about 3m width (Fig. 3.1). This shade strip included sowthisle flowers at the density of about 5 /m^2, together with *Polygonum*, *Atriplex* and some grasses without flowers.

To record the proportion of the population in the rose garden which moved to the shade of *Acacia* trees, 30 *M. viridiceps* and 30 *S. grandicornis* were marked with a fine ground mixture of one part of fluorescent dye with 6 parts of gum Arabic (Reeves *et al.* 1948) from 0900 to 1100 on the day of experiment. The powder-dye was applied by means of a hand-operated powder blower (Fig. 5.1) held approximately 5 cm from syrphid flies resting or feeding on weeds and daisy flowers .

5. 3 Results

5. 3. 1 Winter flight activity

5. 3. 1. 1 Flight activity between 1200-1400

There was a significant inverse relationship between the number of *M. viridiceps* recorded on African daisy and the mean light intensity (Lux) measured between 1200 and 1400 in July 1993 and 1994 (R^2=0.49, p=0.04, F=6.85 for 1993; R^2=0.53, p=0.04, F=6.90 for 1994; Fig. 5. 2). No significant differences between the two regression coefficients (t=0.11, $\alpha = 0.05$, df=13) and the elevations were detected (t=-1.78, $\alpha = 0.05$, df=14). There was no significant relationship (p= 0.05) between the numbers of flies and the mean wind velocity within the range mean 2.3-7.2 km/h, and daily relative humidity between the range of 24-89% either singly or in combination.

Figure 5. 1:The hand-operated powder blower used for marking hoverflies in the field.

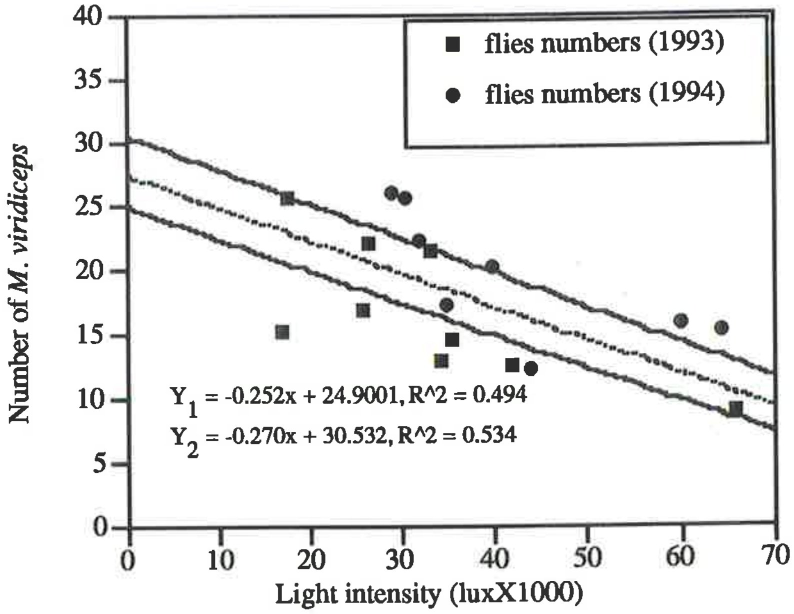

Figure 5. 2: Relationship between the number of *M. viridiceps* and the light intensity; lines 1 and 2 are for 1993 and 1994 respectively. The common regression line with the equation Y=27.5-0.26x is also shown.

5. 3. 1. 2 Diurnal activity and temperature threshold

M. viridiceps did not alight on African daisy plants at temperature less than 13°C (Fig. 5. 3). The mean numbers per hour/day of *M. viridiceps* on African daisy during 8 days in July 1994 are shown in Fig. 5. 4A. Activity started at hour 09.00 (about two hours after sunrise), peaked mostly around hour 12.00 (about 5 hours after sunrise) and declined rapidly in the early afternoon.

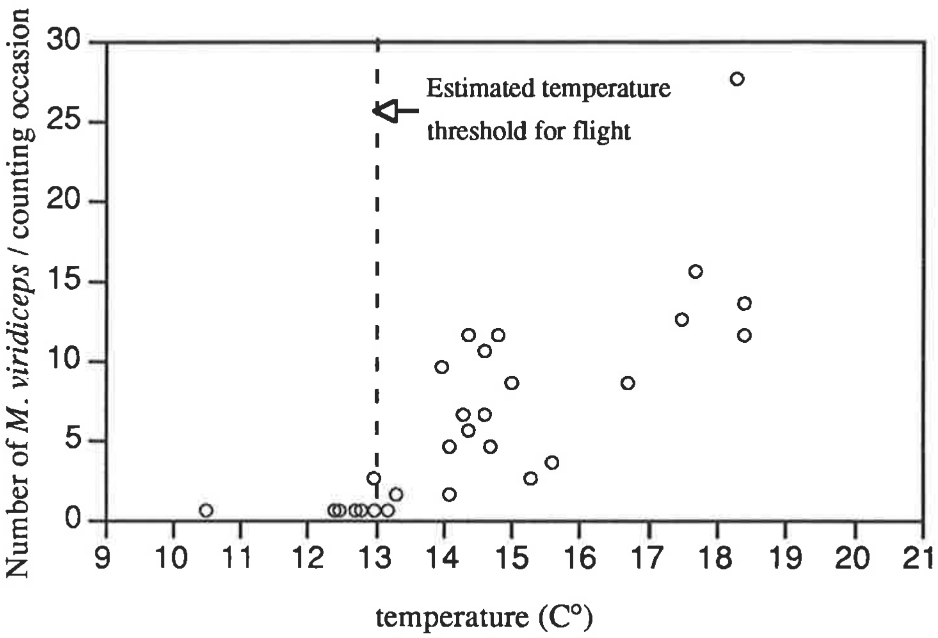

Figure 5. 3: The threshold temperature for the commencement of flight activity by *M. viridiceps* around African daisy, during June and July 1993 and 1994

5. 3. 2 Summer flight activity

5. 3. 2. 1 Diurnal activity on marguerite daisy and weeds

Since African daisy does not flower in summer, diurnal activity of *M. viridiceps* was studied on marguerite daisy at this time of the year. The flight activity of this species started at 0800 (CST) (about two hours after sunrise) and ceased at 1500 after a peak at 1100 (five hours after sunrise) (Fig. 5. 4 B). Thus the commencement and peak activity of *M. viridiceps* in summer were one hour earlier than in winter but at the same number of hours after sunrise.

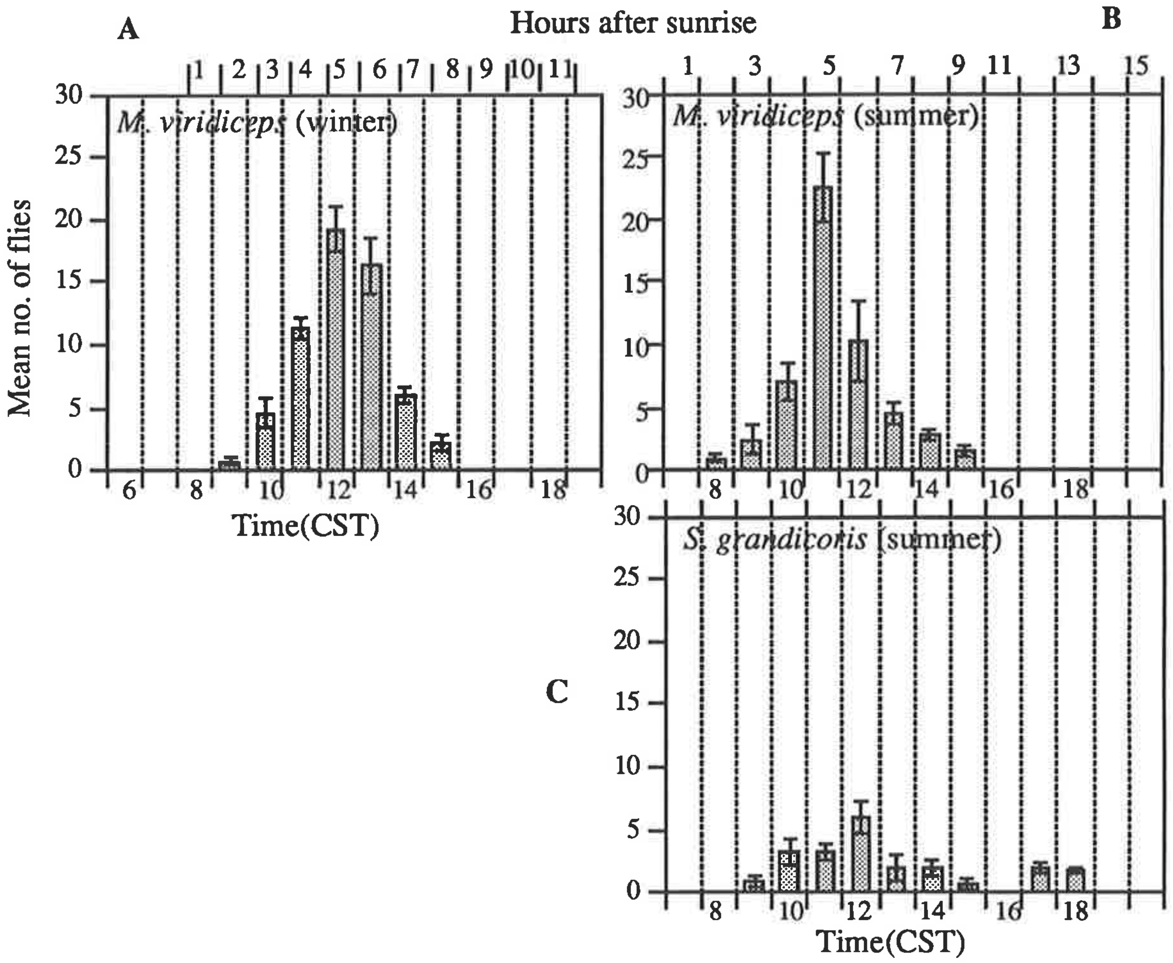

Figure 5. 4. Diurnal flight activity of *M. viridiceps* in winter (A) and summer (B), and of *S. grandicornis* in summer (C). Time in summer is based on Central Standard Time (CST) in South Australia and one hour ahead of winter time. Vertical bars show standard errors of means (4 days in summer and 8 days in winter).

No consistent relationship between the number of flies counted and hourly solar radiation and temperature was detected.

Both species started activity on weeds earlier than marguerite daisy. The data indicate that *M. viridiceps* starts activity and peaks about one hour earlier than *S. grandicornis*. (Fig. 5. 4. B, C).

The mean percentages of each syrphid species on weeds are shown in Fig 5. 5. At the beginning of the daily activity, all individuals of both species were active on weeds. A greater percentage of *S. grandicornis* were counted on weeds than on marguerite daisy. In contrast, *M. viridiceps* tended to forage more on marguerite daisy than on weeds during diurnal activity at the Claremont rose garden.

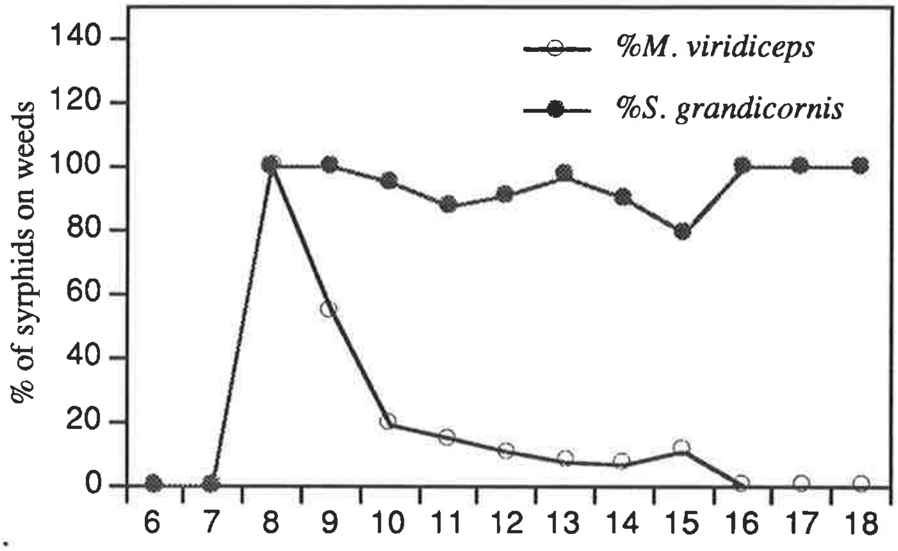

Figure 5. 5: Changes in percentages of populations of *M. viridiceps* and *S. grandicornis* on weeds and on marguerite daisy.

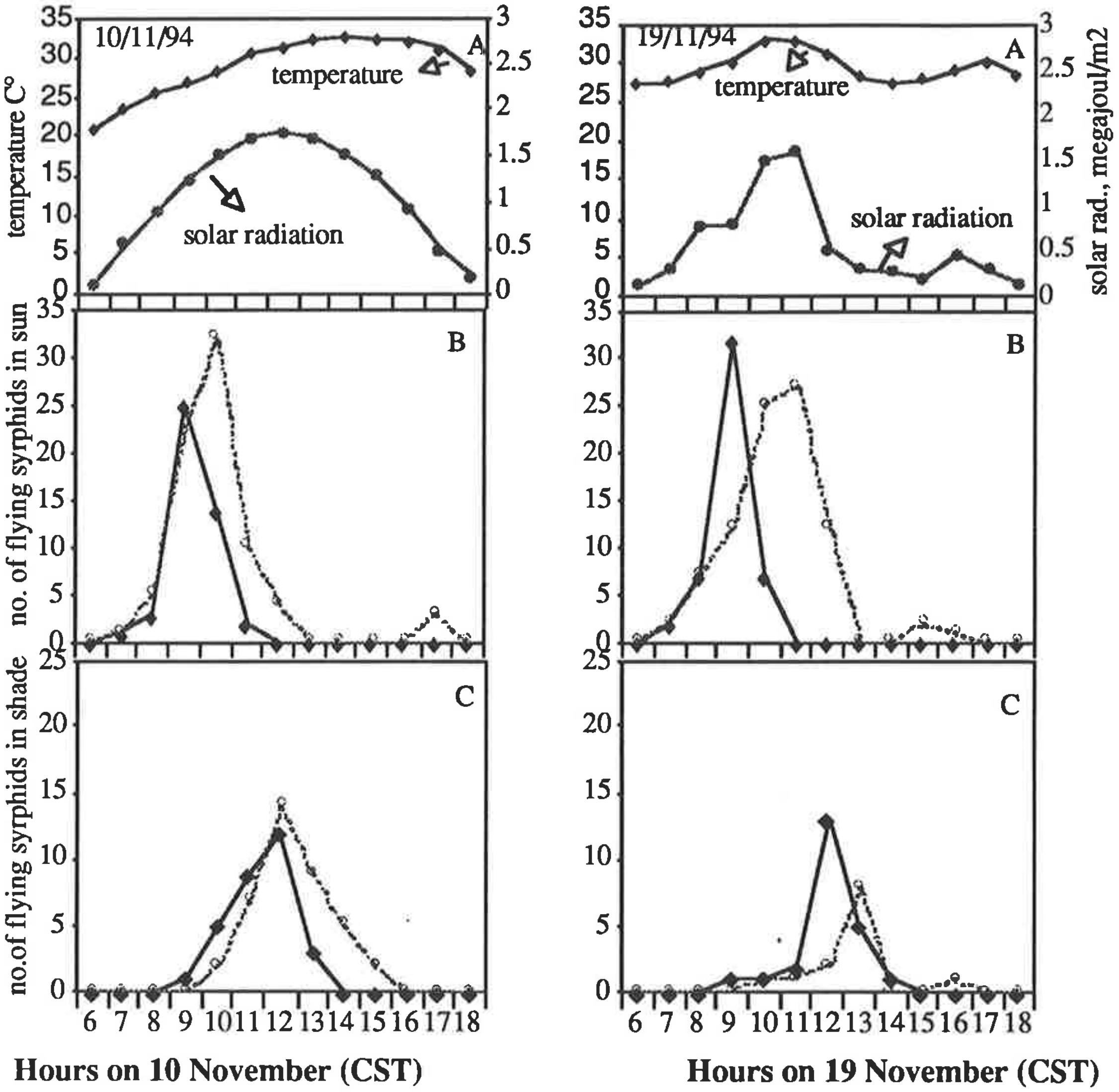

Figure 5. 6: (A) the hourly maximum temperature (°C) and solar radiation (meg. joules/m^2) on each of the 2 days of observation (10 November and 19 November, 1994); and (B-C) diurnal activity pattern of *M. viridiceps* (solid lines) and *S. grandicornis* (dotted lines) at the rose garden (sunny area; B) and in the shade of *Acacia* trees (C) on each day.

5. 3. 2. 2 Diurnal activity in sunny and shady areas

On each of the 2 days of observation, temperature remained between 25 and 33° C from 8.00 hours to 18.00 hours (Fig. 5.6), but the solar radiation decreased in the late afternoon to the same level as in the morning. Both species of syrphids tended to fly earlier in the morning in the sunny area than in the shady area (Fig. 5.7); and they also tended to cease flying earlier in the late morning-afternoon in the sunny area. *S. grandicornis* stopped flying in the sunny areas later than *M. viridiceps* and some were even flying in the late afternoon, between 1500-1800. In contrast, no *M. viridiceps* adults flew after 1200 in the sunny area. Marked *M. viridiceps* and *S. grandicornis* were similarly active in the sunny area earlier in the morning (Fig. 5. 7), but moved to the shade during the afternoon.

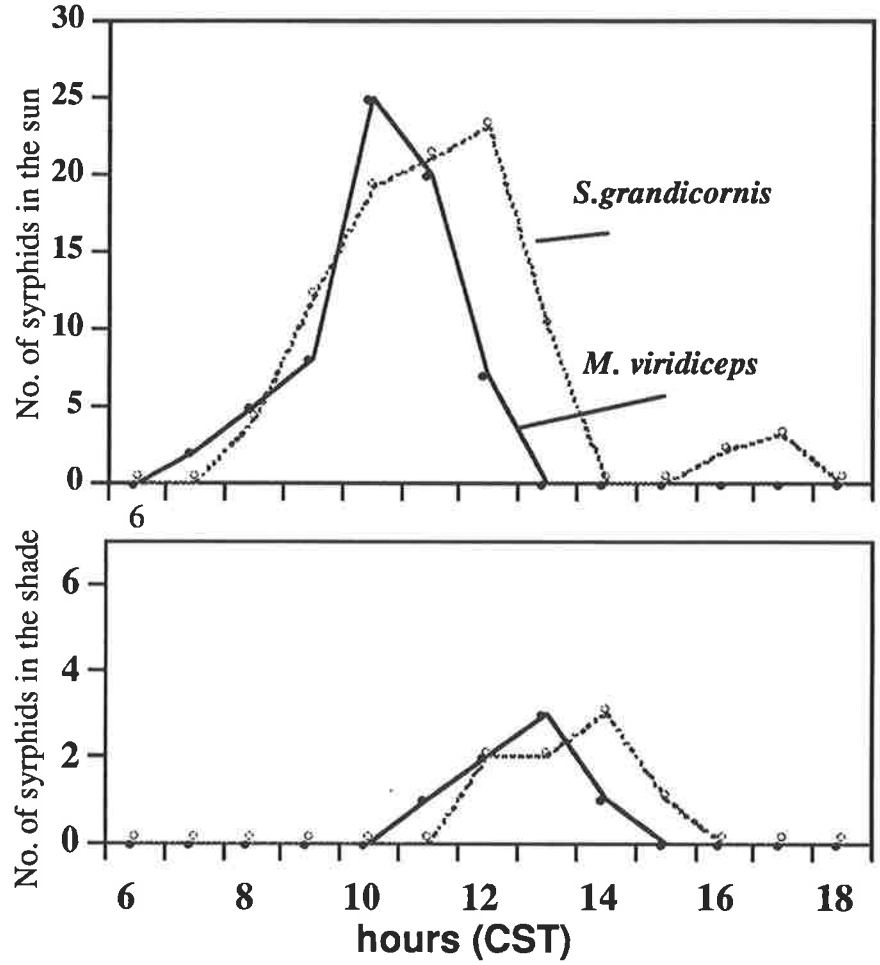

Figure 5. 7 Diurnal activity patterns of marked individuals of *M. viridiceps* and *S. grandicornis* in the sunny and shady areas of the Claremont rose garden on 18/11/94.

5. 4 Discussion

The flight activity of *Melangyna viridiceps* and *S. grandicornis* relates to foraging activity, since none of the plants observed in this study carried aphid colonies. Syrphid flies prefer areas with flowers even for oviposition (Schneider 1969) and it is likely that the duration of activity and the time that hoverflies remain in an area is related to the levels of prey density or feeding on honey dew of aphids in the vicinity of flowering plants.

It has been shown in this study that during summer days, adults of both species may be found in the shade of trees in the afternoon, at a time when they were virtually rare or absent from the open field. The movement to the shade during hot period of the day may minimise the possibilities of insect desiccation (Wilmer 1982). It is concluded that in addition to flowers, provision of shade is important in retaining hoverflies within an area during summer.

M. viridiceps is active between March (early autumn) to late November or December (late spring and the beginning of summer), but particularly during winter and early spring in Adelaide. During that period of the year when the activity of *M. viridiceps* overlaps with that of *S. grandicornis, M. viridiceps* starts activity earlier in the morning and ceases activity earlier in the afternoon. Even during winter, *M. viridiceps* appears to avoid the effects of direct sunlight around mid-day (cf Neilson 1966). In this regard, the start and peak of activity of *M. viridiceps* at the same number of hours after sunrise in summer and winter, suggest that light is a determinant of flight activity of this species, as it is with a number of other syrphid species (Gilbert 1985d).

Temperature is also an important determinant of flight activity of *M. viridiceps*. In winter, the threshold for the start of flight activity of *M. viridiceps* is 13°C, and this is reflected in the later start of activity in winter. Thermal considerations of each species, body size, reflectance properties of cuticle and behavioural and physiological thermoregulation are elements in the optimisation of foraging and commencement of activity (Maier and Waldbauer 1979; Wilmer and Unwin 1981; Wilmer 1983; Gilbert 1985d). Since the body sizes of *M. viridiceps* and *S. grandicornis* are similar, the cuticular colour of the insect may be important in different activity times of the species. The darker colouration of *M. viridiceps* compared with *S. grandicornis* indicates, perhaps, an adaptation to cooler temperature (Wilmer 1983). In summer, temperatures mostly exceed 13°C at sunrise , but activity does not start until two hours after sunrise. This may be influenced by light as a co-determinant of activity, but it also may reflect other factors not measured in this study.

Nectar feeders, such as *S. grandicornis,* may have to await the formation of nectar in their food plants before foraging (Nùñez 1977). Nectar concentration is highly correlated with ambient relative humidity, and microclimate inside flowers may influence the equilibration of nectar with relative humidity of the air or the equilibrium concentration itself (Corbet 1979). On the other hand, pollen feeders, such as *M. viridiceps*, may have to wait until their food dries, since they cannot eat pollen grains aggregated by moisture. Thus, the suitability of available food is a factor which determines syrphid foraging activity on certain flowering plants.

The movement of *M. viridiceps* from weeds to daisy and the tendency of a high proportion of *S. grandicornis* to remain on weeds indicate that the two species differ in their food demands and their response to food availability (cf Opp and Prokoppy 1986).

The duration of the activity of a predator in the field may influence suppression of prey numbers. The pattern of daily foraging activity of *M. viridiceps* is is unimodal, similar to a number of other syrphids (Lewis and Taylor 1964). In contrast, *S. grandicorni* s sometimes returns to the field in the afternoon and although it does not have a clear bi-modal activity pattern, it does have a longer period of activity than *M. viridiceps.* in the field. The re-starting of activity in the afternoon may be due to a combination of physical factors such as sunlight, temperature and food availability, or it may be a result of biological factors such as satiation or changing to a different type of behaviour, such as host finding.

Chapter 6

Pollen and flower selectivity by *Melangyna viridiceps* and *Simosyrphus grandicornis*

6. 1. Introduction

Pollen grains and nectar of flowers are consumed by adult hoverflies. Food resource selection in hoverflies depends partially on the colours of flowers (Haslett 1989a) and different species of hoverflies may respond variously to different colours. *Platycheirus scutatus* and *Eupeodes luniger* were found to be attracted to the pollen of yellow flowers of broom (Dixon 1959). An experiment with sticky traps of different colours (orange, white, lemon, yellow, golden yellow, black, red and green) has shown that white traps were most attractive to the aphidophagous syrphid species, *Episyrphus balteatus*, *Metasyrphus corollae*, *Sphaerophoria scripta*, *Chrysotoxum intermedium* and *Syrphus* sp. (Peschken 1965; Ortu 1990). In addition, Cowgill (1991) showed that *Episyrphus balteatus* and *Eupeodes corollae* preferred many food plants with white flowers (cited by MacLeod 1992), while some investigations have indicated that water-traps with yellow colour were the most attractive to hoverflies (Ssymank and Godesberg 1991).

In New Zealand, Wratten *et al.* (1995) showed that more *Melangyna novaezelandiae* were captured in yellow traps compared with blue, white and green, while *Melanostoma fasciatum* was trapped equally in all these traps. While some investigations on response to different colours have been done on European and New Zealand hoverflies species, there is no information on the attraction of the two common Australian species of hoverflies to different colours.

Colour as a long distance signal and quality of pollen and nectar as a close signal are two factors which determine the relative attractiveness (selectivity) of a flower species to hoverflies. A comparison of pollen and nectar in the gut with availability in the field can be an indicator of plant species selectivity. While identification of nectar in the gut may be difficult, pollen types usually can be easily identified. Haslett (1983) measured pollen digestion by a photographic method and showed that a small proportion of pollen grains remained intact and passed out of the fly undigested. Although pollen is digested as it passes through the gut, the grains retain their shape and can still be identified (Holloway 1976). Therefore, pollen used by the flies can be identified by analysing pollen species in the insect gut.

The selectivity patterns of some syrphid species have been studied in Europe (Haslett 1989 a, b; Ssymank and Gilbert 1993; Rotheray 1994; Klimes 1994). Haslett (1989a,b) showed that some hoverfly species are highly selective in their pollen diet and there were considerable differences in the relative amounts of pollen and nectar ingested by individual insects. Ssymank and Gilbert (1993) distinguished 3 groups of syrphids: the group which visit the flowers of grasses and sedges (*Melanostoma*, *Platycheirus* and *Pyrophaena*); those early spring species which feed on the pollen of anemophilous trees and shrubs (3 *Melangyna* species); and finally the group which consume the anemophilous pollen on the leaf surface of trees and shrubs (mainly in *Xylota*).

The pollen spectra in the gut of New Zealand species of hoverflies have been investigated by Holloway (1976) and Wratten *et al.* (1995). Holloway (1976) indicated that the small and sparsely hairy species of hoverfly with a short proboscis, *Melanostoma fasciatum* , had ingested at least 99% anemophilous pollens while the larger, more hairy species, with elongated proboscis, *Eristalis tenax*, had ingested pollen exclusively from nectar-bearing flowers. Wratten *et al.* (1995) classified gut-pollen contents of *Melangyna novaezelandiae* and *Melanostoma fasciatum* into 13 groups according to plant family or genus. They concluded that pollen-type ranking was similar between the two species and both species had *Taraxacum*-type pollen most frequently in the gut. However, selectivity of Australian hoverfly species has not been investigated.

The aim of this study was to investigate flower selectivity by two native hoverfly species, *Melangyna viridiceps* and *Simosyrphus grandicornis*, relating this to availability of flowers in a rose garden and laboratory in Adelaide, South Australia.

6. 2 Materials and Methods

6. 2. 1 Attractiveness of different colours

Two experiments were conducted in a 2.4m x 3.4m x 3.30m glasshouse. The first experiment was designed as a 4 x 4 Latin Square (reference) and 4 colours (red, yellow, white and orange) were chosen as treatments for *Simosyrphus grandicornis*. The 4cm petri-dishes were painted with each colour enamel (Hubrol), and equal volumes of cubed sugar and hazelnut pollen were put in the middle of each petri-dish. Tissues soaked in water were provided in petri-dishes at four sites in the room.

The petri-dishes were placed 20cm apart on a bench 120cm high. Eight pots of rose plants were set around the petri-dishes as resting places for the flies. 50 *Simosyrphus grandicornis* (equal numbers of males and females) were captured from the field and released in the glasshouse.

The experiment was run over 3 days under natural light. The temperature range was 18-22°C and light intensity was 2000–30000 lux during the course of recording. The numbers of hoverflies were counted on 50 occasions separated by 10 minute intervals. After each count, the flies feeding on dishes were driven away to mix with other flies. The number of flies in the room was kept roughly constant, with a few new flies being released each day to replace dead ones.

The second experiment, for *Melangyna viridiceps,* was conducted in the same place but in a randomised block design with 3 replicates and 5 colour treatments (yellow, orange, white, blue and red). The painted petri-dishes were arranged on the edge of the rotatable round table (Chapter 3) with 17cm spaces between them. The numbers of flies were counted on 27 occasions with at least 20 minute intervals. The ranges of light intensity and temperature were the same as in the previous experiment.

6. 2. 2 Selectivity in the field and pollen determination

6. 2. 2. 1 Description of Claremont site

The Claremont site is part of an experimental field with an area of 70m by 60m located at the Waite campus, University of Adelaide. Fig. 6. 1 shows the site and the approximate area covered by the different vegetation types of trees, shrubs and weeds. A rose garden with some attractive flowers has been made at this site for the selectivity study. A description of the rose garden has been presented in Chapter 3.

6. 2. 2. 2 Sources of specimens and pollen determination

Flies were collected from the field by net sweeping and by using water traps and suction traps. During sweeping surveys, all species of plants flowering at the Claremont site were inspected, and flies collected wherever they occurred.

Five yellow water traps were installed at a distance of 4m from each other at the Claremont rose garden. Two suction traps were also installed in the vicinity of an African daisy plant, *Euryops pectinatus,* and a marguerite daisy plant, *Chrysanthemum frutescens*, at the same rose garden (Chapter 4).

Live flies caught by sweep netting were carried in small plastic tubes and immediately dissected for pollen identification.

The specimens caught in water traps were transferred to the laboratory in 70% ethanol. Those caught by suction traps were transferred in a solution of water and detergent in the suction trap's jar.

Dissection and sex determination were carried out under the stereo-microscope. The complete mid and hind gut of the specimen was taken without rupturing and placed in one drop of 20%

sucrose (O' Brien and McCully 1981) on a glass microscope slide. The guts were then teased apart with two fine forceps to release the pollen grains, the pieces of gut wall were removed and the slide was covered with a glass coverslip. Sometimes the pollen content in the gut was identified immediately, but on other occasions permanent mounts were made by drying for 24 hours and then sealing the edges with colourless nail polish.

Pollen grains in the fly's gut were classified into plant family, genus and species, depending on the levels of taxonomic discrimination achievable (Pike 1956; Heusser 1971; Moore 1978; Iwanami 1988; Punt 1988; Dashorst 1990; Boyd 1992) under the light microscope with a magnification of x400. Permanent slides were also made from pollen grains of flowers on which the syrphid flies had been observed alighting. Photographs of these pollen grains were also provided to compare with the pollen contents of the gut of hoverflies (Appendix 6.1).

Numbers of pollen grains of each plant species in the field of the microscope were counted with a magnification x400. Ten fields chosen at random over the slide were counted and total number of each pollen type was calculated and the percentage of pollen consumption per sampling day was then obtained for each pollen species. The mean percentage of pollen consumption per 15 days was calculated by dividing the total percentage by the number of sampling days during the first and second half of each month.

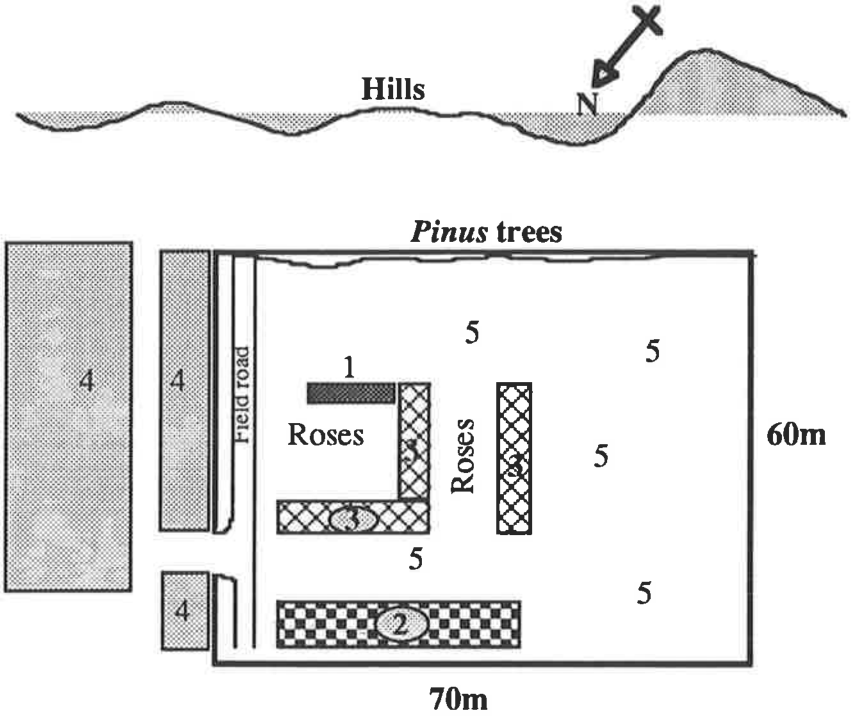

Fig 6. 1: Diagram of the Claremont site. Locations and approximate sizes of three different strata for sampling the availability of flowers for *M. viridiceps* and *S. grandicornis*; 1: African daisy 2: *Acacia* trees, 3: marguerite daisy, 4: *Eucalyptus* and 5: weeds. Diagram is not to scale.

6. 2. 2. 3 Comparison of the quantity and diversity consumed by males and females

Pollen grains in the gut of *M. viridiceps* and *S. grandicornis* can be seen through the clear abdominal integument under a stereo microscope. Depending on the amount of pollen in the gut, each insect was ranked 0, 1, 2 or 3. Those with no pollen ranked as '0' and specimens with full guts ranked '3'. The levels of pollen consumption by males and females were then compared by a non-parametric Mann-Whitney test. The ovarial stages were also categorised into 4 groups: A, B, C and D. Classes C and D categorised as gravids (see Chapter 4).

6. 2. 2. 4 Ranking flower availability

Hoverflies explore flowers from different strata, i.e. high trees, shrubs and herbs, making it difficult to estimate the availability of resources using a similar method for all strata. According to the type of plants, four different methods of flower sampling were used to estimate the relative number of flowers at the Claremont site. These data were then multiplied by two indices: the index for the relative area occupied by each species (Fig. 6. 1) and the index of intrinsic flower density of each flower species. As the first factor, the index of relative area of each species was visually estimated from area covered to one of three categories, large, medium and small, with indices of 1 for *Eucalyptus* and weeds (large area), 0.5 for *Acacia* and marguerite daisy (medium area), and 0.25 for African daisy (small area).

The second factor was the intrinsic density of flowers on different species. Species with dense flowers were given an index of 1 (marguerite and African daisies), those with a medium density of flowers were given an index of 0.5 and species with sparse flowers (at least during sampling) were given an index of 0.25. Therefore, with the assumption of the same attractiveness, the pollen of a plant species with dense flowers which occupies a small area has a similar probability of being taken as the species with dispersed flowers which occupies a large area. Regardless of the sampling technique, the product of the two factors was multiplied from each percentage of flower density obtained by sampling. These indices of availability were ranked and compared with ranked pollen species found in individial flie's guts and the differences in ranks were analysed by Johnson's (1980) procedure, using Genestat 5. (Appendices 6. 2 and 6. 3).

Availability of weed flowers

The relative density of weeds at the Claremont site was measured by randomly placing 20-25 quadrats (70cm by 70cm) in the area of weeds (Fig. 6. 1) and recording the presence or absence of species with flowers in each quadrat. The percentages of quadrats containing each species was then calculated and the product of this figure and two factors mentioned in 6. 2. 2. 4 was used to rank the availability of weed flowers at the Claremont site on each sampling date.

Availability on shrubs

All the flowers on all daisy plants and the percentage of branches with flowers on daisies were recorded weekly and the mean for two weeks was used for the analysis. Flowers on all 6 African daisies were counted, but on marguerite daisy plants, five bushes of 17 were selected randomly and the number of flowers was converted to 17 bushes. When the number of flowers was higher than 100 per plant on each daisy, flowers were estimated by a grid method. The bush was divided into 8 parts using four 1.8m wooden dowels. The number of flowers in one or two parts were counted and then converted to the total number per plant. The percentage of branches with flowers was also recorded by randomly selecting 10 shoots/plant. The percentage of branches with flowers was also recorded by randomly selecting 10 shoots/plant with a maximum of 60 shoots on each sampling occasion.

The preference of the syrphid for either of the two daisy species was compared by a method similar to Haslett (1989a), in which only the two plant species of interest were considered, and also by using the method of Johnson (1980), mentioned previously, which included all flowers in the study area.

The flowering period and percentage of shoots with flowers on the native shrubs which were planted around the rose garden were calculated by counting the number of shoots with flowers out of 15 randomly selected shoots per plants.

Availability of flowers on Eucalyptus and Acacia trees

Australia has many *Eucalyptus* and *Acacia* species which flower at different times of the year. Therefore, the weekly recording was confined to 50 *Eucalyptus* trees and 20 *Acacia* trees (Chapter 3) located 20m and 50m from the rose garden respectively. The percentage of shoots with flowers were estimated using binoculars 12 x 50. Ten *Eucalyptus* trees were selected at random weekly, and the number of shoots with flowers were counted for 10 fields of view on each tree from 20m away.

6. 2. 2. 5 Preference study using suction traps

Daily observations and recording of the number of syrphid adults showed that many syrphids were attracted to African and marguerite daisies at the Claremont site. Therefore, a field experiment was conducted there to compare the attractiveness of these two flower species. Only two 20cm suction traps were available; one trap was set up beside an African daisy and the other beside a marguerite daisy; both plants chosen at random. After 2-11 recording periods, the traps were moved to a new pair of plants.

The effective height above the suction traps was measured in a room with still air by an air velocity meter (Veloci Calci TSI). The air velocity was measured at 2cm intervals until the height was reached where no air movement was detected. At each interval, the mean of 5 readings was calculated by the air velocity meter and about two thirds of the nil velocity height was used as the effective height.

The number of flowers at the effective height was counted in the field. The mean number of flowers per site was then calculated and regressed on the mean number of flies caught per day.

Syrphid flies caught in suction traps, water traps and by net sweeping were dissected and the mean percentages of pollen grains of the two daisy species were obtained. The proportions of each daisy pollen type (in percentage) to availability of daisy flowers (percentages of each flower species at the area of study) were calculated and compared. It is clear that the same percentage of the flower availability was used for all flies captured on each occasion.

6. 2. 3 Preference experiments in the laboratory

6. 2. 3. 1 Wind-tunnel experiment

This experiment was conducted in a wind tunnel with a light intensity of 10000 lux and wind velocity of 20m/s. Twenty *M. viridiceps* were released, one by one, 50cm from two small pots of daisy flowers with 20cm space between them. This experiment was replicated 3 times under similar conditions.

6. 2. 3. 2 Preference experiment in the glasshouse

Three experiments were conducted in a 2.40m x 3.40m glasshouse with a height of 3.30m under natural light. Since the two fly species were available during different times of this study, the experiments for each species were conducted at different times of the year.

Experiment 1: Selection between two species of daisy flowers

This experiment was carried out over a period of 3 days from 31/7 to 2/8/94. Sixteen flowers each of marguerite and African daisies were collected from the field and each was put in a small bottle filled with a 2% solution of "flower fresh", manufactured in Australia. Sixteen bottles of flowers (8 of each species) were alternated on the perimeter of a rotatable round table (Chapter 3) and the rest were put in a circle in the middle such that the spaces between flowers in the outer and inner circles were 19cm and 12cm respectively. Flowers of similar size and condition were used in the experiment. All the flowers were placed about 7cm above the table surface. Wilted flowers were replaced with fresh ones during the experiment.

Seventy *Melangyna viridiceps* captured from the field were released from a 30cm x 30cm x 30cm sleeved cage on the floor of the glasshouse. The number of flies on each type of flower was recorded on 16 occasions. After each recording the flies were brushed off to mix with the other flies until the next recording. Meanwhile, the table was rotated to re-randomise the flowers. Light intensity and temperature were also recorded on each occasion. The total numbers of flies on African daisies versus marguerite daisies were compared with a χ^2 test.

The experiment was repeated under the same conditions on 35 occasions during the beginning of November 1994 by releasing 70 *S. grandicornis*.

Experiment 2: Selection between African daisy (Asteraceae), *Eucalyptus* and *Acacia* flowers

This experiment was conducted in the same glasshouse on the rotatable round table, under natural light conditions (15000-50000 lux) at 15.8-21.3°C. The conditions of the experiment were similar to those for experiment 1, but the experimental design was a randomised block with three treatments and five replicates. The perimeter of the rotatable table was divided into five parts and three different flower species were put at random in each part. Two daisy flowers, a shoot of *Eucalyptus camaldulensis* bearing 11 flowers without leaves, and a shoot of *Acacia microcarpa* bearing young flowers were put in small bottles of water as three treatments. The experiment was run over a period of four days from 19/8 to 22/8/94, and the flowers were replaced every day or earlier if they wilted. Sixty *Melangyna viridiceps* captured from the field were released at the beginning of the experiment. Dead flies which had fallen on the floor were replaced. The numbers of flies on flowers were counted on 29 occasions from 9:00 am to 4:00

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pm with intervals of at least 30 minutes.

A similar experiment was conducted in the glasshouse using 60 *S. grandicornis* during November 1994.

Experiment 3: Selection between African daisy and two weed flowers

The attractiveness of two common weed species, wild radish and sowthistle, whose pollens are naturally consumed by the insect, were compared to African daisy. The experiment was run in the glasshouse over a period of 3 days by releasing 60 adult *Melangyna viridiceps* captured from the field. The numbers of flies were counted on 20 occasions, and light intensity (3000-55000 lux) and temperature (14.1-21°C) were also recorded on each occasion from 22/8 to 25/8/94. The other conditions of the experiment and the statistical design were similar to experiment 2. Since sowthistle flowers are closed in the afternoon, counts were limited to mornings .

A similar experiment was conducted for *S. grandicornis* in the same glasshouse under 5000-70000 lux and 15.1-25°C in November 1994.

6. 3 Results

6. 3. 1 Attraction to different colours

At any one count, the number of flies feeding on the coloured petri dishes was no greater than 3, or 6% of the total for *S. grandicornis* in the room and 7, or 14% for *M. viridiceps*.

The analysis of variance indicates that the mean numbers of flies attracted to different

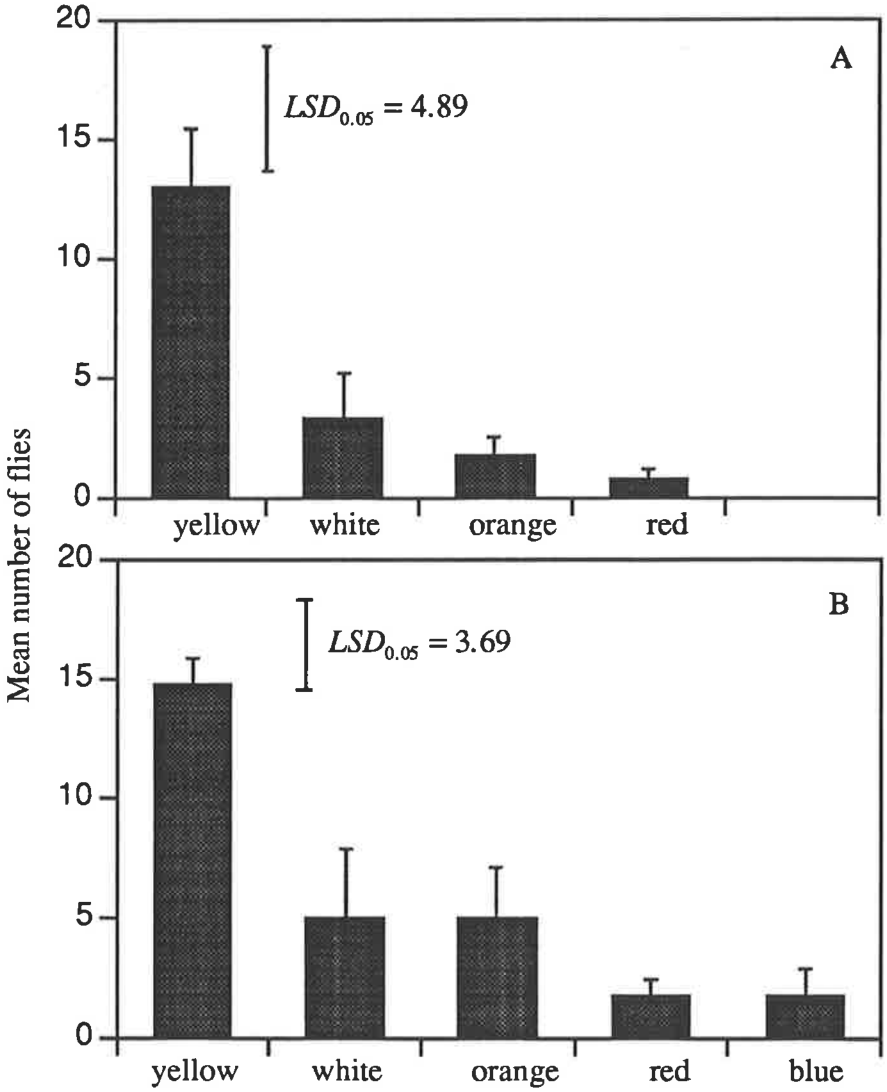

Figure 6. 2: Number of *S. grandicornis* (A) and *M. viridiceps* (B) attracted to different colours in the glasshouse experiments. Standard error bars and Least Significant Differences (LSD) are also shown.

colours are significantly different ($P< 0.01$). The comparison of the means (Fig. 6. 2) showed that yellow was the most visited colour by both species and there was no significant difference between other colours ($LSD_{0.05}=4.89$ and 3.69 for the first and second experiment respectively). By contrast, the red colour attracted only one *S . grandicornis* during the course of the experiment.

6. 3. 2 Selectivity in the field

6. 3. 2. 1 Flower availability and usage of pollen by syrphid flies

The scientific and common name, flower colour and flowering period(s) of each plant species within and around the Claremont rose garden are listed in Table 6. 1 in one of two sub-lists denoted as "Pollen " and "No pollen". The former group comprises those plants whose pollen was found in the guts of either *M. viridiceps* or *S. grandicornis.* No pollen from the second group was found in the guts of the flies.

The monthly abundance of flowers of 6 native plant species and the percentages of their pollen in the guts of *M. viridiceps* are given in Fig. 6. 3. Similar data are given in Fig. 6.4 for 8 species of weeds; and similar data again are given in Fig. 6. 5 for the African and marguerite daisies. Johnson's (1980) method was used to measure the difference between ranked availability of flowers and ranked usage of pollen from these and other species listed in Table 6. 1. An example of the calculations for determining this difference is given in Appendix 6. 2, 6. 3 and 6. 4 for the data for one sampling occasion. In Appendix 6. 2 is given the converted availability of flowers, the ranks of this converted availability, and estimated percentages of pollen (denoted as usage) from the different plant species in the guts of *M.viridiceps* adults. These percentages are converted to ranks, for each fly, and then to a mean rank for each plant species in Appendix 6. 3; and the differences between ranked converted availability and mean ranked usage for each plant species/group are given in the last column of the same table. The formula for the calculation of F is given in Appendix 6. 4.

Table 6. 1: Availability and usage of flowers by *M. viridiceps* and *S. grandicornis* at the Claremont site from February to October 1995. Those plants whose pollen was found in the guts of syrphid adults are listed under "POLLEN". The others are listed under "NO POLLEN". N=Native and E=Exotic (species).

Scientific name	Family	Common name	Flower colour	(N)ative or (E)otic	Months of flowering
POLLEN					
-	Proteaceae	?	?	-	-
Acacia sp.	Mimosaceae	wattle	yellow	N	Mar.-Apr.; Sep.-Oct.
Chrysanthemum frutescens	Asteraceae	marguerite daisy	white	E	Feb.-Nov.
Eucalyptus sp.	Myrtaceae	Eucalyptus	white-pink	N	All year
Euryops pectinatus	Asteraceae	daisy	yellow	E	Feb.-Nov.
Fumaria densiflora	Fumariaceae		blue	E	May-Sep.
Lamium purpureum	Lamiaceae	purple dead-nettle	blue	E	Jun. -Oct.
Malva	Malvaceae		white	E	
Plantago	Plantaginaceae	sago-weed	white	E	Oct.-Mar.
Poa annua	Poaceae	annual meadow-grass	white	E	
Polygonum	Polygonaceae	knot weed	white	E	Mar. Jun.
Portulaca	Portulacaceae	-	yellow	E	
Raphanus raphanistrum	Cruciferae	wild radish	yellow	E	May-Oct.
Sinapis	Cruciferae		yellow	E	May-Oct
Sonchus oleraceus	Asteraceae	sowthistle	yellow	E	all year
Veronica hederifolia	Scrophulariaceae	ivy-leaved	blue	E	May-Oct.
NO POLLEN					
Anagallis arvensis	Primulaceae	scarlet pimpernel	white	E	Jun.-Oct.
Atriplex australasica	Chenopodiaceae	saltbush		E	
*Callistemon**	Myrtaceae	bottle brush	white-red	N	Mar.-Apr.; Sep.-Oct.
Capsella bursa pastoris	Brassicaceae	shepherd's purse	white	E	
Goodenia varia	Goodeniaceae	hop goodenia	yellow	N	Feb.-Oct.
Grevillea crithmifolia	Proteaceae		white	N	Feb.-Mar.; May-Oct.
Grevillea glabrata	Proteaceae		white	N	Aug.-Oct.
Helichrysum sp.	Asteraceae	everlasting fl.	yellow	N	Mar.-Sep.
Heliotropium supirium	Boraginaceae			E	
Cardaria draba	Brassicaceae	hoary pepperwort		E	Jun-Jul
Olearia axillaris	Asteraceae	coast daisy-bush	white	N	Feb.-Apr.
Oxalis pes-caprae	Oxalidaceae	soursob	yellow	E	Jun.-Sept
Rosa	Rosaceae	rose	varies	E	except Jun-Aug.
Solanum nigrum	Solanaceae	blackberry nightshade	white-yellow	E	

*This pollen type included in *Eucalyptus* pollen group (Myrtaceae)

Pollen usage of 77 *M. viridiceps* and 12 *S. grandicornis* was measured by gut examination on respectively 8 and 2 sampling occasions. Appendix 6. 5 gives the percentages of different pollen grains in guts of *M. viridiceps*.

No pollen grains of the two native plant species of Proteaceae, *Grevillea glabrata* and *G. crithmifolia* planted in the site of study were detected in guts of any flies. However, there were some pollen grains of other species of this family in the gut of *M. viridiceps.* In addition, some Asteraceous pollen in guts was obviously consumed from outside the study area and its availability could not be measured. Therefore, these two plant families with unknown pollen species were omitted from the statistical analysis.

The statistical analysis was initially used to test the null hypothesis that these two hoverflies species consume flower resources randomly. This hypothesis was rejected for *M. viridiceps* (F=301.6, df=16 and 61) and for *S. grandicornis* (F=98.6, df=9 and 3). The mean of the differences between ranks was then listed for each plant species and for each species of fly to determine differences between plant species (Table 6. 2). In this table, plant species are arranged from lowest to highest according to the size of the mean of the differences The smaller the mean of the differences, the higher the selectivity.

The means of the difference in rank for any two plant species have been compared with the least significant difference between means, WS_d , where W is obtained from a table in Waller and Duncan (1969) and S_d is the standard error of the difference between two means (Johnson 1980). The least significant difference (WS_d) was estimated as 1.078 for *M. viridiceps* and 2.166 for S. *grandicornis* respectively Table 6. 2).

The least significant differences between any two plant means suggest that *M. viridiceps* and *S. grandicornis* consume flower species from different plant groups selectively (Table 6. 2). *M. viridiceps* consumes pollen mostly from different species of herbs (76.5%).

Table 6. 2: Mean of the differences between ranked flower availability and ranked pollen usage for each of most of the plant species listed in Table 6. 1. Averages connected with one line are not significantly different at the 5% level of probability. Large negative values indicate feeding selectivity by either species of hoverflies.

M. viridiceps		***S. grandicornis***	
Plant name	Average difference (ranks)	Plant name	Average difference (ranks)
Atriplex	-4.208	*Raphanus raphanistrum*	-4.125
Plantago	-3.519	Myrtaceae	-1.875
Polygonum	-3.084	*Euryops pectinatus*	0.083
Solanum nigrum	-2.961	*Acacia*	0.292
Raphanus raphanistrum	-2.058	*Chrysanthemum frutescens*	0.375
Fumaria	-1.513	*Anagallis*	0.417
Lepidium cardaria	-0.740	*Lamium*	0.625
Oxalis	-0.247	*Sonchus*	0.667
Anagallis	-0.195	*Polygonum*	1.458
Euryops pectinatus	-0.084	*Veronica*	2.083
Chrysanthemum frutescens	0.617		
Sonchus	0.818		
Lamium	2.318		
Myrtaceae	2.779		
Veronica	3.506		
Poa	3.799		
Acacia	4.773		
Least significant diff.	**1.078**		**2.166**

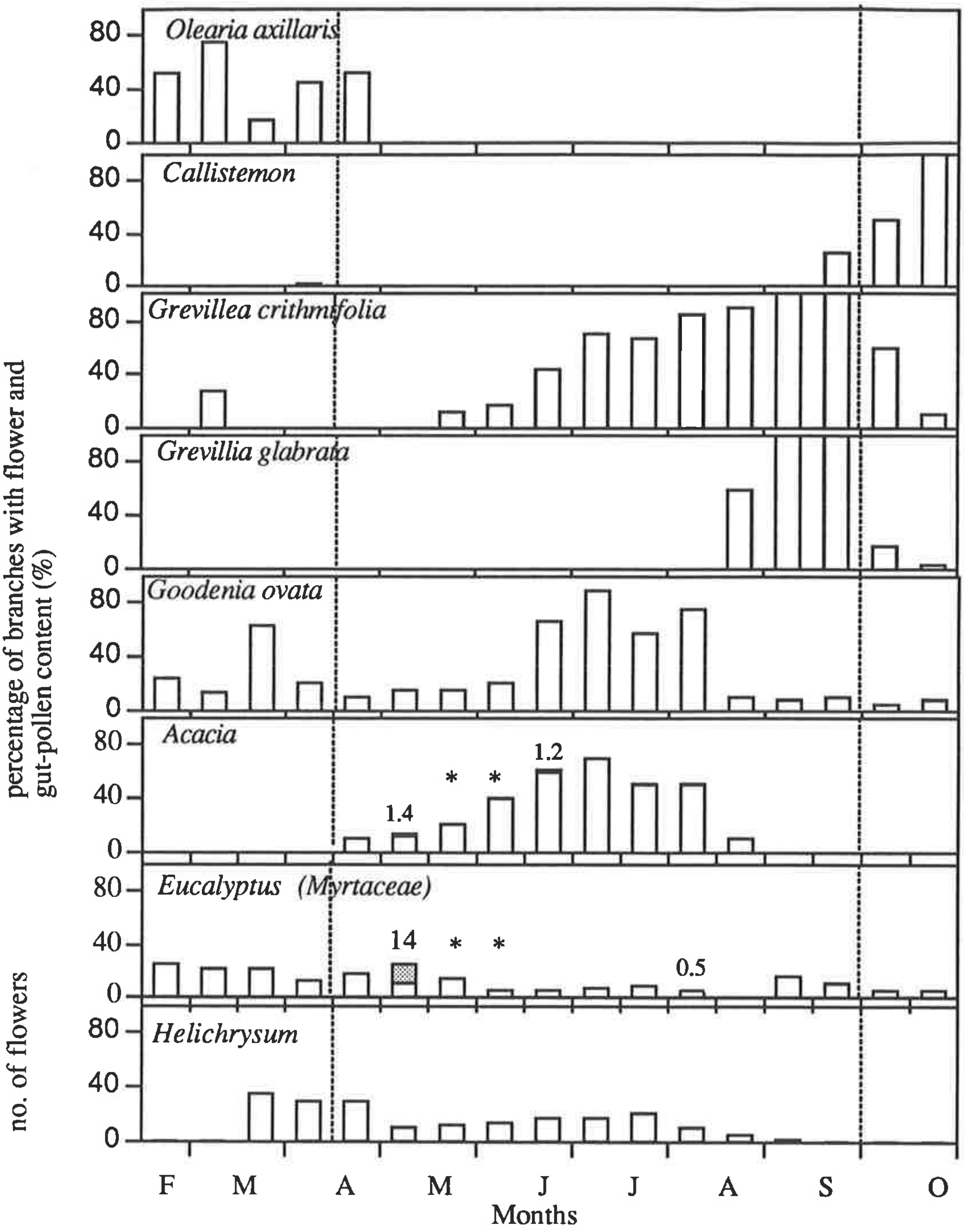

Figure 6. 3: Flower abundance and percentage of pollen in guts of *M. viridiceps* (solid) at the Claremont site in 1995. Above the columns of data values of percentage of pollen in gut are given for those columns for which percentage of pollen is >0. Specimens were dissected on occasions between two dashed vertical lines. No gut dissection were made in *months. Notice that pollen of only *Acacia* and *Eucalyptus* were consumed.

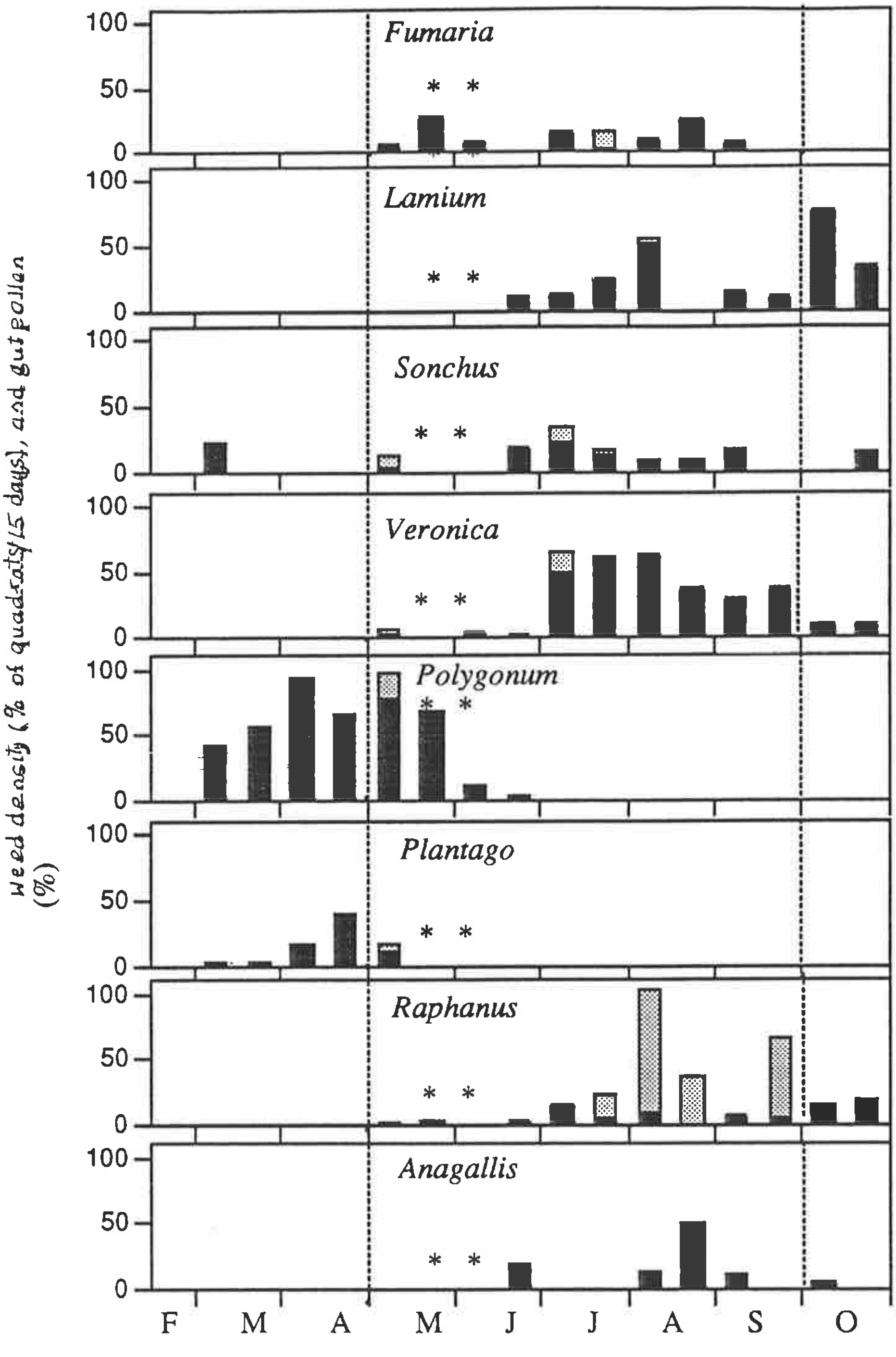

Figure 6. 4: Mean density of weeds in percentage of quadrats per 15 days (solid) and corresponding percentage of pollen in the gut of *M. viridiceps* (stippled) in 1995. Specimens were dissected on occasions between two dashed lines and asterisks show occasions when no flies were dissected.

African daisy and marguerite daisy are consumed equal to *Oxalis, Angallis and Sonchus,* and more than *Myrtaceae* and *Acacia*. These conclusions are the same as those for the glasshouse experiment which showed that this species preferred daisy flowers to *Acacia* and *Eucalyptus*. No difference was detected between the two daisy species which differed from the glasshouse and field experiments.

For *S. grandicornis*, wild radish (*Raphanus raphanistrum*) was the most attractive plant species used (Table 6. 2). Myrtaceae and African daisy were used equally. Similarly, there was no difference in selectivity between marguerite daisy and *Acacia*. But Myrtaceae and African daisy were selected over *Acacia* and marguerite daisy (Table 6. 2). Although *S. grandicornis* is highly attracted to wild radish, it usually prefers trees and shrubs more than does *M. viridiceps*.

6. 3. 2. 2 Availability and usage of daisy flowers

Weekly number of marguerite daisy flowers on 17 bushes and the number of African daisy flowers on six bushes at the Claremont rose garden from March to November have been given in Chapter 4. Pollen grains of the two daisies were detected in guts of *M. viridiceps* from the beginning of May to the 17th of October 1995. To compare the attractiveness of the two kinds of flowers it is necessary to consider the proportion of pollen taken and the availability of the food resource in the habitat (Haslett 1989a).

In this study, flower preference was determined by analysing pollen-gut contents of syrphid flies and estimating the relative abundance of flowers available to the insect (Fig. 6. 5). Two methods were used to compare the utilisation from the two daisies. In the first method the utilisation index (I) for each flower species was calculated by the formula $I = \frac{P}{F}$ where P is the proportion of that species' pollen in the gut of each specimen, F is the corresponding number of flowers of that species in the field which, in this study, had the same values for specimens dissected on each occasion. The calculated I's for marguerite and African daisy were compared by a t-test and the analysis showed that the utilisation index of the African daisy (mean I=0.016) was significantly greater than that of the marguerite daisy (mean I=0.009) for *M. viridiceps* (df=138, p=0.015).

In the second method, the attractiveness of the two daisies was compared by the number of syrphids caught in suction traps. The air velocity provided by the electro-motor of each trap gradually decreased to nil at 34cm above the trap, and the effective height of each trap was arbitrarily considered to be up to 20cm above the trap where the air velocity was 0.25m/s (Fig. 6. 6). The number of flies per trap and the mean number of flowers at the effective height of the suction traps in each site are shown in Fig. 6.7. The linear relationship between the two variables (Fig. 6. 7) is significant (p=0.002, R^2=0.97 for marguerite daisy; p=0.003, R^2=0.96 for African daisy).

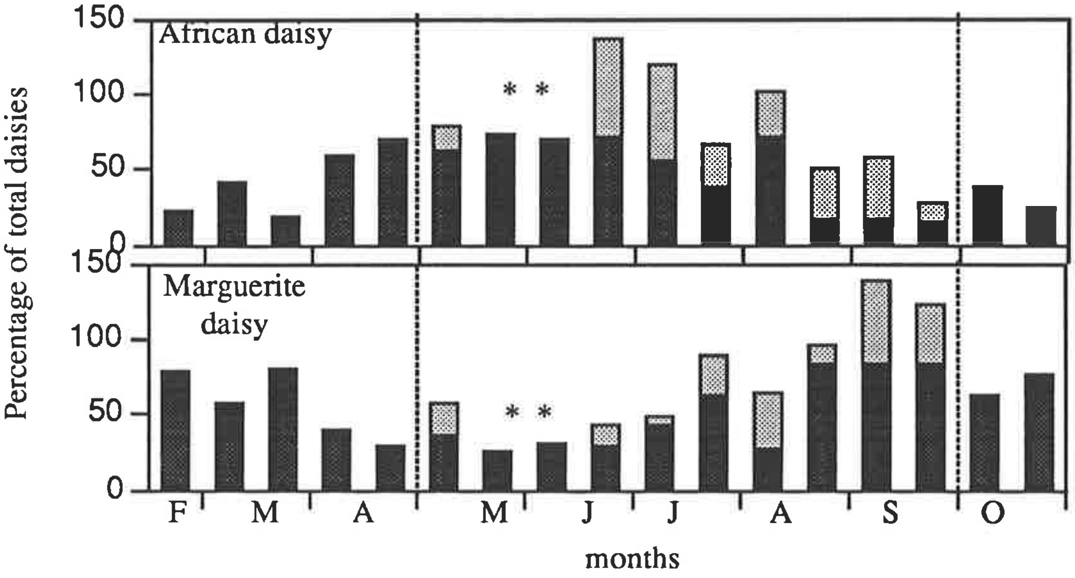

Figure 6. 5: Percentages of each daisy flower species per 15 days (solid) and corresponding percentage of pollen in the gut of *M. viridiceps* (stippled). Specimens were dissected on occasions between two dashed lines and asterisks show occasions with no sampling for pollen gut.

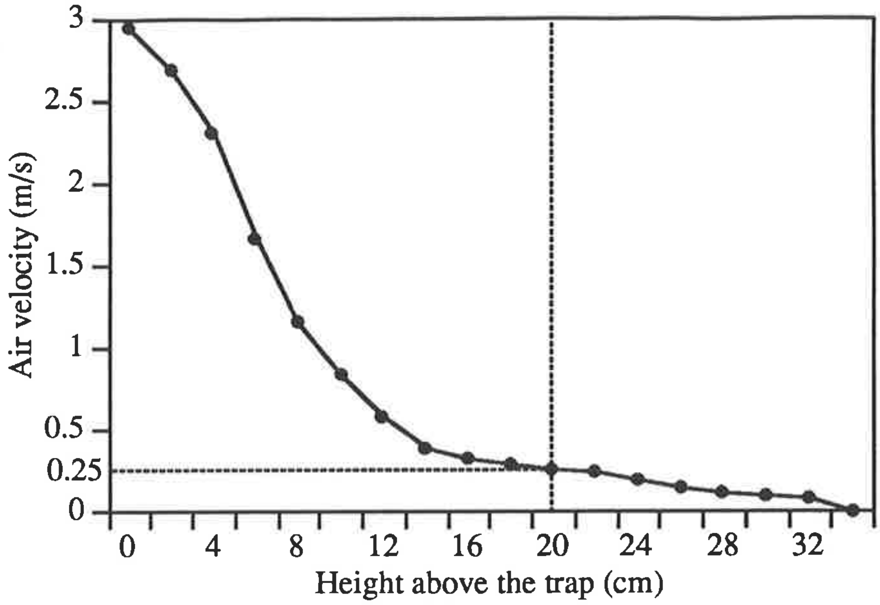

Figure 6. 6: Relationship between the air velocity and the height above suction traps at the room condition.

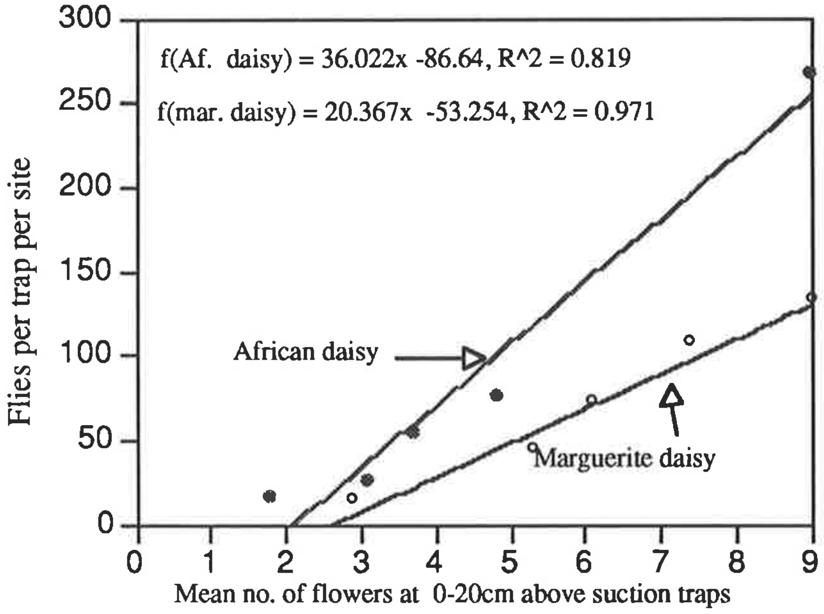

Figure 6. 7: Comparison of the attractiveness of the two daisy species by regressing the total number of *M. viridiceps* caught per site and the mean number of flowers at 0-20cm above suction traps.

Table 6. 3: Total number of syrphids per site caught by suction traps installed in the vicinity of daisy plants. The number of catches per site are the summation of the number of catches per occasion and the number of flowers per site are the mean number of flowers in the period during which the traps were located at one site.

trap sites	no. of occasions of trap emptying	total duration	*M. viridiceps* (numbers)		*S. grandicornis* (numbers)		Mean no. of flowers	
		(days)	African daisy	marguerite daisy/plant	African daisy/plant	marguerite daisy/plant	African daisy/plant	marguerite daisy/plant
1	5	21	27	105	1	0	256	197
2	7	19	17	70	5	2	221	400
3	6	27	77	42	6	3	386	740
4	2	6	54	12	6	2	1201	697
5	2	6	268	130	7	3	411	662
total			443	359	25	10		
χ^2			8.8		6.4			
P			0.003		0.01			

The two regression lines obtained for the two daisy species (Fig. 6. 7) were compared and the null hypothesis that they do not differ in regression coefficient ($t = 3.16 > t_{0.05(2),6} = 2.45$) and elevation ($t = 3.97 > t_{0.01(2),7} = 3.45$) was rejected (Zar 1984). This difference indicates that more *M. viridiceps* were caught in the trap near the African daisy than in the trap near the marguerite daisy. However when the number of flowers at the trap effective-height was low, the number caught was similar for both daisies (Fig. 6. 7). Regardless of the site of the traps, a higher total number of *M. viridiceps* was caught near African daisy than marguerite daisy (Table 6. 3) ($\chi^2 = 8.8$, p=0.003), but more were caught near the marguerite daisy than near the African daisy at sites 1 and 2.

More *S. grandicornis* were caught in the suction trap adjacent to African daisy, than were caught in the suction trap adjacent to the marguerite daisy, regardless of the mean number of flowers on each daisy or the number of flowers at the trap-effective height (χ^2=6.4, p=0.01) (Table 6. 3). However, no relationship between the number of flowers at the trap-effective height and the number of flies caught was found. This is because, during the period when there were a high numbers of flowers at the effective height, *S. grandicornis* was rare in the field; eg. there were 7.4 marguerite daisy flowers at the effective height of the trap at the site 1 from 24/7/95 to 14/8/95 but no *S. grandicornis* were captured near this plant, or only one fly captured on African daisy during 21 days (duration of traps located in site 1).

6. 3. 3 Comparison of pollen quantity and diversity

The ranked quantities of pollen grains in the guts of males and females of *M. viridiceps* in 1995 were compared by a Mann-Whitney U test (Appendix 6. 6). The calculated Z corrected for ties (Z=-0.675) was less than $\alpha = 0.05, t_{0,05(2),-} = 1.96$ and, therefore the null hypothesis that males and females take same quantities of pollen grains was not rejected.

Of 65 females, 11 (17%) were at the oviposition stage (stage D), one (1.5%) at pre-oviposition stage (C) and the rest 53 (81.5%) were at the immature stages (A and B) (Table 6. 4). The ranks for pollen quantities carried by females are also shown in Table 6. 4. Ten specimens (19%) were full of pollen and almost the same percentage were empty. None of the mature specimens (stage D) was full of pollen and 3 (27%) were empty. Eighteen of males (13.5%) examined had no pollen, 61 (45.9%) with the rank quantity one, 32 (24.1%) ranked 2 and 22 (16.5%) ranked 3 (Table 6. 4).

Thirty five specimens of *S. grandicornis* captured in October and November 1995 were examined for pollen and nectar. This species consumes more nectar than pollen (reference?). Table 6. 5 shows the ranks of pollen consumption of *S. grandicornis*. The guts of 15 out of 19

(79%) of males and 12 out of 16 (75%) of females had no pollen and were full of nectar. Four (25%) of females had small quantities of pollen. The Mann-Whitney test for the null hypothesis that males and females of *S. grandicornis* take the same quantities of pollen grains gives Z corrected for ties=-0.273, p=0.78; so the hypothesis is not rejected.

Table 6. 4: pollen quantities (in ranks 0-3) in guts of *M. viridiceps* . Rank 0 is empty and rank 3 is full.

	Ovarial stage	**pollen quantities (ranks)**				**total**
		0	**1**	**2**	**3**	
Females	AandB (immature)	9	20	14	10	53
	C (pre-oviposition)	0	0	1	0	1
	D (mature)	3	5	3	0	11
Total females		12	25	18	10	65
Males		18	61	32	22	133

Table 6. 5: pollen quantities (in ranks 0-3) in guts of *S. grandicornis*. Rank 0 is empty and rank 3 is full.

	Ovarial stage	**pollen quantities (Ranks)**				**total**
		0	**1**	**2**	**3**	
Females	AandB (immature)	11	3	0	0	14
	C (pre-oviposition)	-	-	-	-	-
	D (mature)	1	1	0	0	2
Total females		12	4	0	0	16
Males		15	4	0	0	19

The number of pollen types for each sex and the percentage of pollen grains in the gut of each specimen of *M. viridiceps* are shown in Appendix 6. 5. A significant difference was detectable between pollen types eaten by males and females of *M. viridiceps* in (df=69, p=0.03, t=2.198, mean for males=2.79 and for females 3.39). A t-test with similar data for *S. grandicornis* showed that the females of *S. grandicornis* had a greater variety of pollen grains in their gut than the males (df=28, p=0.04, mean for males=1.6 and for females=2.5)

6. 3. 4 Laboratory selectivity experiments

6.3. 4. 1 Wind-tunnel experiments

Since 92% of individuals of either species of hoverflies used in wind-tunnel flew towards the top of the tunnel instead of flowers, data obtained could not be analysed in selectivity study.

6. 3. 4 . 2 Selectivity study of African and marguerite daisies

The total number of flies on each type of flowers and each circle on the rotatable table is shown in Table 6.6. The calculation of the χ^2 statistic for the goodness of fit test showed that *Melangyna viridiceps* was attracted more to African daisy (75) than to marguerite daisy (43) (χ^2= 8.68, p=0.003). The position of the daisies on outer and inner circle of the round table (different spaces between flowers) did not affect this preference (χ^2=0.01, p=0.91 for African daisy and χ^2=0.02 and p=0.88 for marguerite daisy).

Similar results were obtained in the experiment for *S. grandicornis* (Table 6-6). The number of *S. grandicorn*is attracted to African daisies was grEater than that attracted to marguerite daisy (χ^2=12.33, p=0.0004) and, again, the attractiveness was not influenced by the position on the rotatable table (χ^2=0.82, p=0.37 for African daisy and χ^2=0.55, p=0.46 for marguerite daisy).

Table 6. 6: Number of *M. viridiceps* and *S. grandicornis* respectively attracted to African and marguerite daisy in two different experiments in the glasshouse.

syrphids	**occasions**	**African daisy**		**total**	**Marguerite daisy**		**total**
		inner circle	outer circle		inner circle	outer circle	
M. viridiceps	16	37	38	75	22	21	43
S. grandicornis	35	94	82	176	62	54	116

6. 3. 4. 3 Comparison of the attractiveness of African daisy with *Eucalyptus* and *Acacia* flowers

The total numbers of flies recorded per plant species are given in Appendix 6. 7. The analysis of variance for transformed data to ln(x+1) showed that the 3 species of flowers varied in their attractiveness to *M. viridiceps* (F=77.2; P=0.0001) and African daisy was the most attractive to *Melangyna viridiceps* (LSD=0.588, α=0.05) (Appendix 6. 8).

Similarly, the analysis of variance for transformed data to ln(x) showed that African daisy was the most attractive amongst 3 flower species to *S. grandicornis* (F=65.11, p=0.0001, LSD=0.337, α=0.05). There was no difference between *Eucalyptus* and *Acacia* flowers for attraction of hoverflies (Appendix 6. 9).

6. 3. 4 . 4 Comparison of the attractiveness of the flowers of African daisy, sowthistle and wild radish

The numbers of *M. viridiceps* and *S. grandicornis* recorded on African daisy, wild radish and sowthistle are given in Appendix 6. 10. An ANOVA suggested that there were significant differences between the three species of flowers in attracting *M. viridiceps* (F=5.526, P=0.03); and the comparison of means (Appendix 6. 11) with the LSD (4.408) suggests that African daisy was the most attractive but that there was no difference between sowthistle and wild radish.

Similarly, an ANOVA of the numbers of *S. grandicornis* attracted to the three plant species (Appendix 6. 12) indicates differences between the 3 species in attracting *S. grandicornis* (F=15.95, p=0.001). But, by contrast to the data for *M.viridiceps* , a comparison of the means (Appendix 6. 10) with the LSD (3.94) shows that wild radish was the most attractive and there was no difference between sowthistle and African daisy.

The results from three selectivity experiments in the glasshouse were summarised and ranked as a fraction of the number of flies attracted to African daisy (Table 6. 6). This ranking shows that *Acacia* and *Eucalyptus* had the lowest attractiveness to *M. viridiceps* amongst 6 flower species used in the experiments. *M. viridiceps* was attracted more to wild radish than to sowthistle. However, *S. grandicornis* had more response to sowthistle than wild radish (Table 6. 6)

Table 6. 6: Ranking the flowers used in 3 glasshouse experiments based on the percentage of attractiveness to African daisy

M. viridiceps		*S. grandicornis*	
Flowers	% of African daisy	Flowers	% of African daisy
African daisy	100	wild radish	180
marguerite daisy	57	sowthistle	120
wild radish	52	African daisy	100
sowthistle	50	marguerite daisy	66
Eucalyptus	8	*Acacia*	28
Acacia	2	*Eucalyptus*	22

6. 4 Discussion

6. 4. 1 Attractiveness to colours

The glasshouse experiments on attractiveness of both species to different colours indicated that yellow was the colour most visited by both species and no difference was found between other colours. These results were obtained under conditions which made all plates equally accessible to hoverflies; also different colours were used with similar food quantity and quality. In the field, on the other hand, flowers from different species may have similar colour but different pollen quantity and quality (Baker and Baker 1973). Yellow and white flowers were the most visited during casual field observations on the selection of flowers by these species of hoverflies (Table 6. 1). The result from analysis of selectivity patterns of both species indicates that flowers with yellow and white are preferred by these species. However, *Veronica hederifolia* is a common blue flower with open petals in spring which is used in low intensity by the two species of hoverflies. Wratten *et. al.* (1995) found that *Melangyna novaezelandiae* (the same subgenus, *Austrosyrphus,* as *M. viridiceps*) (Vockeroth 1969); was attracted to yellow colours. The results obtained from this study were used as a guide for selecting plant species with yellow and white flowers to enhance the number of hoverflies at the Claremont site (Chapter 3). In addition, yellow water traps were used for studying the population of adults (Chapter 4).

6. 4. 2 Pollen selectivity

The analysis of data by Johnson's method (Johnson 1980) showed that both hoverfly species used the resource selectively. Although most specimens of *M. viridiceps* had daisy pollen in their guts, this ranked less attractive than some weeds. However, this may be a result of the abundance of African and marguerite daisies from the beginning to the end of the experiment (Fig. 6. 5) which increased the availability rank and consequently increased the average rank (Table 6. 2). *R. raphanistrum* (wild radish) with a yellow flower conspicuously attracted *M. viridiceps* in the field. However, the glasshouse experiment showed less attractiveness of wild radish compared to African daisy. The difference between glasshouse experiment and field study is probably due to different rates of pollen availability in a limited space (glasshouse) and learning optimal foraging.

Although *M. viridiceps* is native, and South Australia is rich in the flora of *Eucalyptus* and *Acacia* plants, native pollen types were not used in proportion to their abundance. *Acacia* is little used by *M. viridiceps* (Table 6. 2; Fig. 6. 3) even though the peak flowering period of *Acacia* synchronises with the presence of both hoverfly species in the field during spring. The casual census-walks at the peak of *Acacia* flowering periods showed that very low numbers (4 individuals) of *M. viridiceps* were attracted to all *Acacia* trees compared to daisy flowers (600 individuals on both daisy species) (Chapter 4).

Myrtaceae pollen is used more than *Acacia* but both groups of pollen (*Acacia* and Myrtaceae) are consumed less than Asteraceae (two daisy species and *Sonchus*) and other introduced species.

S. grandicornis differs from *M. viridiceps* in its use of pollen resources. *R. raphanistrum* pollen is the most preferred of all pollen types measured for usage and availability during the field study. In the laboratory, *S. grandicornis* was also attracted to wild radish more than sowthistle and African daisy. In addition, *S. grandicornis* is attracted to *Eucalyptus* and African daisy equally (Table 6. 2). However, this result differs from the glasshouse experiment in which African daisy was preferred to *Eucalyptus* (Myrtaceae) by *S. grandicornis*. This may be due to a different utilisation of flowers. In the glasshouse experiments, the number of flies alighting on each plant species was measured, whereas percentages of pollen were measured in the field.

In South Australia, the hot period in summer limits the number of pollen resources; eg. only some species of Myrtaceae and *Sonchus* from the list of Table 6. 1 flower in summer. *Sonchus oleareus* which grows well in the shade during summer is the host of the aphid *Hyperomyzus lactucae* and it was the main oviposition site for *S. grandicornis* in the study area. Compared to *M. viridiceps*, however, *S. grandicornis* consumes only a small quantity of pollen and most specimens dissected in this study carried more nectar than pollen in their gut.

While methods of measuring food ingestion by herbivores have been widely investigated, methods of relating this to food availability have been largely ignored (Norbury and Sanson 1992). In some studies, frequency of occurrence or presence and absence of plant species within a sampling unit (Halford *et al.* 1984), plant density or number of plants per sampling unit (Bailey *et al.* 1971), cover or the proportion of ground occupied by the perpendicular projection of plants on to the ground (Williams and Cameron 1986) and measuring the biomass (Taylor 1983) have been used for estimating the availability of food for animal herbivores; and the advantages and disadvantages of these methods have been reviewed by Norbury and Sanson (1992). Haslett (1989a) studied flower selectivity of hoverflies by analysing gut-pollen contents relative to flower abundance.

In the present study, a single technique could not be used to estimate the availability of flowers in different types of vegetation. The method which was devised was to measure both the area occupied by a plant species and the flower density of each plant species. The data were then ranked for analysis. However, this method, like others, may give distorted result if pollen feeding occurs outside the area of study, especially for highly mobile syrphids (Chapter 5).

This study showed that *M. viridiceps* and *S. grandicornis* explore flowers from three different strata in a garden: weeds, shrubs and trees. However, each hoverfly species may differentially use plants from various strata. *M. viridiceps* utilises more pollen from weeds and shrubs and less from trees (*Eucalyptus* and *Acacia)*. In contrast, *S. grandicornis* selects more trees and shrubs than *M. viridiceps* in addition to some weed species. The very low numbers of *S. grandicornis* during summer may, perhaps, be due to more feeding activities of this species on trees and were not detected by the methods used. Ssymank and Gilbert (1993) stated that the reason for many *Melangyna* spp. being rare is that they feed in early spring high up in the canopy.

In this study, the two daisy species were visited more frequently than native shrubs and there was a high proportion of these pollen grains in guts of both syrphid species. Although the mean differences between ranks of African daisy was higher than that of marguerite daisy (Johnson method), no significant differences were detected between either species. However, when both plant species were more intensively compared by two methods (suction trap and selectivity index), African daisy was more frequently used than marguerite daisy.

Pollen grains from Asteraceae (undetermined Asteraceae) comprise an important part of the diet of syrphid flies in South Australia. A similar preference was found for New Zealand *Melangyna* novaezelandiae (Wratten *et al.* 1995).

6. 4. 3 Pollen diversity and quantity

The numbers of pollen species in the gut of hoverflies are different in various species. Some syrphid species are highly selective whereas others are more generalist in their pollen diets (Haslett 1989a). In this study a maximum of six pollen types was recorded in the gut of *M.*

viridiceps and *S. grandicornis* and females of either species feed on more different pollen types than males. Amongst other syrphid species, for example, *Episyrphus balteatus* was recorded visiting 122 flower species and *Melangyna lasiophthalma*, has been observed on one flower species in Europe (see Ssymank and Gilbert 1993).

Similarly, New Zealand syrphid flies range from very selective, for example *Allograpta ropalus* and *M. novaezelandiae* [= M. ortas (Walker)]which feed on 2 and 6 types of pollen respectively to non-selective, eg; *Eristalis tenax* and *Helophilus campbellicus* (Hutton.) which consume the widest range of pollen per individual (Holloway 1976). However, Wratten *et al.* (1995) indicated that a higher proportion of *M. novaezelandiae* females contained pollen for 12 out of the 13 pollen types.

Holloway (1976) classified syrphid flies based on the body hairiness. "Non-hairy" syrphid species are selective and "most hairy" are non-selective in feeding pollen (Holloway 1976). Based on Holloway's classification, *M. viridiceps* and *S. grandicornis* are less hairy hoverflies and, therefore, data obtained from this study confirms Holloway's classification. Different consumption of pollen types in males and females may be related to exploring different flower resources by females for the maturation of their reproductive system.

Although some *M. viridiceps* were observed with only nectar and honeydew in their guts (7.8% of dissected specimens), this species mostly feeds on pollen. In contrast, *S. grandicornis* mostly consumes nectar and honeydew which may be an adaptation to a hot summer. For example, on 9/11/95 at 8:30 am, 66 *S. grandicornis* were counted on 70 infested and non-infested roses with aphids at the Claremont rose garden during 30 minutes and then they left the area. Since no eggs were observed on infested rose buds, they were probably feeding on honeydew of rose aphids.

Additionally, no differences were detected in amounts of pollen carried in the guts of males and females of either species. These results differ from those obtained by Haslett (1989b) and

Wratten *et al.* (1995) who found greater quantities of pollen in the guts of females of other species of hoverflies.

In this study, most females dissected at stages A and B (immature stages) contained more pollen grains than the other stages. Haslett (1989b) classified the ovary development of syrphid flies into 10 stages and indicated that the maximum consumption of pollen by *Rhingia campestris* was when the ovaries were at stage 6 which is equal to stage B of this study.

Chapter 7

Oviposition of adults and feeding behaviour of larvae

7. 1 Introduction

The total number of eggs laid by a female syrphid varies according to species and types of food consumed (Schneider 1969). Laboratory observation on syrphid reproduction may not be a true reflection of field behaviour. While some species of syrphids have been recorded to copulate in the laboratory, others do not (for overview see Schneider 1969). In the laboratory, food consumed by the flies and the arena for activities differ from those in the field , so the fecundity (number of eggs laid), fertility (the proportion of which are fertile) and the longevity may be different from the field. Nevertheless, data obtained from the laboratory may be used as a first estimate of fecundity in the field.

Understanding the oviposition behaviour of natural enemies and their responses to different prey densities can be a guide to the efficacy and use of these beneficial agents in biological and integrated control. Predators which respond to low prey densities or lay eggs prior to infestation are likely to be more effective in controlling pests than predators which mainly occur after the prey has increased in numbers (Chandler 1967). In addition to number, quality of prey is important for survival of larvae. Thus, eggs should be ideally laid where the young larvae are able to catch prey of appropriate size(s).

Solomon (1949) suggested two types of responses for the relation between predators and prey; namely 'functional' (i.e: changes in feeding behaviour in relation to prey density) and 'numerical' responses (i.e: changes in predator density in response to prey density). However, populations of polyphagous predators, such as some syrphid flies, may change their behaviour in respect of one prey species if other prey species are present at the same time (Schneider 1969; Dusek and Laska 1966).

Oviposition sites for aphidophagous Syrphidae are relatively rare and, in spite of the wide flight range of hoverflies, they must be able to find suitable host plants with aphid colonies (Chandler 1966). Many investigations on syrphids have concentrated on oviposition stimuli and factors which determine the specific prey-predator-relationship (Dixon 1959; Völk 1964; Chandler 1966, 1967, 1968 a, b, c) (chapter 2). Hemptinne *et al.* (1993) have recently investigated the importance of the quality of aphids as well as their abundance and found that females of *Epistrophe nitidicollis* (Meigen) select young colonies of aphids for oviposition in preference to colonies of older aphids. Exuviae which are usually found on old or dispersing colonies may be used as oviposition cues by females. However, other cues are important in oviposition behaviour, depending on the syrphid species (Chandler 1968a, b). For example, over 50% of eggs of *Syrphus luniger* are laid touching aphids and less than 1% on uninfested buds while less than 5% of eggs of *Platycheirus manicatus* are laid touching aphids and 50% on uninfested buds in similar conditions. Syrphids which oviposit in the near vicinity of aphid colonies are known as aphidozetic or aphid-seeking species while those which lay eggs in the absence of aphids are known phytozetic or plant-seeking species (Chandler 1968a, b).

Rose aphids are abundant on suitable rose buds (stages 1-5, see Chapter 9) in Adelaide rose gardens in spring and autumn. *M. viridiceps* and *S. grandicornis* are two common species of hoverflies which oviposit on infested rose buds (Maelzer 1977; Maelzer unpublished data 1992), and amongst other hosts (Carver 1989). While *M. viridiceps* adults are more abundant around Adelaide rose gardens than *S. grandicornis*, they lay fewer eggs on rose-aphid infested buds (Chapter 9).

Capture efficiency of a predator is the ability to capture successfully the prey and it is important in its ability to control a prey population (Yakhontov 1966). The number of prey caught by a predator depends on the number of encounters between predator and prey, age or size of the prey and predator, and defence behaviour of prey (Dixon 1958; Hussein 1982; Kitt 1996; Völkl and Stadler 1996).

The survival of syrphid larvae is related to the location of eggs by the female. In the field, females of *M. viridiceps* and *S. grandicornis* oviposit in or adjacent to colonies of rose aphids. Since most colonies of *Macrosiphum rosae* comprise a mix of all instars, the hatching syrphid larvae have a choice between more than one age or size of prey. Then, the ability of larvae to capture the prey depends on the size of aphids and the physical contact between the larvae and aphids. Therefore, it is important to study oviposition behaviour and capture ability of larvae in relation to density and quality of prey.

The aims of this study were to:

(i) compare the fecundity, fertility and longevity of *M. viridiceps* and *S. grandicornis* in the laboratory.

(ii) study the oviposition response of females to different densities of aphids in field cages, and in the field.

(iii) investigate the response of *S. grandicornis* to aphid exuviae as an indicator of old or dispersing colonies.

(iv) measure capture efficiency of different larval instars of both syrphid species when different sizes of rose aphids were offered to them.

(v) determine the effect of phytophagy on the propensity of first instar larvae to capture their prey.

7. 2 Materials and Methods

7. 2. 1 Fertility, fecundity and longevity

Larvae of *M. viridiceps* and *S. grandicornis* were reared on *Acyrthosiphon pisum* on broad bean, *Vicia fabae*, in the laboratory at 20°C, 70% R. H., 60000 lux light intensity (Chapter 3). The egg production of 10 females of each species was individually recorded. Each newly emerged female was isolated with 1 or 2 males in a 25cm x 25cm cylinder cage made from clear plastic with two holes on the sides and one on the top, covered by gauze for ventilation (Chapter 3).

The adults were given the same physical environment as were the larvae, except that the light intensity was 10000 lux and the adults were offered ground hive pollen and cubed sugar on tissue paper within the cage. Water was also made available to the flies in the cage by placing some in a small vial lid. To prevent drowning of the flies, a small piece of tissue paper was also placed in each vial lid. Cages were cleaned and tissue papers, food and water were changed every 3 days.

Rose aphids on rose buds in a vial of water were offered for laying eggs. Numbers of eggs per day were recorded for each female. Eggs laid on the cage walls were also recorded and removed each day. To estimate the percentage of fertile eggs, different numbers of eggs from each female were reared separately. The mean longevity of males and females were calculated from records of the numbers of dead flies each day. The life span of each female was divided into three equal parts and the number of eggs per fly was calculated for each part of the life span. In addition to observations of mating, 10 newly emerged females of *M. viridiceps* were dissected after being kept with males and the presence of sperm in spermathecae was determined by crushing the spermatheca under a coverslip on a microscope slide and examining under a microscope (×450).

7. 2. 2 Oviposition behaviour

7. 2. 2. 1 Cage experiments

A series of experiments were conducted in a 2m x 2m x 2m metal frame cage covered with gauze (Chapter 3) installed at the Claremont rose garden during the spring of 1993 and 1994.

The effect of different aphid densities on oviposition

A randomised block design with five treatments and three replications was run on a rotatable round table (Chapter 3) in the cage in November 1993. The treatments comprised 5 densities of rose aphids, 0, 5-20, 21-70, 71- 100 and more than 100 per bud. Highly infested buds at stage 1-2 (Chapter 9) were cut from roses in the field and the number of aphids reduced to the appropriate densities. Adults and fourth instars fell off easily during picking and handling, so the remaining aphids were mostly a mixture of first to third instars. Each bud with 20cm long stem was placed in a small bottle of water and kept vertical by plastic sponges around the stem. The bottles were arranged randomly on the edge of the rotatable table. The bottles were placed in petri-dishes with water to prevent inter-infestation. Food (hive pollen and cubed sugar) and water were provided in the middle of the table for the adult hoverflies.

Three gravid females of *S. grandicornis* were released in the middle of the table in the morning and the number of eggs laid was recorded after 8 hours. To randomise the location of the buds in the cage, the table was rotated randomly 3-4 times during the course of experiment. This experiment was repeated three times and data were combined for ANOVA.

Response to exuviae of aphids

This experiment was similar to the previous experiment but with three treatments and four replicates. The treatments were: 71-100 aphids/bud; 71-100 aphids plus 20 third instar exuviae of rose aphid/bud; and an uninfested bud (control). 71-100 aphids per bud was used because it was the optimum density of aphids for laying eggs in the previous experiment. Exuviae were delicately fixed between leaves using a small amount of 30% sucrose solution. Again, three gravid females were released in the cage in the morning and the number of eggs laid was counted eight hours later. This experiment was repeated three times and data were combined for ANOVA.

7. 2. 2. 2 Field study

Data of this study were obtained from four sampling sites in Adelaide, Claremont rose garden, Urrbrae rose garden, Centennial Park and Mercedes College, from August 1993 to October 1995. The locations and the sampling technique have been described in Chapters 3 and 9 respectively.

On each weekly sampling, the number of aphids for each bud with syrphid eggs was compared to the Mean Number of Aphids for all Infested sample buds (MNAI) on that occasion by a χ^2 test. For example, if the mean number of aphids per 20 infested buds on a sampling day is 130, and there are four buds with syrphid eggs on that occasion, the densities of these four buds (e.g. 180, 85, 145 and 320) are compared with 130. In this example, three densities are higher than the MNAI and one density is lower than the MNAI.

The total number of eggs laid on buds with (a) more and (b) less than the MNAI were summed respectively and compared by a χ^2 test. The mean numbers of syrphid eggs per month were calculated and regressed on the mean number of aphids per bud for those buds with eggs.

7. 2. 3 Capture efficiency

Capture efficiency of *M. viridiceps* and *S. grandicornis* was measured by the encounter method of Hågvar, 1974. Larvae of *Melangyna viridiceps* were reared from eggs laid by females captured in the Claremont rose garden. The laboratory arenas for first instar larvae of the flies were hatching vials, 10mm x 5mm diameter, while second and third instar larvae were tested in 55mm (diameter) x 25mm petri-dishes. Larvae were reared at 20±1°C, light: dark 16:8 and R.H=70%, but capture efficiency was measured under a stereo-microscope at room temperature (20-25°C). First instar larvae were tested after 5-6 hours starvation, while second and third larval stages were starved for 24 hours.

Physical contact or 'encounter' was established by pushing a single prey into contact with a single larva by means of a fine brush. This was repeated until the larva either captured the aphid, or no captures were recorded after 10 encounters. Once the aphid was captured, the number of 'encounters', including the last was recorded. The larva was not used again until it had moulted to the next instar. Capture efficiency was calculated by dividing the number of larvae which successfully captured prey by the total number of encounters and multiplied by 100 (Hågvar 1974).

To test whether first instar larvae would eat leaf tissue in the absence of prey, larvae were also reared on fresh rose leaves. Small pieces of fresh rose leaves were placed adjacent to each egg and after hatching; leaves were replaced with fresh pieces as needed until the time of measuring capture efficiency.

7. 3 Results

7. 3. 1 Fertility, Fecundity and longevity

Oviposition initially occurred 4-11 and 3-9 days after adult emergence for *M. viridiceps* and *S. grandicornis* respectively (Table 7. 1). The pre-oviposition periods for the two species were not significantly different ($p \leq 0.66$, $t= 1.43$). The longest oviposition period of females was 26 days and 22 days, and the highest number of eggs laid was 476 and 407 eggs for *M. viridiceps* and *S. grandicornis,* respectively. No difference was detected between the number of eggs laid by either species ($p \leq 0.64$, $t=-0.47$). The analysis of variance indicated that *M. viridiceps* deposited the highest number of eggs during the middle of the life span, whereas *S. grandicornis* laid the highest number of eggs equally during the middle and the final third part of the life span (Fig. 7. 1).

In the laboratory, the mean longevity of females was 32.9 and 19.9 for *M. viridiceps* and *S. grandicornis* respectively, which were significantly different ($p=0.0001$, $t=6.09$). Females which lived longer laid more eggs than those with shorter longevity ($p= 0.05$, $R^2=0.4$ for *S. grandicornis* , $P=0.0001$, $R^2=0.85$ for *M. viridiceps*) (Fig. 7. 2 a, b). Additionally, the longevity of males and females did not differ significantly in either species ($p= 0.58$, $t=-0.56$, df=18 for *M. viridiceps*; $p=0.46$, $t=-0.78$, df=21 for *S. grandicornis*).

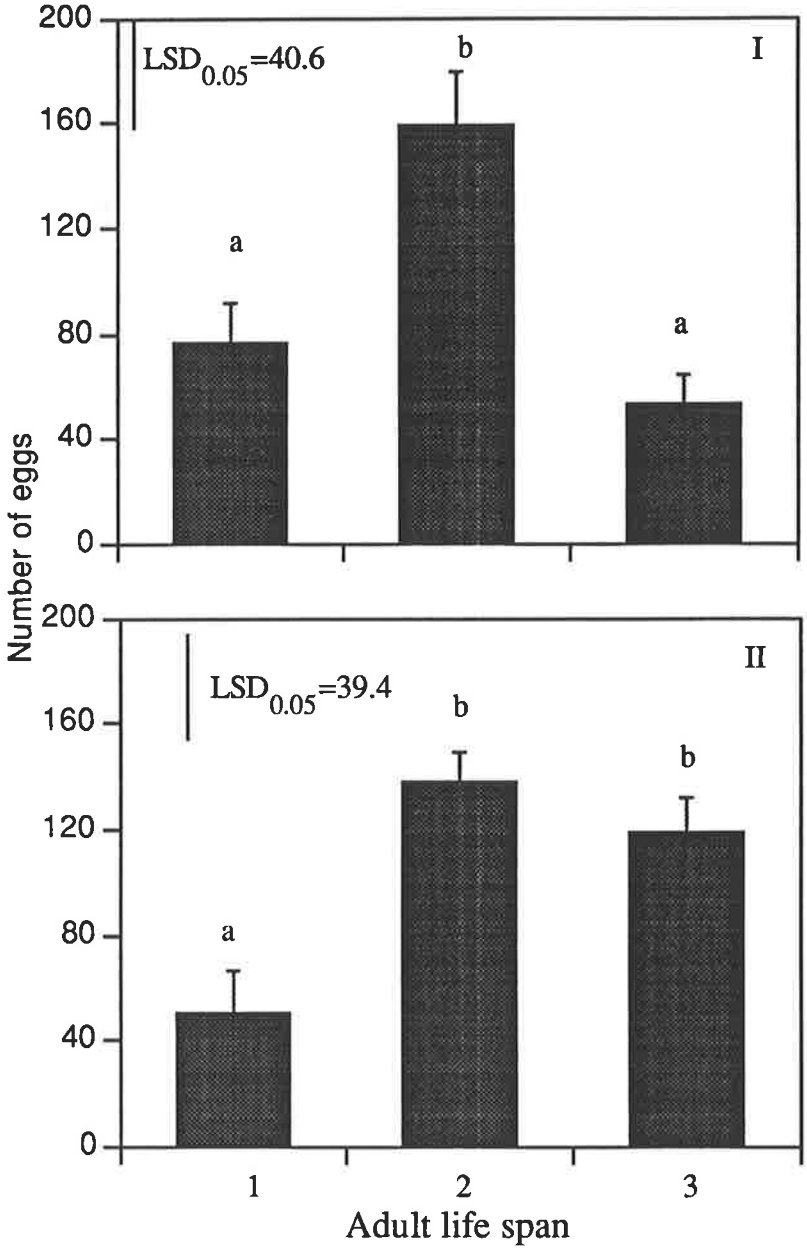

Figure 7. 1: The mean number of eggs laid in each third of the life span of I: *M. viridiceps*, II: *S. grandicornis*.

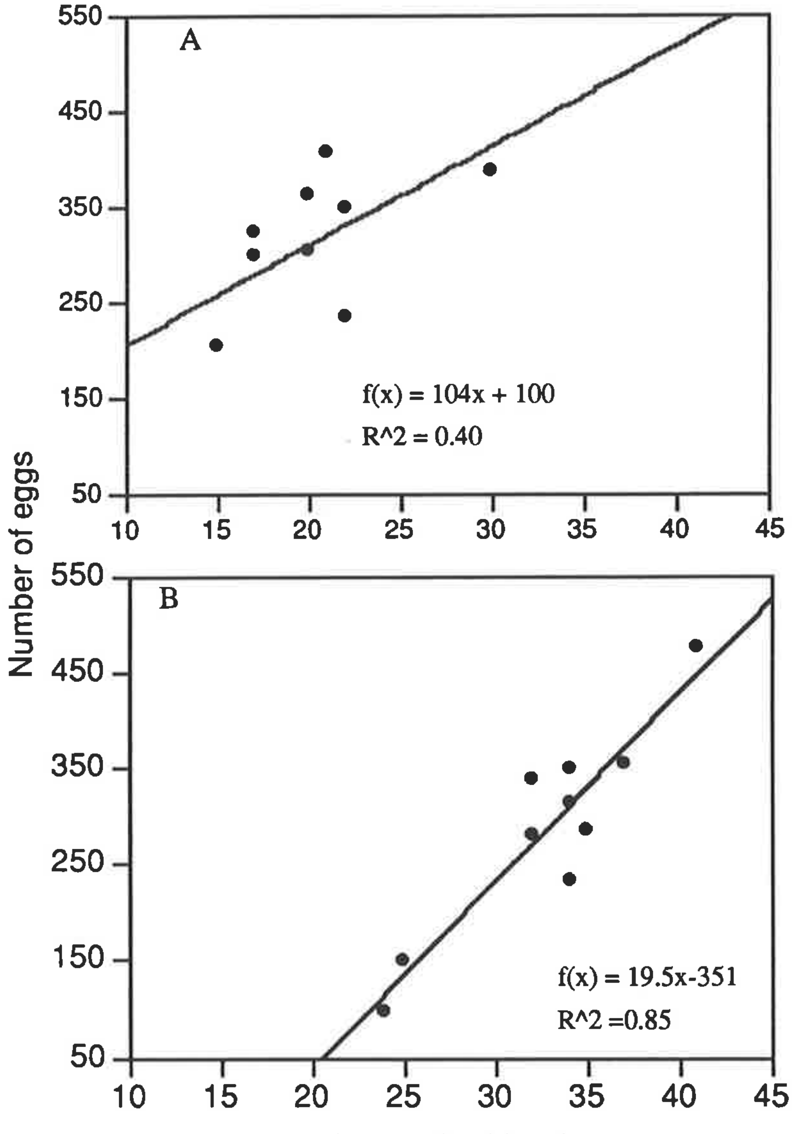

Figure 7. 2: Relationship between longevity of syrphid flies and total numbers of eggs laid, A: *S. grandicornis*, B: *M. viridiceps*.

Table 7. 1: Oviposition and longevity, and range in brackets of *M. viridiceps* and *S. grandicornis* in the laboratory. Mean± standard errors; n=10 for each species.

Syrphid species	Longevity (days)		Mean eggs per female	Pre-oviposition period (days)	Oviposition period (days)
	females	males			
M. viridiceps	32.9±1.6 (24-41)	31.5±1.94 (20-41)	288±34 (99-476)	6.8±0.66 (4-11)	19.5±1.65 (9-26)
S. grandicornis	19.9±1.4 (15-30)	18.5±1.27 (13-30)	307.9±23.2 (204-407)	5.6±0.64 (3-9)	13.8±1.3 (7-22)

Neither mating nor sperm in the spermathecae were observed in *M. viridiceps* in the course of the study, and all eggs of *M. viridiceps* laid in cages were infertile, In contrast, mating was observed in *S. grandicornis* and of 298 randomly selected eggs of this species 236 were fertile (79.2%).

7. 3. 2 Oviposition behaviour

7. 3. 2 . 1 Cage study

In the first group of cage experiments with *S. grandicornis,* a significant effect of aphid density on oviposition was demonstrated ($\alpha=0.05$, F=18.58, p= 0.0001); the number of eggs laid increased with aphid density up to 100/bud then decreased (Fig. 7. 3-A). The optimum prey density was on 71-100 aphids ($LSD_{0.05}=4.67$). *S. grandicornis* laid only one egg on all of 21 control buds (4.8%) used in both experiments (Fig. 7. 3-A, B).

The second group of cage experiments showed that *S. grandicornis* laid significantly fewer eggs on buds with exuviae than those without exuviae ($\alpha=0.05$, F=44.37, p= 0.0001; $LSD_{0.05}=4.48$) (Fig. 7. 3-B).

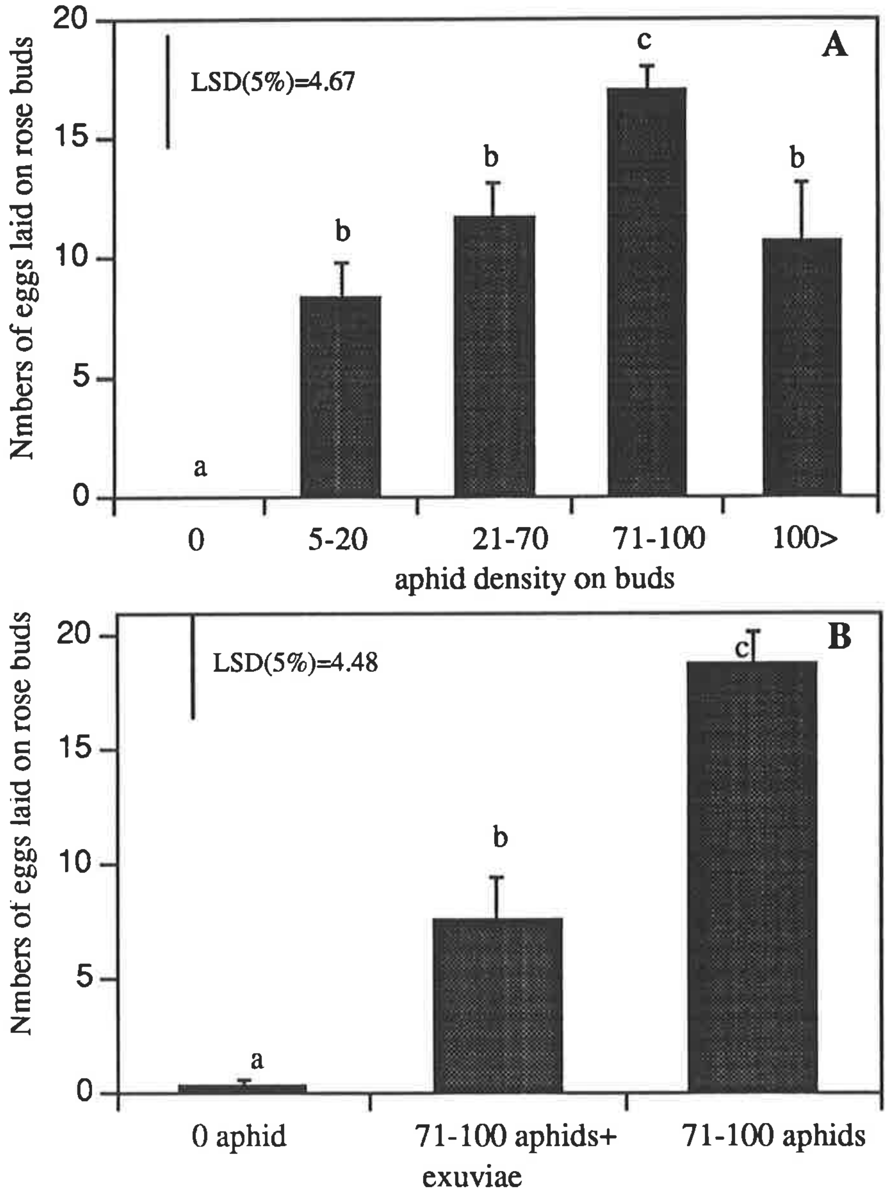

Figure 7. 3: Field cage experiments with *S. grandicornis*: A, Relationship between different densities of aphids and the number of eggs laid on rose buds ; B, The effect of aphid exuviae on the number of eggs laid. Vertical bars represent SE of the mean.

7. 3. 2. 2 Field study

S. grandicornis deposits eggs on infested buds singly (not in clumps) in the field. On 48.9% of buds on which eggs were laid, only one egg was found per bud. However, eggs can also be scattered in aphid colonies, varying in number from 2 (26.4%) to 10 (Fig. 7. 4). The frequencies of egg numbers on buds in the field differed from those in the cage. The percentage of buds with one egg was smaller in the cage than in the field, and the percentage of buds with > 4 eggs was greater in the cage than in the field. The higher degree of clumping of eggs on buds in the cage perhaps reflects the lower degree of choice available to the ovipositing females

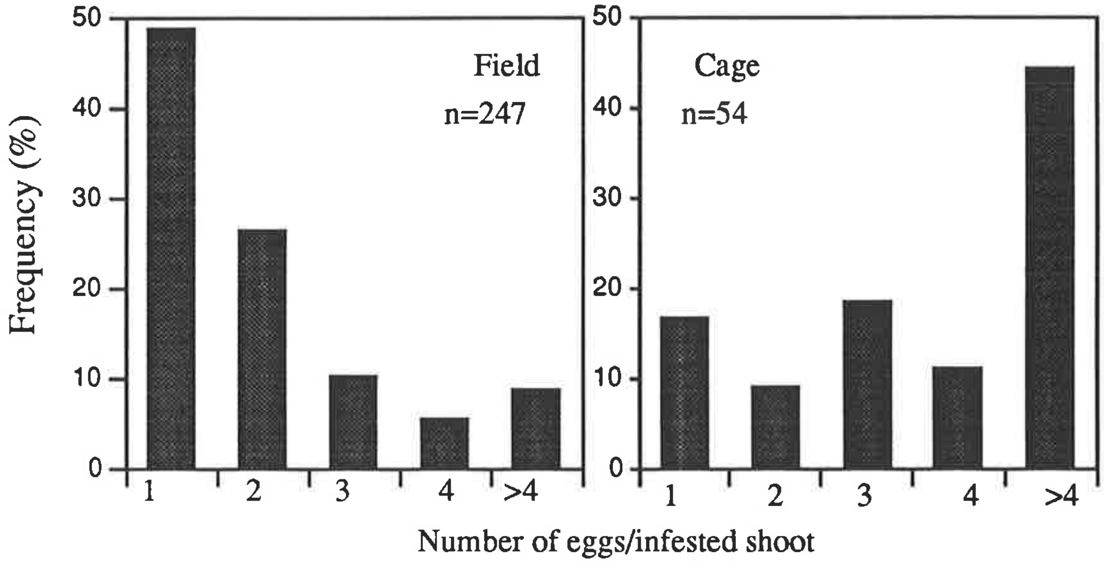

Figure 7. 4: Frequency of the number of eggs of *S. grandicornis* on infested rose buds in the field and in cage of field.

No relationship was found between the number of aphids per bud and the number of *S. grandicornis* eggs per bud on different sampling occasions (Fig. 7. 5, A-H). On most sampling occasions the number of buds with eggs was too low for statistical analysis but during November and January-March when enough buds with syrphid eggs were available, data were analysed for 8 sampling occasions (Fig. 7. 5, A-H). The pooled data during these eight sampling occasion give 29 buds with aphids per bud < MNAI and 30 buds with aphids per bud > MNAI. The difference is not significant (χ^2 = 0.2, p = 0.9).

Because of the low numbers of syrphid eggs at individual sites, all weekly data of the number of buds on which syrphid eggs were laid were combined from four sampling sites. A total of 34 aphid-infested buds with *M. viridiceps* eggs were sampled from all sites during this study;16 buds with aphids per bud>MNAI and 18 buds with aphids per bud<MNAI (Table 7. 2). Further, the data for *S. grandicornis* had to be bulked for different sites and sampling occasions to obtain reasonable numbers. Because of this, it was difficult to directly relate aphid density to oviposition. To overcome this, egg laying was related to mean density of aphids/bud at the time and place of the sample was taken.

Mean numbers of aphids were calculated from *all* infested buds on each sampling occasion (MNAI). Then, the mean number of aphids on buds on which syrphid eggs were found was compared with the MNAI. Eggs were laid equally on buds with aphids densities above and below the MNAI for any particular site and sampling occasion. However, once eggs were found on buds, total number of eggs was significantly higher on these buds which were infested with numbers of aphids higher than the MNAI (Table 7. 2).

Table 7. 2: Pooled data showing the relation between syrphid eggs and the MNAI (mean number of aphid/ infested bud) per sampling occasion : The frequencies of buds on which eggs were laid, and the total numbers of eggs laid on rose buds with aphid numbers less than the MNAI and greater than the MNAI.

	Syrphid species	Lower than MNAI	Higher than MNAI	χ^2	p
Frequency of buds on which eggs were laid	*S. grandicornis*	122	125	0.04	0.9
	M. viridiceps	18	16	0.12	0.732
Total eggs	*S. grandicornis*	198	240	4.03	0.05
	M. viridiceps	18	32	3.92	0.048

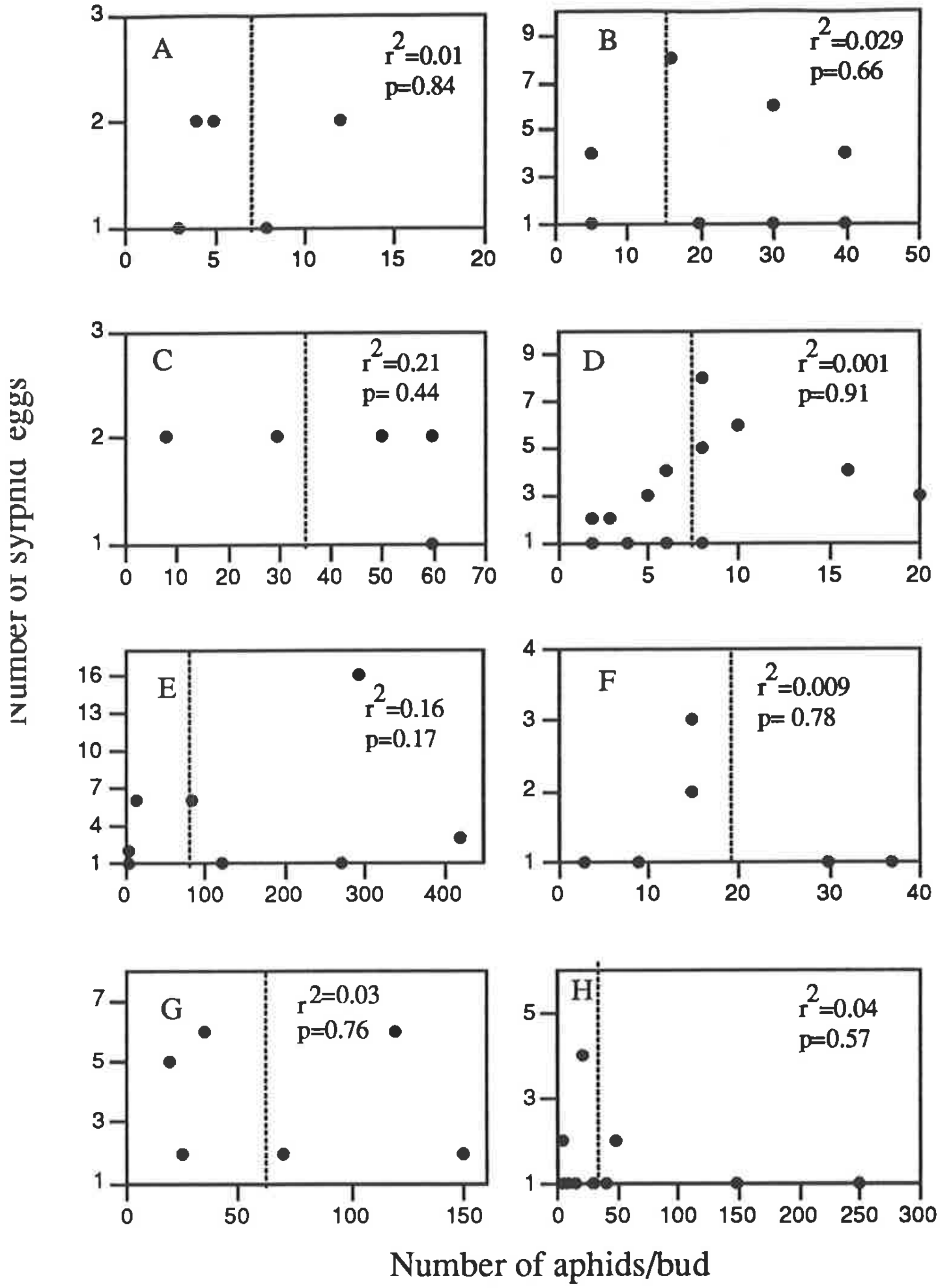

Figure 7. 5; Relationship between numbers of aphids/bud and numbers of eggs of *S. grandicornis* /bud at different sites and on different sampling occasion;A andB, Centennial Park, 18/1/94 and 23/1/94; C, Urrbrae House 16/1/94; D, Mercedes College 2/2/94; E, Urrbrae House, 25/11/93; F and G, Mercedes Collage, 17/3/94 and 23/3/94 respectively; H, Urrbrae House, 20/2/94. Dashed lines indicate the mean number of aphids per infested bud (MNAI) on each sampling occasion.

7. 3. 3 Capture efficiency

Capture efficiencies of different larval stages of *M. viridiceps* and *S. grandicornis* offered various nymphal stages of *Macrosiphum rosae* are shown in Table 7. 3 and 7. 4. The mean numbers of encounters (before capture of prey) for each larval instar feeding on each aphid instar were compared by ANOVA and the estimated LSD. No significant differences were detected between the mean numbers of encounters of first instar larvae of *M. viridiceps* fed first or second instars of rose aphid, but first instar larvae had more significant encounters with third instar aphids than with first and second instar aphids. No fourth instar aphids could be captured by the first instar larvae of *M. viridiceps*. (Table 7. 3).

There were no significant differences between the number of encounters of the first instar larvae *S. grandicornis* in capturing instars 1-3 of rose aphids (Table 7. 4). However, only one of 25 first instar larvae of *S. grandicornis* could capture a fourth instar aphid.

Table 7. 3: Capture efficiencies of individuals of different instars of *M. viridiceps* larvae offered different instars of *Macrosyphum rosae*.

syrphid larvae (instars)	aphid instars	numbers of larvae tested	success-ful captures (%)	mean encounters/ larva	capture* efficiency %
first	1st	23	87^{a}	1.45±0.15	69
	2nd	23	87^{a}	1.75±0.14	57
	3rd	31	80.6^{b}	3.12±0.31	32
	4th	28	0	>10	0
Second	1st	31	90.3^{a}	1.18±0.07	85
	2nd	29	86.2^{a}	1.16±0.07	87
	3rd	21	85.7^{a}	1.39±0.27	72
	4th	32	59.4^{b}	2.58±0.29	39
Third	1st	30	76.7^{a}	4.00±0.41	25
	2nd	26	84.6^{b}	1.08±0.05	91.7
	3rd	23	91.3^{b}	1.05±0.05	95
	4th	26	76.9^{a}	2.00±0.24	50

Table 7. 4: Capture efficiency of individuals of different instars of *S. grandicornis* larvae offered different instars of *Macrosyphum rosae* .

syrphid larvae (instars)	aphid instars	numbers of larvae tested	successful captures (%)	mean encounters/ larva	capture* efficiency %
first	1st	34	85.3^{a}	1.83±0.16	55
	2nd	24	83.3^{a}	1.95±1.29	51
	3rd	33	78.8^{b}	2.50±0.30	40
	4th	25	4^{c}	9±0.00	11
Second	1st	33	81.8^{a}	1.48±0.15	67
	2nd	35	82.9^{a}	1.72±0.17	58
	3rd	38	81.6^{a}	1.74±0.18	57
	4th	32	68.8^{b}	2.86±0.24	35
Third	1st	35	80^{a}	4.00±0.32	25
	2nd	41	92.7^{b}	1.05±0.04	95
	3rd	23	100^{b}	1.0±0.00	100
	4th	26	76.9^{a}	1.35±0.13	89

Second instar larvae of both species captured first second and third instar aphids equally well, but the fourth instar aphid, with the highest number of encounters was captured less frequently. The lowest capture efficiency occurred when first instar aphids were offered to the third instar larvae of both species. The highest capture efficiency was obtained for third instar larvae of either syrphid species when second or third instar aphids were offered to them. Both species were more efficient in capturing the third instar aphids than the fourth instar.

When eggs were hatched near fresh leaves, the capture efficiency of the first instar larvae of *M. viridiceps* decreased to 40% of encounters with the first instar aphid, compared with 69% when no fresh leaves were present (Table 7. 5). Mean number of encounters were compared by a two tailed t-test; first instar larvae had more encounters after rearing on fresh leaves

Table 7. 5: capture efficiency of first instar larvae of *Melangyna viridiceps* and *S. grandicornis* offered fresh leaves 5-6 hours prior to being offered 1st instar aphids.

Syrphid species	total number of larvae	successful larvae			capture eff. of syrphids not offered	unsuccessful larvae
		successful (%)	mean encounters/larva	capture* efficiency %	leaves (from table 6. 3)	%
M. viridiceps	60	75	2.49±0.20	40	69	25
S. grandicornis	62	87.1	1.93±0.10	52	55	12.9

(t=3.34, p=0.001, df=63). In contrast, no significant differences were detected between the first instar larvae of *S. grandicornis* before and after rearing the larvae had access to fresh leaves (t=3.34, p=0.59, df=81) (Table 7. 5). This indicates that *M. viridiceps* probably shifted to phytophagous behaviour during the 5-6 hours starvation period. As evidence that leaf tissue was consumed by aphid-starved larvae the green colour of larval guts could be observed through transparent cuticle under the stereo-microscope.

7. 4 Discussion

7. 4. 1 Fertility and fecundity

The pre-oviposition period for both species varied between 3 and 11 days in the laboratory with the mean of 6.8 and 5.5 for *M. viridiceps* and *S. grandicornis* respectively. Therefore, in Chapter 10, a pre-oviposition period of one week was included in the calculation of the number of generations. Different species of syrphid flies may have different pre-oviposition periods; for example, *Syrphus corollae* oviposited in the second day of emergence (Barlow 1961).

Virgin adults of *M. viridiceps* and *S. grandicornis* lay eggs in the absence of males, and although these eggs were infertile, the number of eggs laid were used to estimate fecundity in the laboratory. *M. viridiceps* was not reared for successive generations because they could not be induced to copulate in the laboratory. Similarly, I have never seen copulation of this species in the field during my 3-year study. Males and females probably need particular conditions for mating, for example, males of some species of hoverflies have an ambushing flight under isolated groups of trees (Schneider 1969; Heinrich and Pantle 1975). In contrast, males and females of *S. grandicornis* mate in the laboratory and they copulate in the cages or in the field. Mating in the field was observed to last more than 30 minutes in flight whereas, in small cages, mating occurred on the floor of the cage as well.

M. viridiceps lived longer than *S. grandicornis* when both were fed with honeybee hive pollen and cubed sugar. However, no differences were detected between longevity of males and females. In the field, both species consume pollen grains from a variety of sources (Chapter 6). So, perhaps, their different demands of food nutrient requirement may influence their longevity in the laboratory. However, when fed the same diet, the number of eggs laid by both species was not significantly different, but *S. grandicornis* laid at a greater daily rate than *M. viridiceps*.

7. 4. 2 Oviposition behaviour

S. grandicornis was seldom found to lay eggs on uninfested buds (0.8% of buds with eggs in the field and 4.8% in the cage) indicating that adult females can distinguish between infested and uninfested buds, and is therefore an aphid-seeking or aphidozetic species (Chandler 1968 a, b). The few cases in which eggs were found without a colony could be explained by (a) colony extinction after oviposition, (b) in response to residual honeydew as contact kairomone after extinction of colony (Völk 1964; Budenberg 1990; Budenberg and Powell 1992), (c) imperfect ability of the fly to withhold eggs in the absence of suitable hosts (Dixon 1959) or (d) ageing females of some species lose their ability to discriminate between hosts (Chandler 1966, 1967). This last (d) is the most likely explanation why, in these cage experiments, one of 21 uninfested buds (4.8%) was recorded with eggs, because females were captured in the field and were used regardless of their age. Combined with the relatively short distance (17cm) between shoots, older females may have lost their discriminative ability.

The selection of the sites of plants or habitat by syrphids for feeding or oviposition may be determined by the number, colour, type and form of flowers and plants in the area (Dixon 1959; Chandler 1966). In her studies, Dixon (1959) observed syrphid adults were attracted to broom plants whilst they were in flower and when they also had colonies of aphids. Each year the largest numbers of syrphid eggs were laid on broom during its flowering period compared with non-flowering time. Thus, when food for adults and suitable prey for larvae are available on the same plant, it is likely that females lay eggs close to the feeding site. However, in the presence of more suitable prey on nearby plants of different species, flowers occurring in one place are used as a food resource and eggs may be laid on suitable prey in other places. Further, it has been shown in this study that syrphids will lay eggs in aphid colonies on non-food plants Observations and gut dissection have shown that *M. viridiceps* and *S. grandicornis* are rarely attracted to rose flowers (Chapter 6). A large number of *M. viridiceps* were attracted to African and marguerite daisies planted inside or around the Claremont rose garden, but the number of eggs was low in comparison with the number of eggs of *S. grandicornis* (Chapter 4 and 9). Even when marguerite daisy with high numbers of flowers were infested with *Macrosiphum euphorbiae*, no syrphid eggs were recorded on this plant species. Therefore, flowers may attract syrphid flies for feeding, but the number of eggs laid depends on the prey preference and availability of suitable prey for the syrphid species.

S. grandicornis and *M. viridiceps* can discriminate rose buds with aphid colonies perhaps by olfactory, gustatory and optical responses (Dixon 1959; Chandler 1966). This species shows no preference for buds with aphid densities either relatively greater or less than the mean density on a particular sampling occasion. However, once an infested bud is selected, females deposit more eggs on infested buds with higher than the (MNAI) than on buds with lower than the MNAI.

In the cage experiments, the number of eggs increased to an optimum of 100 aphids per infested bud and then decreased at greater densities. Density-dependence of oviposition behaviour of Syrphidae has been demonstrated in a number of species (Dixon 1959; Hughes 1963; van Emden 1963; Bombosch 1963; Clark 1963; Kuchlein 1966; Chandler 1968). The results obtained from the present cage experiments are similar to the data of Clark (1963), which indicated that the number of eggs laid by *Syrphus sp* on *Eucalyptus* infested by psyllids increased until an optimum density, and then decreased. Additionally, females of hoverflies respond to the quality as well as the abundance of the prey (Hemptinne *et. al.* 1993). When the number of aphids on a bud increases or the host plant is unfavourable, the colony disperses by walking off and by the formation of alates. Aphid exuviae remain at the site of the colony and females of some species of aphidophagous Syrphidae avoid laying eggs close to old aphid colonies (Kan 1988a,b; Kan and Sasakawa 1986). Present results showed that fewer eggs were laid by *S. grandicornis* and *M. viridiceps* on buds with exuviae than those without. By avoiding oviposition on aphid-infested buds bearing older colonies, the syrphid minimises the risk of starvation for the offspring (Hemptinne *et al* 1993) and optimises larval foraging by laying eggs at the most suitable time of colony development (Kindlmann and Dixon 1993).

In contradiction to the results of the cage experiments, data obtained from the field indicated that *S. grandicornis* oviposition behaviour in response to prey numbers is not density-dependent (Fig. 7. 3). These differences can be explained as follows:

(a): In the field, females can select attractive prey whereas, in the cage experiments, only one prey species is available and females deposit eggs on the most suitable oviposition site (optimum aphid density).

(b): In the field, eggs were laid on only a small proportion of infested buds and, of these, only one egg was oviposited on 50% of egg-bearing buds infested, regardless of density of aphids. This may mask any density-dependent pattern of oviposition of *S. grandicornis* on rose buds.

7. 4. 3 Capture efficiency

First instar larvae of either species were not able to catch fourth instar aphids. In rare cases, when first instar larvae were observed to pierce the cuticle of fourth instar aphids, the larvae could not stabilise themselves on the stratum and were overpowered by the aphids. In addition, aphids secrete a waxy liquid which may adhere to the body of the prey and makes its movement difficult. One of the defence functions of aphid cornicles by secretion of waxy liquid against predators and parasites has previously been noted by Edwards (1966) for syrphids and by Kitt (1996) for *Macrosiphum rosae* against the parasitic wasp, *Aphidius rosae* (Haliday.).

Hagen *et al.* (1976) suggested that the composition of prey cuticle may be important in prey acceptance. However, syrphid larvae pierce the cuticle and feed on inside-body contents. Capture efficiency experiments, and some casual laboratory observations, indicated that the cuticle of the fourth instar *M. rosae* can be pierced by first instar larvae. Thus, it may be the large size, fast movement and defence secretion of the fourth instar rose aphid which enables it aphid to escape from the first instar syrphid. In general, predators need to be larger than their prey (Harvey and Gittleman 1992).

The first instar larvae of syrphid flies are vulnerable to starvation and predator defence. The ability of female *S. grandicornis* to discriminate between young and old colonies is important for survival of offspring. Laying eggs on buds with dispersing colonies and with a high proportion of large aphids is dangerous for their offspring because (i) they are not able to catch the large prey and (ii) they are also in danger of death by the defence of the large aphids.

The third instar syrphid larva is the largest and most voracious larval stage and is large enough to capture all stages of rose aphids, but it is less efficient in capturing first and fourth instars aphids than second and third instar aphids. Energy gained from prey consumption may compensate for the energy larvae expend during prey capture. This may be recognised by physical contact (thigmokinesis) between the larvae and aphids.

The capture-efficiency experiments and laboratory observations showed that most first instar larvae of *M. viridiceps* consumed green plant materials when deprived aphids. The larvae of some species of syrphids are able to shift to another food in emergency; e.g., larvae of *Allograpta obliqua* (Say.) are able to sustain themselves on plant food (for overview see Hamrum 1965). This survival mechanism is important for the first instar larvae, which have little movement and have difficulty in finding prey, especially when the prey is rare. It is possible that the observed decrease in capture efficiency of the first instar larvae of *M. viridiceps* when they are first reared on fresh leaves without aphids, is due to satiation of the larvae. The low mortality due to facultative phytophagy, which is characteristic of first instar *M. viridiceps* in the absence of prey, may be a reason for the abundance of adults of this species in Adelaide.

Chapter 8

Temperature-dependent development in eggs, larvae and pupae of *M. viridiceps* and *S. grandicornis* in the laboratory

8. 1 Introduction

Temperature influences the rate of development of insects. This is particularly obvious when cohorts of an insect species are reared at different constant temperatures. Computer technology and the use of non-linear regression techniques facilitate the application of rate and distribution data to the building of sophisticated population models of development time (Wagner *et al.* 1984). The data and equations on temperature-dependent development for each species are input for simulation models which can be used to predict the seasonal phenology of the species (Jud *et al.* 1994) and are currently being used in pest management programs (Jud *et al.* 1994).

Since the syrphid larvae had to be fed on aphids during the course of the temperature experiments, it was convenient to record the numbers of aphids eaten and hence to measure the voracity of each instar of syrphid larvae. Much has been done on the voracity and development of European species of hoverflies (Chapter 2). However, although *M. viridiceps* and *S. grandicornis* are the two commonest species of entomophagous hoverflies in South Australia, little is known of the quantitative aspects of their voracity.

The aims of these experiments were to study:

(i) the development of eggs, larvae and pupae at different constant temperatures.

(ii) the voracity of *M. viridiceps* and *S. grandicornis* larvae reared on rose aphids.

(iii) the number of generations per year, by using a temperature-dependent simulation model.

8. 2 Materials and Method

8. 2. 1 Voracity

Gravid females were captured in the field and put in 25cm x 25m x 30cm oviposition cages.

Rose aphids on favourable buds (stages 1-4) were offered to them for oviposition. The flies were supplied with bee hive pollen and daisy flowers, *Euryops pectinatus* and *Chrysanthemum frutescens*. Infested buds were inspected at 4h intervals and the eggs laid on each occasion were used for each set of experiments. To avoid damage, each egg was removed from the plant by cutting off the small piece of plant tissue the egg was fixed to. Each egg was put in a 10 x 20mm plastic vial with gauze on the lid for ventilation. The eggs were inspected at 12h intervals until they hatched.

A series of experiments was conducted in a growth chamber under 10000 lux, 70% R.H. and 16:8 light to dark photoperiod at different times of the year depending on the availability of hoverfly adults. 20 first instar larvae of each syrphid species were used at each of 3 different temperatures, 10, 15 and 20°C (a total of 120 larvae).

Neonates are fragile and consume few aphids per day and were fed in vials after they hatched. Rose aphids were provided from the field. Infested rosebuds were shaken over a 20 by 30cm white metal plate. Second instar rose aphids were transferred to the vials using a fine brush. On reaching the second instar, hoverfly larvae were transferred to larger vials. They were supplied with a surfeit of third instar aphids aspirated directly into each vial from the white metal plate. As the larvae developed through the 2nd and 3rd instar stages, more aphids were aspirated into the vials as required.

The numbers of aphids consumed was recorded twice a day until pupation and summed to obtain the total consumption. The number of aphids eaten between inspections was calculated by subtracting the number of aphids remaining at an inspection from the number offered at the previous inspection. The number of second instar aphids eaten by first instar syrphid larvae was converted into third instar equivalents (TIEs) based on the relative weights of the 2 aphid instars.

At 20°C, larvae were weighed every day and the increase in their weights was recorded. Then the number of aphids required for a 1mg gain in the wet weight of larvae was calculated.

8. 2. 2 Temperature-dependent development and number of generations

Eggs of the same age (±2h) were used to start the voracity experiments. Eggs were put in vials in groups of 5 or less to minimise cannibalism by neonates. The eggs were incubated at 4, 8, 10, 15, 20, 25 and 30°C in the dark. In some cases the experiment was run 2-3 times to obtain reasonable numbers.

As first instar larvae (a maximum of 12h old) emerged at different temperatures they were put singly in vials (10 x 25mm). Approximately 20, 40 and 150 rose aphids (mixed instars), were offered to the larvae in the vials during the 1st, 2nd and 3rd instars respectively. At 4°C, larvae of both species failed to survive. Eggs, larvae and pupae were examined daily for evidence of hatching, moulting and adult emergence. Larvae were transferred to clean vials with fresh aphids daily as in the previous experiment. Total numbers of aphids per individual larvae at each temperature were used in ANOVA and t-test to compare the voracity within and between each species at different temperatures.

Two computer programs were used to fit models and calculate the number of generations per year. The PMDS computer program (Logan and Weber 1991) was used to fit the appropriate curve to each immature stage. The program chooses the best model from 8 functional relationships between temperature and the median rate of development (Logan 1988) and gives a graphic display and a simulation analysis.
A Day Degree program (R. Laughlin, unpublished data) was used to calculate the number of generations per year based on temperature data from the Waite Institute meteorological station and using the functions suggested by PMDS.

R. Laughlin's program calculates the duration of an insect stage or stages under fluctuating temperatures. Two input sets are needed. Daily maximum-minimum temperatures for the period under study and figures defining the relation between growth and temperature for the different stages of the insect. These figures can be any of 5 functions (linear regression, exponential, exponential $_b$, Logan t_b, Stinner) or a look-up table describing a growth rate/temperature curve at 1 degree intervals.

When the program is run it asks for a starting date. Given a starting date, it calculates an hourly temperature curve for each day using sine curves between successive values of the maximum-minimum set. Taking each stage in turn, it calculates the percentage of the stage completed in each succeeding hour, accumulating these amounts until the sum reaches 100. When the last stage reaches 100, the life cycle is complete. The program outputs the length of each stage and of the whole life cycle.

8. 3 Results

8. 3. 1 voracity

The mean weights of second and third instar rose aphids used in the experiment were 0.13± 0.005 and 0.51± 0.03 respectively. Thus, 3.9 second instar aphids were equivalent to 1 third instar aphid. Numbers of aphids consumed have all been converted to third instar equivalents (TIEs) below.

The cumulative numbers of third instar equivalents (TIEs) of rose aphids consumed over all the larval stages of *M. viridiceps* and *S. grandicornis* at different temperatures in the laboratory are plotted in Fig. 8.1 against larval development time in days; and the mean total numbers of TIEs consumed over all larval stages of each species are given in Table 8. 1A. A model 1 2-way ANOVA of the latter data (Table 8. 1B) indicated no significant differences between temperatures. A comparison of the means of the temperatures (Table 8. 1A) with the appropriate LSDs (Table 8. 1B) indicated that more TIEs were eaten at 10°C than at 15°C ($p<0.05$) and significantly fewer ($p<0.01$) were eaten at 20°C than at 15°C. The most interesting aspect of the analysis, however, was the significant interaction

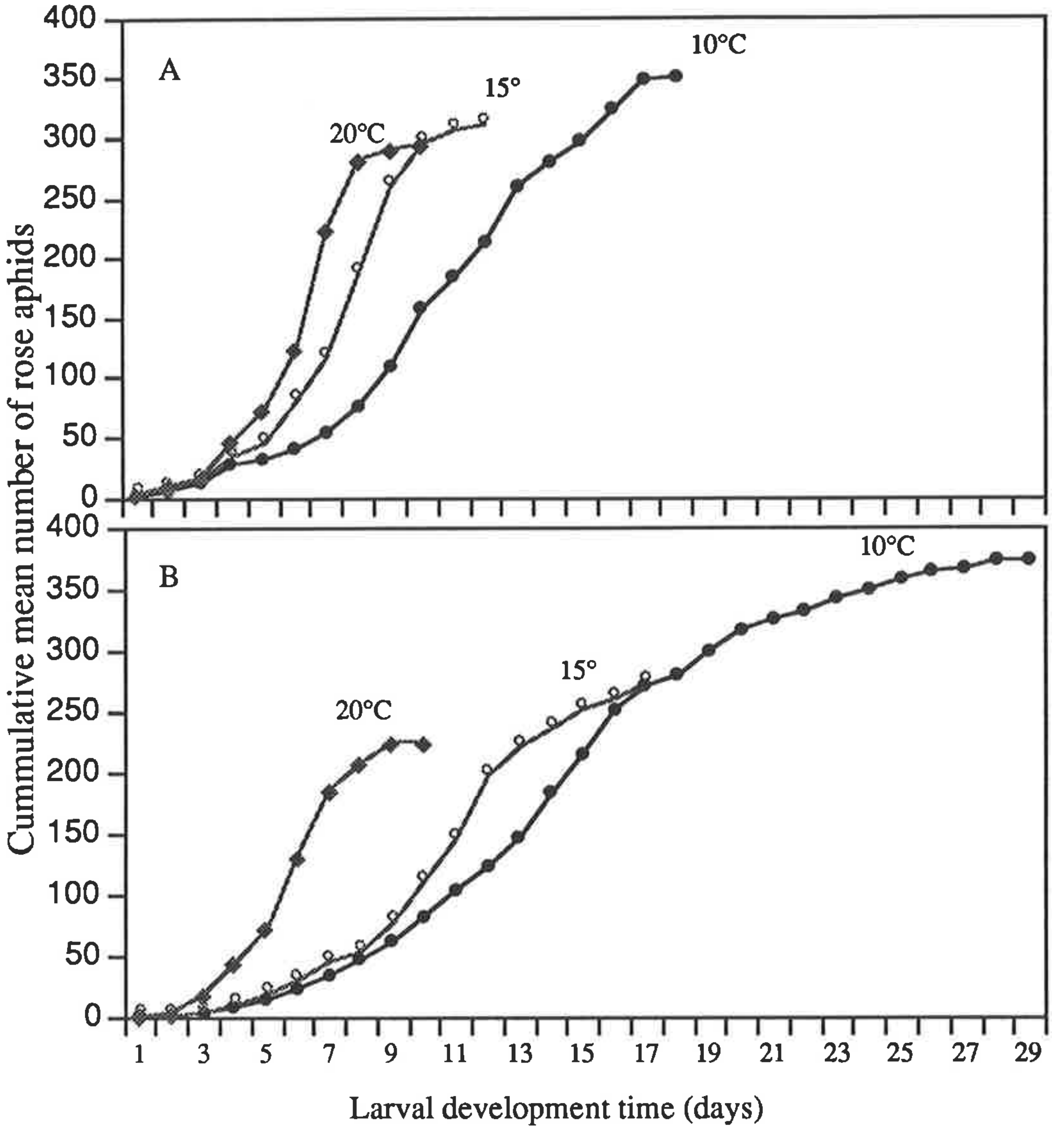

Figure 8.1: Cumulative number of third instar equivalents (TIEs) of rose aphids consumed by larval instars 1-3 of (A) *M. viridiceps* and (B) *S. grandicornis* at three different temperatures.

between species and temperature (Table 8. 1B). Thus, there was no difference between the TIEs consumed by *M. viridiceps* and *S. grandicornis* at 10°C (Table 8. 1A). At 15°C, *S. grandicornis* ate more TIEs than did *M. viridiceps* (significant at p=0.05), but at 20°C *S. grandicornis* ate significantly fewer TIEs (significant at p<0.01) than did *M. viridiceps* (Table 8. 1A, B and Fig. 8.1).

Table 8.1A: Total numbers of third instar equivalents (TIEs) of rose aphids consumed over all larval stages of *M. viridiceps* and *S. grandicornis* at different temperatures in the laboratory.

Species	10°	15°	20°	Means of species
M. viridiceps	351.5 (±9.1SE)	310 (±11.5SE)	296.1 (±14.2SE)	319.2
S. grandicornis	373.4 (±22.4SE)	357.5 (±14.6SE)	224.3 (±5.9SE)	318.4
means of temperatures	362.5	333.8	260.2	

S=significant, NS=non-significant

Table 8. 1B: ANOVA for the data in Table 8. 1A.

Source of variation	d.f.	SS	M. S.	F	p
Total	119	743967.3			
Treatments	5	302512.1			
Species	1	6.9	6.9	<1.0	N.S.
Temperatures	2	225096.4	112548.2	29.1	<0.001
Interaction	2	77408.8	38704.4	10.0	<0.001
Error	114	441455.2	3872.4		
LSD between any 2 temperatures			27.6 36.5	p=0.05 p=0.01	
LSD between species at any one temperature			39.0 51.6	p=0.05 p=0.01	

d.f.=degrees of freedom, SS= Sums of Squares, M.S.=Mean of Squares, F=F-test , N.S.= not significant at 0.05 probability level or better.

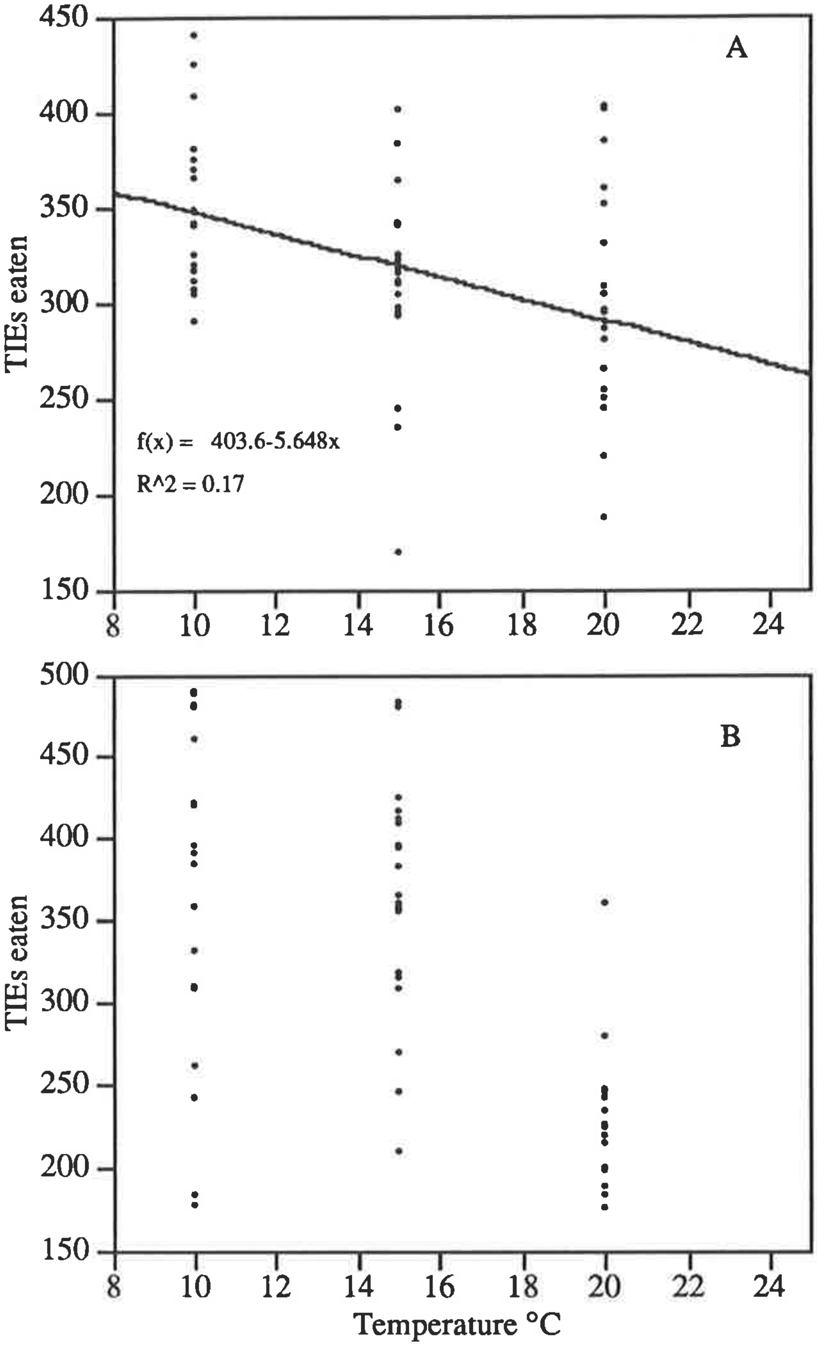

Fig. 8. 2: The total numbers of TIEs eaten over all larval stages by A; *M. viridiceps* and B, *S. grandicornis* at 3 different temperatures.

For *M. viridiceps* the line Y= 403.6-5.648x was fitted by regression with replication (see text and Appendix 8. 1). No curve was fitted for *S. grandicornis*.

Another interesting difference between the two species was suggested in the plot of the the number of TIEs consumed by each individual against temperature (Fig. 8. 2). The points suggest that the numbers of TIEs consumed by *M. viridiceps* decreased linearly with increasing temperature; but the numbers eaten by *S. grandicornis* at 20°C decreased so sharply that the relation of TIEs and temperature for that species could probably be fitted only by a polynomial curve. However, testing linearity of regression with only the means at each temperature results in most of the information being wasted. Linearity of regression was tested for each species by regression with replication (Zar 1984) which used all 20 TIEs at each temperature. The ANOVAs confirm the impressions from Fig. 8. 2 that the hypothesis of linearity of regression should not be rejected for *M. viridiceps* (Appendix 8. 1) but should be rejected for *S. grandicornis* (Appendix 8. 2). The line: $Y=403.6-5.648x$ was fitted to the data for *M. viridiceps* and is given in Fig. 8. 2. No curve was fitted to the data for *S. grandicornis* but any such curve would cross the line fitted to the data for *M. viridiceps*. (as suggested in Fig. 8. 2), and the crossing of the trend lines for the 2 species would graphically illustrate the significant interaction which is indicated in the ANOVA of Table 8. 1B.

M. viridiceps were incubated for 18, 12 and 10 days and *S. grandicornis* were incubated for 29, 17 and10 days at 10, 15 and 20°C respectively. *M. viridiceps* consumed 19.5, 25.8 and 29.6 third instar equivalents (TIEs) of rose aphids per day at 10, 15 and 20°C respectively while the other species consumed 13.3, 16 and 22.4 TIEs under the same conditions. 89.1 and 80.5% of consumption occurred during the third stadium of the hoverflies which occupied 55.5 and 56.7% of the larval development period of *M. viridiceps* and *S. grandicornis*. respectively.

Both species were also compared with respect to the number of aphids consumed and weight at the end of each stadium at 20°C (Table 8. 2).

Table 8. 2: Mean numbers of third instar equivalents (TIEs) of rose aphids consumed and the weight of syrphid larvae at the end of each stadium at 20°C (± standard error).

syrphid species	1st instar		2nd instar		3rd instar	
	aphids	weight	aphids	weight	aphids	weight
M. viridiceps	3.1 ±0.4	0.2 ±0.03	29.3 ±2	1.9 ±0.2	263.7 ±14.2	20.7 ±8
S. grandicornis.	2.8 ±0.12	0.6 ±0.06	41.0 ±4.1	3.1 ±0.17	180.5 ±6.18	24.2 ±95

The weight of the neonate first instar larva of both species was approximately 0.03mg. This figure was used for calculating the weight gain in the first instar. *S. grandicornis* required fewer aphids for a weight gain of 1mg (Table 8. 3).

Table 8. 3: The mean number of TIEs (± standard error) required for a 1mg weight increase in larvae of *M. viridiceps* and *S. grandicornis* at 20°C.

syrphid species	first instar	second instar	third instar	overall
M. viridiceps	7.2±1	25±3.1	14.2±0.8	14.5±0.7
S. grandicornis.	5.7±3.5	17.2±2.0	8.7±0.29	9.4±0.41

8. 3. 2 Temperature-dependent development

The mean durations of development of all stages of *M. viridiceps* and *S. grandicornis.* are given in Table 8.4. The details of the development times of eggs of both species are presented in Appendix 8. 3; those of the larvae are given in Appendix 8. 4A and 4B, and those of the pupae are given in Appendix Table 8.5. The fitted curves are given in Figs. 8.3 and 8.4, and the parameters of the fitted curves are given in Appendix Tables 8.6A and 8.6B. For eggs, the PMDS program fitted the Stinner curves $R_t = C/(1+e^{k_1+k_2 t'})$ and $R_t = C/(1+e^{k_1+k_2 t''})$ (Stinner *et al.* 1974) for each species; R_t= median development rate, C= maximum rate of development at T_{opt}. $k1$ and $k2$ are constants; t = temperature (°C); t' = T_{opt} - t for t ≤ T_{opt}; t" = t - T_{opt} for t > T_{opt}. The curves are plotted in Figures 8.3a and 8.4a.

Table 8. 4: The means of duration of each stage (days) at 5 constant temperatures

temperature °C	*S. grandicornis*				*M. viridiceps*			
	egg	larvae	pupa	total	eggs	larvae	pupa	total
8	8.3	41.6	27.4	77.3		not measured		
10	3.9	29.0	24.4	57.3	6.3	21.2	20.0	47.5
15	3.5	18.5	17.3	39.3	2.9	10.9	14.3	28.1
20	1.5	12.3	7.7	21.5	1.8	10.8	8.3	20.9
25	1.5	7.7	8.2	17.4	1.9	8.8	7.1	17.8

The median rate of egg development (Fig. 8.3 and 8.4) increases with temperature to a peak of 23.5 and 27.6°C (T_{opt}) for *M. viridiceps* and *S. grandicornis* respectively. Then the rate decreases with the same slope above T_{opt}. All eggs of *M. viridiceps* died at 4°C whereas 70.1% of the eggs of *S. grandicornis*. survived at this temperature. In the laboratory, the rate of development of individuals that did develop at 20°C was similar to those at 25°C for *M. viridiceps*. In contrast, eggs of S. *grandicornis* incubated at 25 and 30°C had similar rates of development (Appendix 8. 3). These results indicate that the eggs of *M. viridiceps*. require a lower optimum temperature of development than those of *S. grandicornis*.

For larvae, the fitted curves of median developmental rates (1/days) at different temperatures are also plotted in Fig.8. 3, (b-d) and 8. 4, (b-d) for each larval instar of *S. grandicornis* and *M. viridiceps* . Development times for the first and second instar larvae of *S. grandicornis*. (Appendix 8 4A) declined sharply when the temperature increases from 8°C to 10°C, whereas

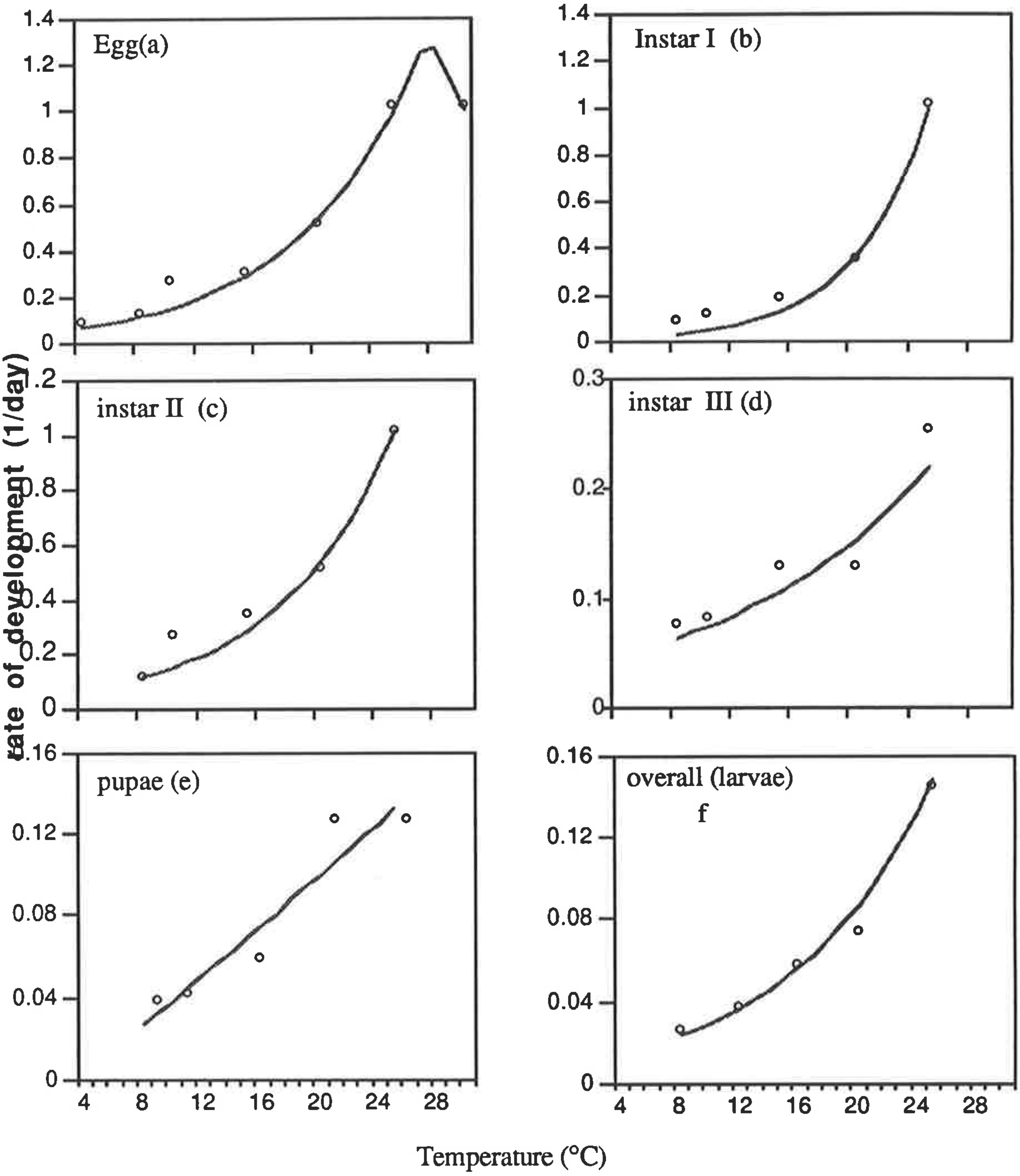

Figure 8. 3: Median developmental rates (1/days) of *S. grandicornis.* at 6 constant temperatures, 4, 8, 10, 15, 20, and 25 °C.

increased from 8° to 10°C, whereas this rise in temperature did not affect development times of the third instar larvae. Therefore, it seems that the development time of the third instar larvae of this species is less sensitive to changes in temperature under the conditions

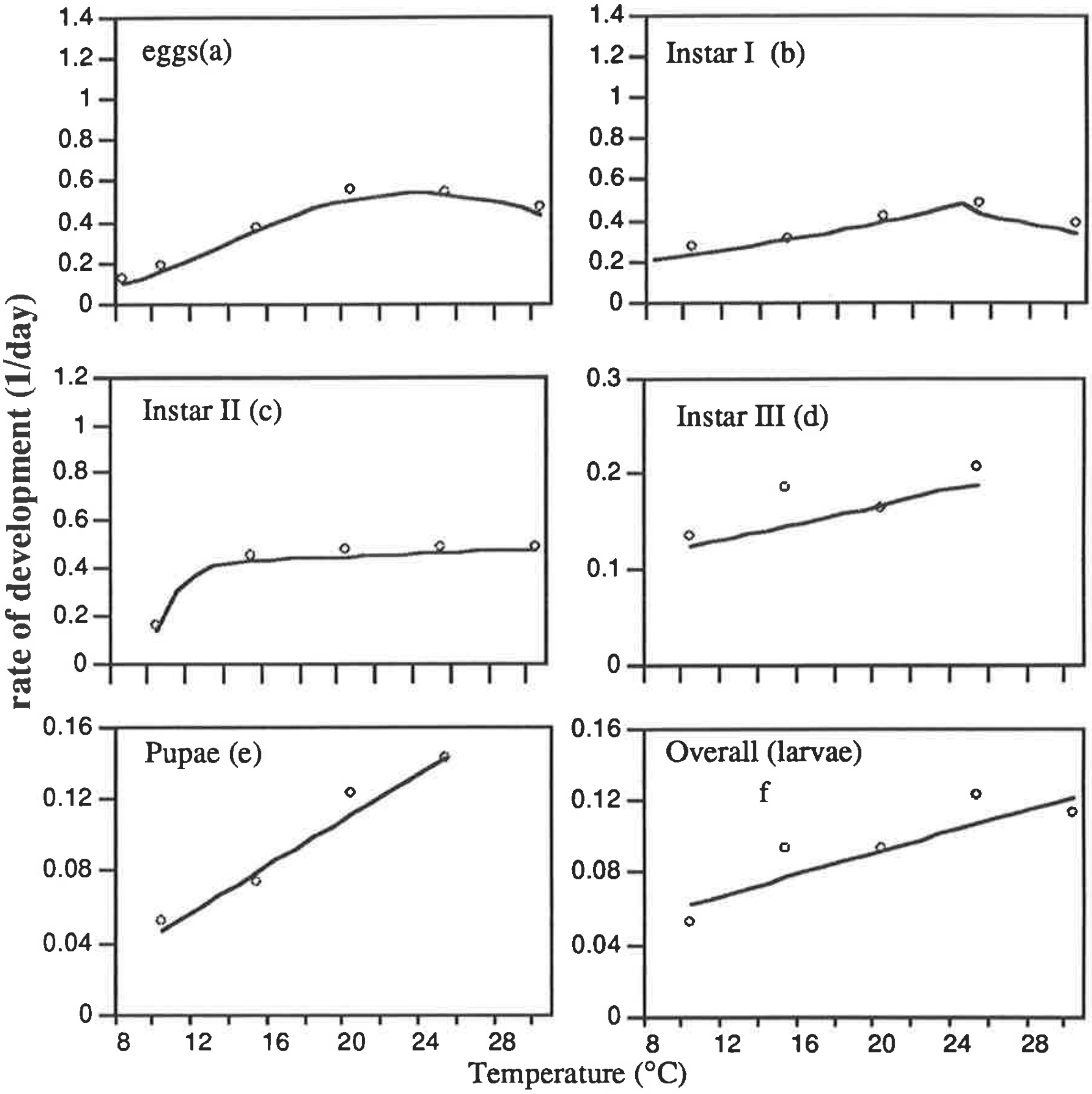

Figure 8. 4: Temperature-dependent development curves fitted to median development rate (1/day) of *M. viridiceps* at constant temperatures, 5, 10, 15, 20, 25 and 30°C.

this rise in temperature did not affect development times of the third instar larvae. Therefore, it seems that the development time of the third instar larvae of this species is less sensetive to changes in temperature under the conditions of this experiment. Two different models were used for fitting curves for the median development rates of *S. grandicornis.*, namely, Stinner's for the first instar (Fig.8.3-b) and exponential for the second and third instars (Fig. 8.3c,d). The exponential equation (Logan 1988) is $r(t) = \psi e^{\rho T_T}$ where ψ is the minimum rate of development and ρ is the slope of a regression line, $r_i^T = \ln(r_i)$, obtained from the natural logarithm of the observed developmental rates against temperature (T_T) above the lowest experimental temperature (in this experiment, 8°C for larvae of *S. grandicornis.*). The two parameters, ψ and ρ are given by the PMDS as p1 and p2 respectively (Appendix 8.6A, 8. 6B).

The trend of the developmental rate of the larvae of *M. viridiceps* at different temperature differed from that of *S. grandicornis.*. This species had a lower development response to increasing temperature during the second and third stadium (Fig. 8.4, c *and* d). The difference is clearly demonstrated by the two types of curves fitted to the second stadium of both species; exponential for *S. grandicornis.* and Logan Tb for *M. viridiceps.* When the total larval development times from hatching to pupation at each temperature were considered, an exponential and linear model were fitted to the median rate of development against temperature in both species (Fig. 8.3f and 8. 4f).

For pupae, an exponential T_b model (Logan and Weber 1988) with the equation $r(t) = e^{\rho(T_T - T_b)}$ (ρ and Tb are respectively the slope and intercept) was fitted to the observed median development rates of the pupae of *S. grandicornis* ; whereas a linear relationship with the equation of $r(t) = \rho(t - T_b)$ (ρ=slope and T_b = intercept) was fitted for *M. viridiceps.*. However, pupae of both species had a similar trend of development. In fact, the program fits the best curve based on the largest adjusted coefficients. For example, the shape of the exponential curve for *S. grandicornis.* pupae suggested by PMDS is similar to a linear because the adjusted coefficients are nearly the same (0.7494 and 7470 for exponential and linear respectively). Obviously, either function could be used to describe the experimental results. I have chosen linear to use for *S. grandicornis*. development.

8. 3. 3 Numbers of generations per year

S. grandicornis

S. grandicornis became active in August, after the days became warmer. Few males and females were captured in suction traps or observed during winter (Chapter 4). The first eggs were recorded on roses on 30/8/93 and the last eggs on 15/6/94 (9.5 months later) in the Claremont rose garden. In the second year, the first egg was found in the Urrbrae rose garden on 21/8/94 and the last one was observed on 16/4/95 (about 8 months later). During this period, 10 generations per year were calculated for *S. grandicornis* in Adelaide (Table 8.5).

M. viridiceps

The flight activity of *M. viridiceps* starts in March-April and continues until December. Since very few eggs and larvae were observed on roses, the first and last records of flight activity were used for calculation of the number of generations per year. First flight activity was observed on 1/3/93, 6/3/94 and 23/4/95 and the last flight activity was observed in 1/12/93, 24/11/94 and 15/11/95. However, in the exceptionally cool summer of 1994, when the minimum temperature suddenly decreased to less than 10°C for more than 10 days in January, flight activity of *M. viridiceps* re-started in this month. Disregarding this anomaly, activity of this species was recorded between 1/3/93-1/12/93 and 6/3/94-24/11/94 and 11-13 generations were calculated for these periods (Table 8. 6) However, very few adults were captured in water traps when there was no other evidence of flight activity in summer (Chapter 4).

In the laboratory, the pre-oviposition period for adults at 20°C and 16: 8h light:dark was about 7 days. This period was added to the calculation of each generation.

8. 4 Discussion

8. 4. 1 Voracity

The quantification of the potential voracity of the larvae of the two native syrphid flies, *M. viridiceps* and *S. grandicornis* confirms that temperature has a marked influence on the voracity of the larvae of the two species. Low temperature extends the larval development period and increases the total number of aphids consumed even though the mean number of aphids consumed per day decreases.

M. viridiceps consumed 296 and 351 and *S. grandicornis* consumed 224 and 373 third instar equivalents (TIEs) of rose aphids at 20 and 10°C respectively. This increase in the number of TIEs eaten at 10°C is due to the longer larval development period (Tenhumberg and Poehling 1995). In other words, the mean number of TIEs consumed per day (consumption rate) decreased for both species at 10°C. At 10°C, although there was no difference between the number of aphids consumed by the two species, *M. viridiceps* had a greater consumption rate than *S. grandicornis*. *M. viridiceps* is a cold-loving species and its activity period is in winter and spring whereas *S. grandicornis* is a warm-loving species and most of its activity period is in late spring, summer and autumn. Therefore, *M. viridiceps* shows less response to lower temperature than *S. grandicornis*.

At 20°C both species pupate after an 8-10 day larval period. However, more TIEs are eaten by *M. viridiceps* than by *S. grandicornis*. In contrast, the latter uses fewer TIEs to gain 1mg body weight (9.4 TIEs. for *S. grandicornis*. and 14.5 TIEs for *M. viridiceps*). This is probably an adaptation to shortage of prey during summer when *S. grandicornis* is active in Adelaide. In addition, hosts other than aphids are present in the summer. However, larvae of syrphids show a functional response when the number of prey changes (Tenhumberg and Poehling 1991). Thus the two species may have different functional responses, exploring different ranges of prey at the same prey density.

Estimating the potential voracity of a syrphid larva in the laboratory may lead to overestimation of field voracity (Tenhumberg and Poehling 1995). These authors showed that, depending on the temperature, a single larva of *Episyrphus balteatus* consumed 660-1140 third instars of the aphid

Metopolophium dirhodum. In contrast, in 10m^2 cages of winter wheat, a single larva of the predator consumed a maximum of 396 aphids which was only half of the mean potential voracity given in the literature (Tenhumberg 1995). In spite of overestimation, investigating the voracity of syrphid larvae in the laboratory can be a good indication for comparative studies and is valuable when field data are not available.

8. 4. 2 Temperature-dependent development and number of generations

Comparison between median growth rates (1/day) for all stages of both species indicates that eggs and larvae of *S. grandicornis* complete egg and larval development on aphids quicker than *M. viridiceps* at high temperatures and grow more slowly at low temperatures (Fig. 8. 1, 8. 2, 8. 3). This difference between the species is especially clear in the second and third stadium in which an increase in temperature within the range of experimental conditions has little effect on the growth rate of *M. viridiceps*. However, eggs of *S. grandicornis* hatched at 4°C whereas all eggs of *M. viridiceps* died at this temperature. Pupae of both the species gave a similar response to changes of temperature.

S. grandicornis is active during spring, summer and autumn whereas *M. viridiceps* is active in autumn, winter and spring. The minimum temperature in Adelaide does not usually go any lower than 4°C for an extended period. Therefore, low temperature probably does not affect the survival of the eggs of either species. However, eggs of *S. grandicornis* at 4°C developed 1.4 timesmore slowly than at 8°C, and eggs of *M. viridiceps* did not survive at 4°C. In addition, the first instar larvae of both species died at 4°C.

In the laboratory, *M. viridiceps* had more possible generations per year (11-13) than *S. grandicornis* (10) during 1993-95 . However, natural fluctuating temperatures in the field may give a different result from development times calculated from constant temperature data obtained in the laboratory. In summing hourly percentages of development the calculation assumes that there is no modifying effect of smooth temperature change *per se*. It is possible that fluctuating temperatures may change growth rates from the rate expected from constant temperature experiments, but such examples are rare and Liu *et al.* (1995) concludes that the majority of insects show no such effects.

The calculation also assumes that the daily temperature cycle of a study area can be adequately represented using the maximum-minimum/sine curve calculation. Obviously, a continuous temperature record taken from the actual development site of the insect would be preferable but maximum-minimum temperatures were, in this case, all that were available.

Table. 8.5: Durations of generations of *S. grandicornis.* in the field in 1993-94 estimated by Laughlin's Day Degree program.

Start day	end day	duration (days)	Start day	end day	duration (days)
1993-94			1994-95		
01/09/93	30/09/93	29	21/8/94	17/09/94	27
07/10/93	31/10/93	24	24/9/94	21/10/94	26
07/11/93	25/11/93	18	28/10/94	19/11/94	22
2/12/93	18/12/93	16	26/11/94	11/12/94	15
25/12/93	14/01/93	20	18/12/94	02/1/94	15
21/01/93	03/02/94	12	09/01/94	20/1/95	11
10/02/94	26/20/94	16	27/01/95	12/02/95	11
5/03/94	23/03/94	18	19/2/95	03/03/95	13
30/3/94	17/04/94	18	10/3/95	01/04/95	22
24/04/94	16/05/94	21	8/4/95	02/05/95	24

Table. 8.6: Duration of generations of *M. viridiceps* in the field in 1993-94 estimated by Laughlin's Day Degree program.

1993			1994		
Start day	end day	duration (days)	Start dates	end day	duration (days)
1/3	21/3	20	2/3	17/3	15
28/3	9/4	12	24/3	6/4	11
16/4	3/4	13	13/4	27/4	14
10/4	23/4	14	4/5	21/5	17
30/4	14/5	14	28/5	14/6	17
21/5	8/6	18	21/6	10/7	20
14/6	5/7	22	17/7	9/8	23
12/7	1/8	27	16/8	2/9	17
8/8	27/8	19	9/9	28/9	19
3/9	23/9	20	6/10	22/10	16
1/10	19/10	18	29/10	14/11	16
23/10	7/11	15			
14/11	28/11	14			

Chapter 9

Seasonal occurrence of *M. viridiceps* and *S. grandicornis* and their synchronisation with rose aphids

9. 1 Introduction

Identification of the causes of numerical changes in populations and explanations for these changes may be of practical use in biological control. Since aphids may cause damage to plants, it is important to anticipate the changes in numbers of their populations. Aphid populations may respond very quickly to changes in abiotic and biotic factors. Of the biotic factors, natural enemies influence aphid numbers in many agro-ecosystems. In this study, a simple model agro-ecosystem is used to evaluate the effectiveness of two common Australian syrphids.

Thirty species from 14 genera of aphids feed on roses in the world (Blackman and Eastop 1984). In Australia, the four introduced species, *Macrosiphum rosae*, *M. euphorbiae*, *Rhodobium porosum* (Sanerson.) and *Aphis gossypii* were all found on roses during the survey at all sites of study. In Adelaide, *M. euphorbiae* is the most abundant species in early spring, but at other times *M. rosae* was by far the most common and abundant aphids on roses.

Macrosiphum rosae is cosmopolitan in distribution and follows the world-wide cultivation of the rose (Maelzer 1977). The life history of *M. rosae* has been described in Europe by Börner and Heinz (1957), the population growth and the effects of temperature on natural populations of this aphid have been studied in Germany (Tomiuk and Wöhrmann 1980, 1982) and Schlinger and Hall (1959) studied the effects of introduced parasites on the aphid's abundance in California. In Australia, Maelzer (1977) studied the biology and main causes of changes in numbers of the rose aphid on cultivated roses and the phenology of cultivated roses. Maelzer (*ibid*) suggested that, except in early spring and early autumn, the main factor maintaining the number of rose aphids below the economic injury level was native predators, including the syrphids *Melangyna viridiceps* and *Simosyrphus grandicornis*. However, the numbers of aphids on rose buds are annually so high that rose growers and gardeners use chemicals to contol damage (Kitt 1996).

Many workers (e.g. Wratten 1992; Harwood *et al.* 1992; Cowgill *et. al* 1993a,b; Lövei *et al.* 1993a,b), have suggested that the numbers of aphids in a crop can be decreased by growing certain species of plants, e.g. *Phacelia* sp., whose flowers are especially attractive to syrphids and provide them with pollen and /or nectar to increase their fecundity. The aims of my study, therefore, were:

(1)- to study the changes of numbers of rose aphids and of the two syrphid flies *M. viridiceps* and *S. grandicornis* in different rose gardens in Adelaide.

(2)- to study the changes in the number of eggs laid on buds infested with rose aphids when certain other plants with attractive flowers were added to the rose garden.

9. 2 Materials and Method

The population dynamics of rose aphids and the two syrphids, *M. viridiceps* and *S. grandicornis* were investigated at 4 rose gardens during August 1993 to October 1995. Sample intervals were mostly one week, depending upon the weather conditions and the abundance of aphids. However, in mid-summer and mid-winter, when the numbers of aphids were very low, sample intervals were much longer.

Sampling techniques were developed and used to estimate the following variables at different times of the year:

(i) the mean number of aphids per infested bud ,

(ii) the mean number and percentage of "favourable" buds per plant,

(iii) the mean number of infested buds,

(iv) the mean number of eggs and immature stages of syrphids per infested bud,

(v) the total number of aphids and syrphids per area (at the sites other than the Claremont rose garden, the numbers of aphids and syrphids were calculated for equal to the 70 plants in the Claremont rose garden,

(vi) the numbers of other predators (two coccinellids, *Harmonia conformis* and *Coccinella transversalis* and one hemerobiid *Micromus tasmaniae* (Walker.) and the numbers of adults of the syrphid larval parasitoid, *Diplazon laetatorius* , and

(vii) a cumulative index for both aphids and syrphids at each site per season (Wratten and Lee 1979); see **9. 2. 4**.

9. 2. 1 Sites of study

All the sites of study were located in 3 suburbs of Adelaide; Glen Osmond, Pasadena and Netherby, a maximum distance of 5 km apart, on an undulating plain, with similar weather and soils. Descriptions of the sites of study have been given in Chapter 3.

9. 2. 2 Sampling aphids and syrphids

M. rosae feeds mainly on developing buds and young leaves. The dispersion and density of the aphid on rose plants depends on the distribution of different stages of leaves and flower buds. Maelzer (1976) classified rose buds /shoots from 1 to 10, according to the stage of growth of the terminal flower buds. Aphids mainly feed on buds of stages 1-5 which he called "favourable" buds (Maelzer 1976, 1977) (Fig. 9.1). In this study, the concept of favourable buds was retained, and samples were confined to the universe of favourable buds.

The numbers of aphid predators can usually be estimated in the same place in which their prey occur. Most predators of aphids are highly mobile, except syrphid larvae (Heathcote 1972). Most syrphid flies lay their eggs close to aphids (aphidozetic) and the larvae feed on aphids after hatching, but some species lay eggs on uninfested plants (phytozetic) (see literature review). Preliminary observations have shown that *M. viridiceps* and *S. grandicornis* are aphidozetic species which oviposit close to rose aphids on bud stages 1-5. The third instar larvae may also occur on buds in stages 6-7 but the numbers of such larvae compared with those occuring on stages 1-5 are low. Therefore, the sampling unit used for rose aphids was also used for estimating the numbers of eggs and larvae of the two syrphid flies on roses.

Figure 9. 1: Bud stages of rose buds Rosa sp., variety Tea hybrid "McGreydy's sunset" which are favourable for development of *Macrosiphum rosae* (after Maelzer 1977).

Since the two syrphid flies mostly lay eggs on the buds in the presence of aphids, only the infested buds were sampled and the sample sizes were based on the numbers of aphids. The number of sampling units (infested buds) for each sample depended on the percentage of bud infestation, the number of favourable buds per plant and the distribution of aphids on infested buds.

In the Claremont rose garden, roses were numbered between 1 and 72, and a maximum of 21 plants were randomly selected on each sampling day. One favourable bud (stages 1-5) was then selected from each rose plant, cut off, placed in a plastic bag and the aphids counted later under the microscope. During the first year of sampling (1993-94), the buds were selected randomly by using a wooden frame consisting of two 1.2m panels. Each panel had 11 holes numbered 1-11 with a 10 cm space between successive holes. To select a bud from a plant, the frame was placed around the plant and two holes from two panels were selected at random. Two sticks 1.20 m high with a pointer at the end were then inserted into the selected holes. The intersection of the two pointers selected a random point in 3-dimensional space, and the infested bud which was closest to this point was selected for sampling.

The above method was changed in the second year because it was too time consuming and the apparatus was too difficult to erect. Instead, a number between 10 to 20 (called weekly number) was selected from a random number table for use at all sampling sites in one week. Then at a randomly selected plant, first the buds on the perimeter and then the central buds were counted anti-clockwise until the "weekly number" was reached. The sequential bud corresponding to the "weekly number" was collected if it was infested. Otherwise, counting was repeated but started from another point until an infested bud was encountered.

In each of the other rose gardens, plants were similarly selected at random and 1-2 favourable buds per plant were selected by the anti-clockwise counting method. The selected buds/shoots were sampled destructively when :

(i) in the Claremont and Urrbrae rose gardens, the number of aphids per bud were higher than 50 or when there were many favourable buds,

(ii) in the other rose gardens, the selected buds contained eggs and/or first instar larvae of syrphids which could not be identified by a hand lens.

Otherwise, the numbers of aphids and syrphids were counted *in situ* and the numbers of syrphid eggs and larvae were counted with a hand lens.

For destructive samples, the number of aphids and syrphids on infested buds in the Claremont rose garden were counted in the laboratory. Since the aphids, especially adults and fourth instars, tended to drop from the buds, the infested shoots were cut into opened plastic bags. A piece of tissue paper was put into each plastic bag to absorb water and prevent aphids being squashed. From each bud, the aphids were gently brushed down on to a white plate to check the syrphid eggs and larvae which might otherwise be overlooked. Then the bud was examined with a x3 hand lens for eggs and larvae of syrphids. The aphids were collected by a fine brush and poured into 50% alcohol. If the number of aphids was less than about 100, the numbers of different instars were counted in a petri dish under a stereo-microscope. Otherwise, the sample was counted by means of a counting grid or disk (Southwood 1978; Heathcote 1972). The eggs and first instar larvae of *M. viridiceps* and *S. grandicornis* were identified (see **9. 2. 3**).

A ranking procedure was used in other rose gardens to estimate the number of aphids, in which each colony of aphids was allocated to one of 10 size categories. This procedure ranks colonies as very small, small, medium and large, and further classifies them according to their occurrence on either bud stages 1-2 or 3-4 (Table 9. 1) (Maelzer 1976). The numbers of aphids in very small and small colonies were counted *in situ* on infested buds. But counting aphids in medium and large colonies is time-consuming, so Maelzer suggested 4 linear regression equations for estimating the numbers of aphids in medium and large colonies. The ranking method is quick, non-destructive, has a low cost in time and effort, and makes easier the population study of rose aphids. However, it should be checked repeatedly to avoid misclassification (Maelzer 1976).

To check Maelzer's (*ibid*) regression estimates, the actual number of aphids on each of 20 infested shoots with large colonies and 20 with medium colonies were counted in the laboratory at the beginning of each spring in 1993 and 1994. The estimated numbers from Maelzer's regressions were 10 and 17% higher than the real numbers. Therefore, all data obtained by the ranking procedure were converted to real data by using a correction factor.

The total number of eggs and larvae of syrphids were also counted, but each bud which contained egg(s) or the first instar larva(e) was put in a separate vial and brought to the laboratory for identification. The second and third instars of two species could be easily identified in the field.

Table 9.1: Regression equations of the relationship between the lengths of colonies and the number of aphids on different bud stages (Maelzer 1976).

	Size of Colonies	
Bud stage	**large colonies**	**intermediate colonies**
1-2	$\hat{Y} = 166.3 + 63x^{*}$	$\hat{Y} = 18.2 + 28.2x$
3-4	$\hat{Y} = 49.3 + 56.3x^{**}$	$\hat{Y} = 42.5 + 31.1x$

*x = length of colony in cm.

** the length of colonies on stages 3-4 measured from the base of the bud proper backwards down the stem.

9. 2. 3 Identification of the eggs and the first instar larvae

The colours and sizes of the eggs of *M. viridiceps* and *S. grandicornis* are similar, and identifying either species by eye or with a low magnification lens is difficult. The eggs of both species are white when they are laid and become dark grey before hatching. The mean lengths and mean widths of their eggs are not significantly different (Table 9. 2).

Table 9. 2: Comparison between the sizes of eggs of *M. viridiceps* and *S. grandicornis*.

Species	n	*M. viridiceps*	*S. grandicornis*	t value (p)
width (mm)±Sd	20	0.275±0.02	0.285±0.16	-0.5 (0.62)
width (mm)±Sd	15	0.801±0.057	0.781±0.033	1.26 (0.22)

The patterning of the chorion refers to the surface appearance of the intact eggs under low magnification; sculpturing is the structure of the chorion when the chorion is removed and examined under higher magnification (Chandler 1968e). Although I could distinguish the species of the intact eggs under a binocular microscope (x63), electron microscopic photographs (x1000 and x2350) of the chorion of both species were prepared to show not only the distance between rows but also the shape of outgrowths (Fig. 9. 2). In addition, the sculptures are usually different on the dorsal and ventral surfaces (Chandler 1968e) so the dorsal sculpturing were used for identification of eggs.

Both species have distinguishable patterning. *M. viridiceps* has shorter and denser outgrowth sculptures and the distances between longitudinal rows of *S. grandicornis* eggs are greater than those of *M. viridiceps*.

The larvae of the two species at the second and third instars were identified by x3 lens or by eye in the field. Those of *M. viridiceps* have a paired posterior respiratory process which is prominent on the second instar and is very conspicuous on the third instar larva. In contrast, the larva of *S. grandicornis* has a posterior respiratory process which is very short, or absent.

The length and colour of setae on the body of the first instar larvae were used to identify the first instar larvae of the two species. The setae on the body of the first instar larvae of *S. grandicornis* are dark and longer whereas *M. viridiceps* is less setaceous, and the setae are white.

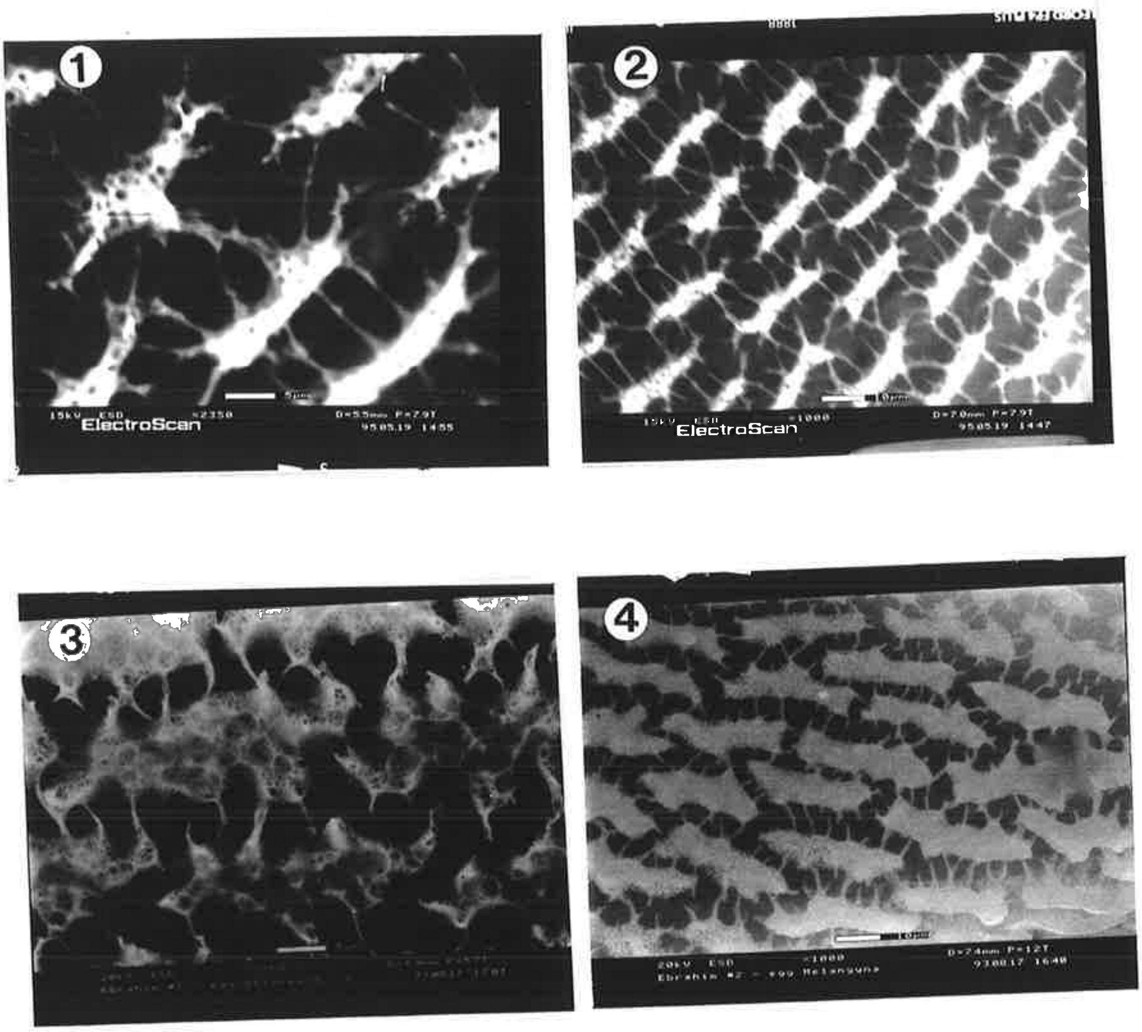

Figure 9. 2: Surface sculpturing of eggs of *M. viridiceps* and *S. grandicornis*

1, 2) *S. grandicornis*; 1, x2350; 2, x1000

3, 4) *M. viridiceps*; 3, 2350; 4, x1000.

9. 2. 4 Numbers of aphids and syrphids converted to indices

To obtain an index of aphids for each site per season, the mean numbers of aphids per infested shoot (bud) on each sampling occasion were converted to aphid-days (Wratten and Lee 1979) and denoted as the index :

$(t_n)(X_n + X_{n+1})$; n = 1,k-1 ; where :

X_n = mean number of aphids per infested bud on the nth. sampling day,

Xn+1 = mean number of aphids per infested bud on the (n+1)th. sampling day,

t_n = the number of days between the nth. and the (n+1)th. sampling days,

k = number of occasions (sampling days) on which aphids were counted.

However, the aphid index was not obtained by giving different weights to different stages of aphids, as was done by Wratten and Lee (*ibid*), but simply by multiplying (numbers of aphids) by (time in days). This simpler index allowed a similar index to be calculated for syrphids on each sampling day by, similarly, simply multiplying (the total number of immature stages of syrphids per infested bud) by (the number of days since the last sampling day). A weighted index along the lines of that used by Wratten and Lee (*ibid*) would have necessitated including an estimate of the number of syrphid adults.

The aphid indices were further used to calculate cumulative indices for aphids, denoted as C_A, and calculated by the following formula (Wratten and Lee 1979):

$$C_A = \sum_{n=1}^{k-1} \frac{t_n(x_n + x_{n+1})}{2}$$

A similar index, denoted as C_S, was calculated for syrphids with the same formula.

Rose aphids are mostly abundant during spring and autumn. Thus, the indices were calculated from late August to the end of November for spring, and from the beginning of February to the end of May for autumn. Then, the syrphid-aphid ratio, denoted as R, was calculated for each site during spring or autumn by the formula:

$$R = \frac{C_S}{C_A} \times 1000$$

where,

C_A=the cumulative index of aphids in aphid-days

C_S=the cumulative index of syrphids in syrphid-days.

Notice that R is really the number of syrphids per 1000 aphids.

9. 3 Results

9. 3. 1 Sampling precision

Table 9. 3 shows the means and ranges of the number of samples and the coefficient of variation (cv) calculated for each rose garden during two different years of sampling. Detailed data for each sampling occasion and the cv values are given in appendices 1-5. In 1993-94, the values of cv were lower in the Claremont rose garden than in the Urrbrae garden but were lowest at Mercedes College. The cv values for syrphids were higher than those for aphids because the densities of eggs and larvae were lower. The cv values were highest for *M. viridiceps* whose eggs and larvae were relatively scarce, patchily distributed and relatively infrequent.

The numbers of samples required were initially calculated by the formula $N = (\frac{S}{D\overline{X}})^2$ (Southwood 1978) with an accuracy (D) of 0.20 and the standard deviation of previous sampling. But the number so estimated was too high to be practicable and fewer samples, with a lower accuracy, had to be taken in this study because :

(1) the number of favourable buds per plant was relatively small, especially in the beginning of spring and autumn. In 1993-94, the plants were fairly young and the number of samples taken never exceeded 21 with a mean of 11.26. In 1994-95 the number of samples increased to 25 with a mean of 14.72 (Table 9. 3).

(2) when the percentage of infestation was low, only small numbers of buds or colonies could be taken without seriously influencing the numbers of aphids in the population, e.g., in the last week of November 1993, only 2.3% of buds were infested, and

Table 9. 3. The mean number of samples (of suitable rose buds) and its range, in brackets; and the mean and coefficient of variation (with its range in brackets) of: aphids, and of the syrphids *S.grandicornis* and *M. viridiceps* , at different sites of sampling in 1993/95.

Sites	Mean no. of suitable rose buds	Mean no. of aphids	Aphids CV	Mean no. of *S. grandicornis*	*S. grandicornis* CV	Mean no. of *M. viridiceps*	*M. viridiceps*
Claremont 1993-94	11.26 (3-21)	58.02±59.56	92.46 (9.24-166.76)	0.48±0.69	188.5 (70.00-460.00)	0.07±0.15	260.38 (57.45-362.5)
Claremont 1994-95	15 (2-25)	71.33±111.4	96.98 (43.69-171.49)	0.38±0.71	205.61 (61.82-390.80)	0.03±0.09	347.17 (274.17-371.43)
Urrbrae house 1993-94	20.27 (5-34)	112.13±101.9	127.98 (34.31-351.13)	0.56±0.59	237.10 (26.92-633.33)	0.03±0.09	298.62 (174.29-448.33)
Centennial park 1994-95	17.48 (6-29)	25.42±27.93	124.57 (64.75-215.52)	0.12±0.19	311.56 (122.95-500)		–
Mercedes Col. 1994-95	19.7 (2-40)	93.40±110.50	91.36 (20.57-172.92)	0.16±0.36	262.96 (172.41-460)	0.03±0.07	457.5 (437.50-460)

there were only 13 infested buds in the field of which 3 were selected as samples. The low percentage of infestation and the high mean number of favourable buds sometimes made sampling time consuming. For example, in the second week of November 1994, with the infestation of 8% and the mean number of 18.38 buds per plant (total of 1268 buds) (Appendix 9. 2) only 2 infested buds were found during the course of sampling.

(3) the distribution of buds on plants was not homogenous because different rose varieties were planted in the rose garden. On some occasions, many bushes had no buds while a few had more than 20 buds. With these restrictions, the number of samples per plant was usually 1-2 and the total number of buds sampled was sometimes less than 10.

9. 3. 2 Seasonal occurrence of syrphids and aphids

As similar trends in numbers of aphids and syrphids were observed in all the rose gardens in each of the two years, the seasonal occurrence of aphids and syrphids at the Claremont rose garden will be described as representative of all sites. Details of the numbers in the other rose gardens are given in appendices 9. 1 to 9. 5. The combined results will be discussed later.

The two-weekly mean numbers of aphids and syrphids at the Claremont rose garden during 1993-95 are shown in Fig. 9.3, and the total numbers are shown in Fig. 9.4. In the spring of 1993, aphids appeared about the second-half of August and peaked in the second-half of September. In the spring of 1994, they similarly started in late August but peaked during the first half of October.

In 1993-94, after the spring peak, aphid numbers declined to near zero in December 93 and January 94 and aphids were seen only occasionally until mid-February 1994. During this period, the density of aphids did not exceed 20 aphids per infested shoot. The highest total number of aphids in the Claremont rose garden was 28 in December 1993 and 692 in the second half of January 1994. These low numbers were due to the small number of favourable buds and the low percentage of infestation of such buds (Fig. 9. 4 and Fig. 9. 3C). Although a higher density of aphids (97.5) was recorded in the first half of February 94, the

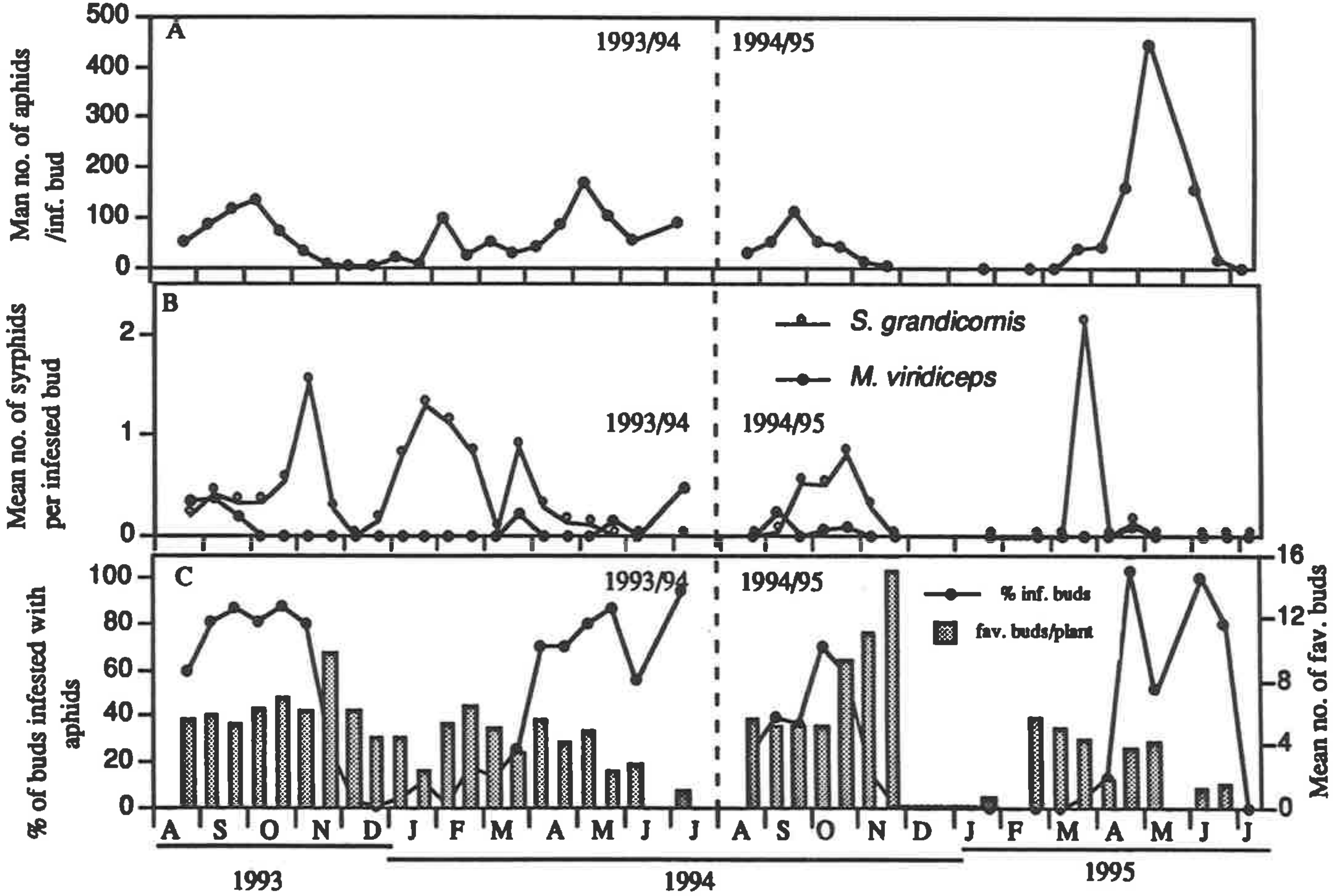

Fig. 9. 3: Claremont rose garden: Mean number of aphids (A) and syrphids (B) during 1993-1995. Fig C shows the mean number of favourable buds and the mean percentage of infestation of such buds

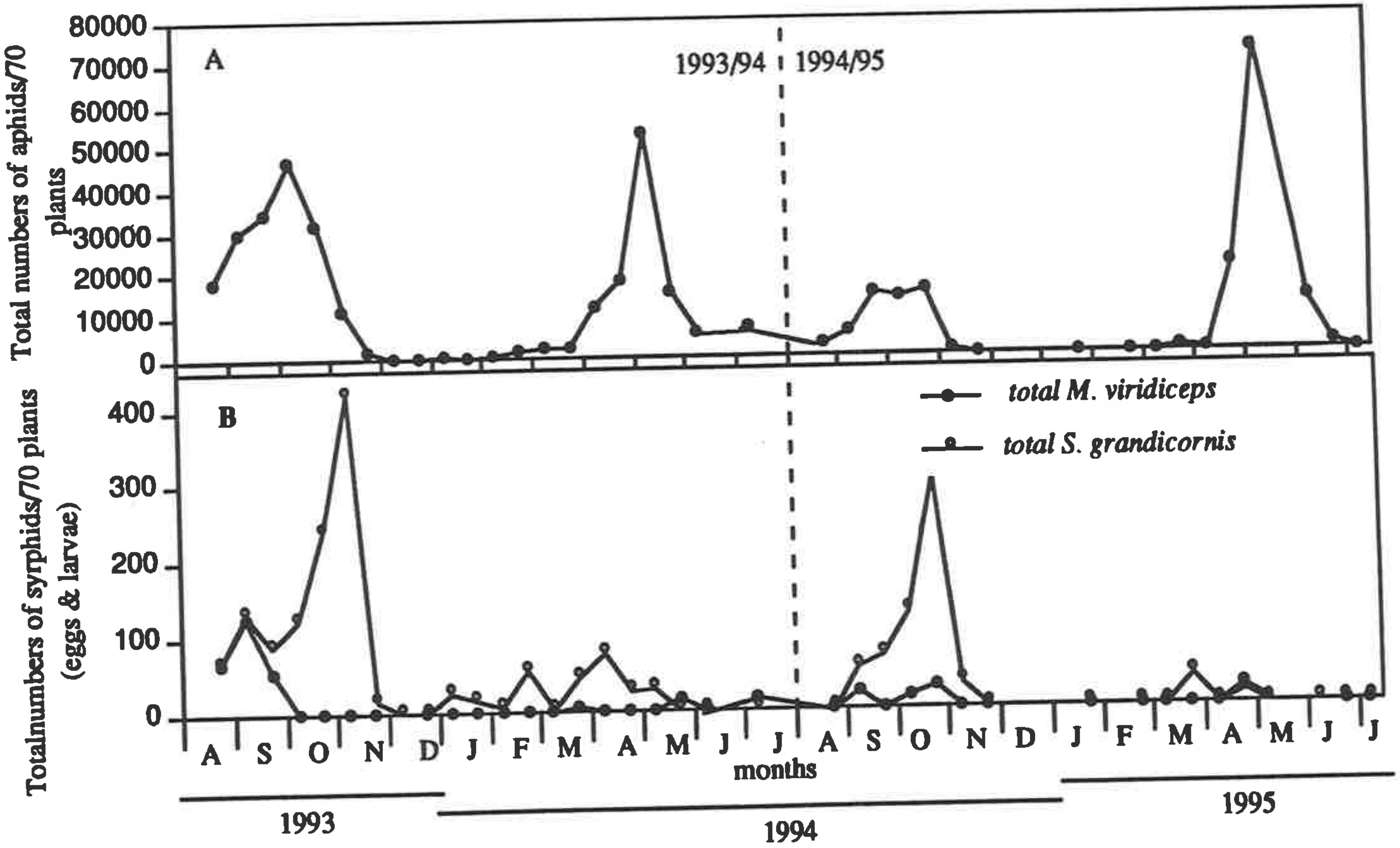

Fig 9. 4: Claremont rose garden:Total number of aphids(A) and syrphids (eggs and larvae)(B) on rose plants at the in each of the year 1993-94 and 1994-95.

total number of aphids did not exceed 688 on all plants. The aphids then increased to a peak in May 1994 (Fig. 9.3A, 9.4A).

Both the mean density of aphids and the total number of aphids were higher in autumn (March-May) than in spring (Sept.-Nov.) in both : 1993/94 and 1994/95 (Fig. 9.3A, 9.4A). In both years, the population of aphids started to increase from the first-half of February and reached a peak in autumn of 169.6 per infested bud in 1993-94 and a peak of 445.8 in 1994-95. The total number of aphids at the peak in autumn was 52893 (per 70 plants) in 1993-94, and71802 in 1994-95. The numbers then declined to zero or near zero in the winter (July-August) of each year (Fig. 9.3A, 9.4A).

The numbers of syrphids fluctuated more than the numbers of aphids. *M. viridiceps* started activity earlier than *S. grandicornis* on roses (Appendix 9. 1 and 9. 2). However, both species were observed from the second half of August in both years (Fig. 9. 3B, 9.4B). Eggs of *M. viridiceps* were observed from the second half of August to the second half of September and also during the second half of May and June 1993-94. However, in 1994-95, no *M. viridiceps* immature stages were observed in June 1995 and 0.08 eggs and larvae were recorded in the second half of April instead of the second-half of May. The density of eggs and larvae of this species never exceeded 0.5 per infested bud in the first-half of July (Fig. 9.3A; 9.4A).

S. grandicornis was obviously more abundant than *M. viridiceps*. (Fig. 9.3B; 9.4B). In 1993-94, the immature stages of this species were observed on roses from the second-half of August 1993 to the second-half of May 1994. The peak of the spring population of *S. grandicornis* occurred in the first-half of November 1993 when it reached 1.5 per infested bud and a total of 417 per 70 plants in the Claremont rose garden. The population declined following a decrease in the aphid population and dropped to 0.25 per infested bud in the second-half of November 1993. From December 1993 to mid-March 1994, the percentage of infestation of buds by aphids was low (Fig. 9.3C) and the density of *S. grandicornis* per infested buds was high (Fig. 9.3B). However, compared to the spring population, the total numbers of eggs and larvae were low and reached a peak of only 75 per 70 plants in the first-half of April (Fig. 9.4B). The peak in numbers in the autumn of 1993-94 occurred before the peak of aphids (Fig 9. 3A, B; Fig. 9.4A, B).

Similar peaks in the density and total numbers of *S. grandicornis* occurred in the spring and autumn of 1994-95 (Fig.9.3B, 9.4B), but the population was very low from November 1994 to March 1995 during which period the numbers of aphids were also very low (Fig. 9.3C).

Trends in the numbers of aphids and of the two species of syrphids in the other 3 rose gardens were similar to those described above for the Claremont garden ; so, general trends in the numbers of aphids and syrphids were obtained by averaging the weekly data in all four rose gardens. The resultant trends are shown in Fig. 9.5A, 9.5B. Also shown, in Fig.9C, are the mean numbers of adults of *M. viridiceps* per day per trap for each month which were obtained from the data in Chapter 4.

Seasonal characteristics of the syrphid and aphid populations in Adelaide (Fig. 9. 5) can now be explained as follows:

(1) There are two main peaks in aphid numbers which occur in spring and autumn. The peak in autumn is usually higher than that in spring (Fig. 9.5A).

(2) The number of aphids are not detectable on roses in June and July because of the pruning of old shoots or unsuitability of the host plants. However, a small number of aphids may live on old leaves. For example, 154.7 and 16.4 aphids per infested bud were recorded in the first and second-half of June 1995.

(3) The aphid populations on roses start to grow in August, after the arrival of alate adults. The time at which the infestation starts in this month depends on the local temperature and the amount of new growth of roses.

(4) Although the aphids are usually in very low numbers in December because of the high summer temperatures (Maelzer 1977), some aphids live for a short time on favourable buds. But a bud matures and becomes unfavourable for aphids very rapidly at

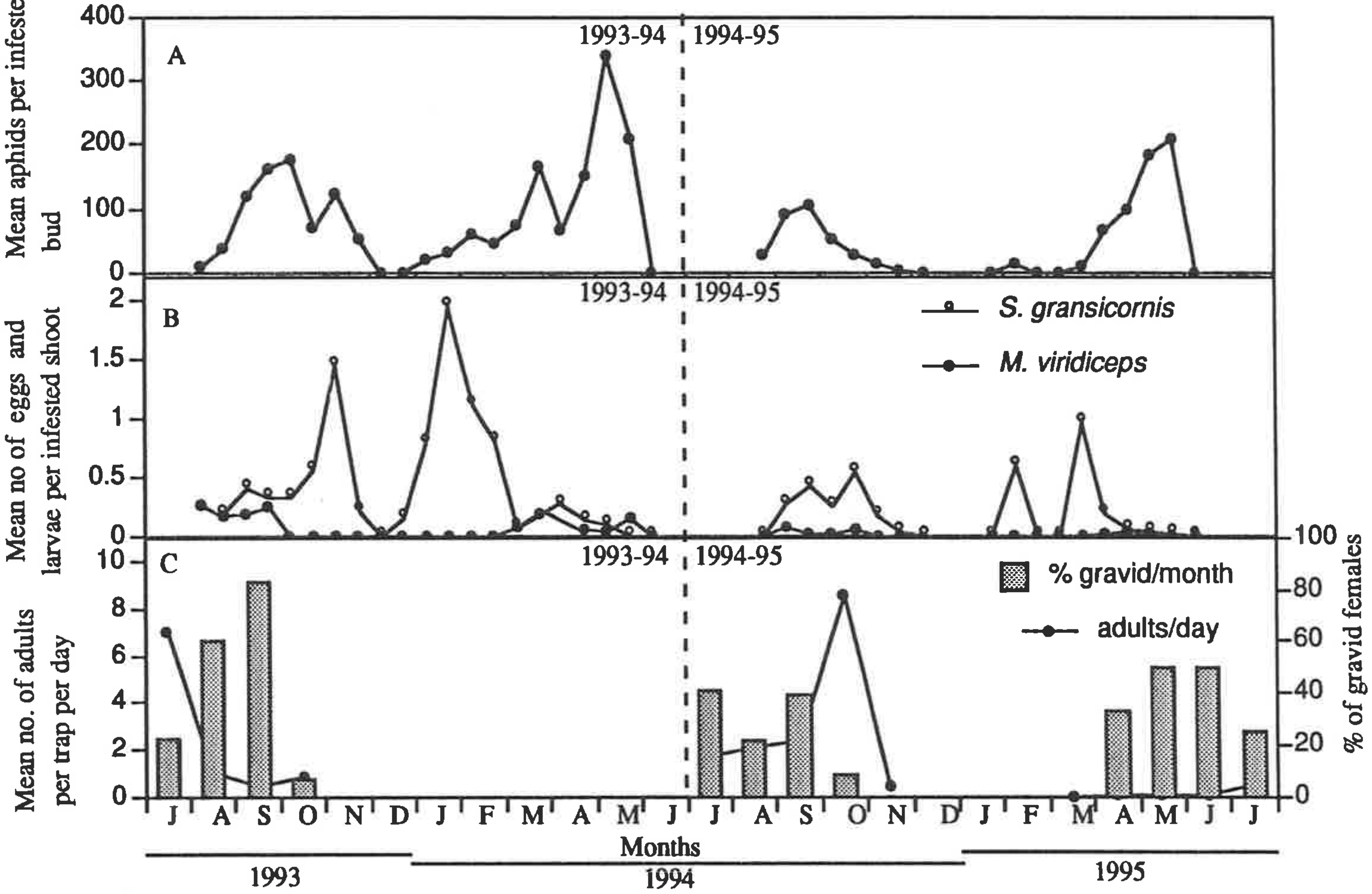

Fig.9. 5: All sites combined; A, the mean number of aphids per infested shoot; B, the mean number of eggs and larvae of *M. viridiceps* and *S. grandicornis* per infested shoot; C, the mean number of adults of *M. viridiceps* per day per trap and the percentage of females with eggs (% gravid females)

high temperatures; so there is little time for aphids to increase in numbers on such buds and, consequently, the mean number of aphids per infested bud and the percentage of infested buds are low (Maelzer 1977) (Fig. 9.3C, 9.5A).

(5) The numbers of *M. viridiceps* per infested bud are much lower than those of *S. grandicornis* on roses. The adults of the former species are active from April to October in Adelaide. However, only small number of immature stages per infested bud were recorded in April and May, and August to October (Fig. 9.5B).

(6) *S. grandicornis* adults lay eggs on roses from August to March or April, although flight activity was observed during the whole year except in June and July. When the mean number of aphids per infested bud declined during summer time, the mean number per bud of immature stages of this species increased (Fig.9.5A,B). By contrast, as the mean number of aphids per bud increases to the autumn peak, the mean number of syrphid eggs and larvae per bud decreases (Fig. 9.5A,B). However, a similar pattern of increasing aphid numbers and simultaneously decreasing syrphid numbers is not evident in spring each year (Fig. 9.5A, 9.5B).

9. 3. 3 Syrphid-aphid ratios

The indices in aphid-days and syrphid-days for each site during spring and autumn are given in Table 9. 4, and the ratios of the mean number of syrphids per 1000 aphids in each rose garden are given in Table 9. 5. The nature of the syrphid-aphid ratios does not allow statistical comparisons of the ratios between syrphid species or seasons or rose gardens. As a rough rule of thumb, a difference of 50% will be considered to be significant. On this basis the following conclusions can be suggested.

In 1993-94, when sampling was confined to the Urrbrae and Claremont rose gardens, the ratios of syrphids per 1000 aphids for *S. grandicornis* in both rose gardens were higher than those for *M.viridiceps* in both spring and autumn (Table 9. 5). The ratios for *S. grandicornis* were similar within each of the gardens in spring and autumn; but the ratios in Claremont were higher than those in Urrbrae in both seasons.

The ratios for *M.viridiceps* within seasons and within gardens were similar except for the ratio in Claremont in spring which was higher than the others.

In 1994-95, the syrphid-aphid ratios of *S. grandicornis* in each of 3 rose gardens were again higher than those of *M.viridiceps* in both spring 1994 and autumn 1995 (Table 9.5). Moreover, in spring 1994, the ratios of both species of syrphids to aphids were higher in Claremont than in the other two gardens (Table 9.5). In contrast, very low ratios for *M. viridiceps* were calculated for Claremont in autumn 1995 and for Mercedes College in both seasons. No *M. viridiceps* were observed at Centennial Park (Table 9. 5).

Generally, the ratios of eggs and larvae of *M. viridiceps* to the number of aphids were smaller than those of *S. grandicornis* and the ratios for both syrphid species were higher in the Claremont rose garden than in the other gardens.

The syrphid-aphid ratios for *S. grandicornis* for each week can further be used to examine the role of the syrphid species in the population dynamics of the rose aphid during the weeks in which some syrphid eggs and larvae were recorded on the buds. The relationship between the mean numbers of aphids per infested bud and the syrphid-aphid ratios is shown in Fig. 9. 6. The horizontal line represents the Economic Injury Threshold (EIT) which according to Maelzer (personal communication) is about 50 aphids per infested bud. Of 75 week-sites data obtained from all sample sites during the study, 35 week-sites had fewer aphids than the EIT (50) and 40 week-sites had equal or more aphids than the EIT. The numbers of week-sites above and below the EIT were not different significantly ($\chi^2 = 0.33; p = 0.56$).

The numbers of weeks with aphid numbers either higher or lower than the EIT are shown for each rose garden in Fig. 9.7. These numbers have been given only for *S. grandicornis*. In the Claremont garden there was obviously no difference between the number of weeks with aphid numbers higher or lower than the EIT. In the Urbrrae garden, there were more weeks

Table 9. 4 : The cumulative aphid and syrphid indices (see text for explanation) during spring and autumn of 1993-95 in different rose gardens.

seasons and years	**sites**	**aphid index**	**syrphids index**	
			M. viridiceps	*S. grandicornis*
	Claremont			
Spring 93		7056	9.45	41.73
Autumn 94		9036	2.8	49.38
Spring 94		4079	5.57	38.52
Autumn 95		11072	1.28	25.34
	Urrbrae			
Spring 93		14865	6.06	38.58
Autumn 94		8938	2.70	30.9
	Centennial			
spring 94		14845	0.00	15.96
autumn 95		3272	0.00	9.39
	Mercedes College			
Spring 94		6865	0.95	15.38
Autumn 95		10322	0.86	16.56

Table 9. 5: Syrphid - 1000 aphids ratios for the two syrphid species, *S. grandicornis* and *M. viridiceps* , in 3 different rose gardens in spring and autumn of each of the years 1993-94 and 1994-95.

	S. grandicornis				*M. viridiceps*			
	Claremont	Urrbrae	Mercedes College	Centennial Park	Claremont	Urrbrae	Mercedes College	Centennial Park
Spring 1993	5.94	2.60			1.34	0.41		
Autumn 1994	5.46	3.46			0.31	0.30		
Spring 1994	9.44		2.24		1.37		0.14	0
Autumn 1995	2.29		1.60		0.12		0.08	0

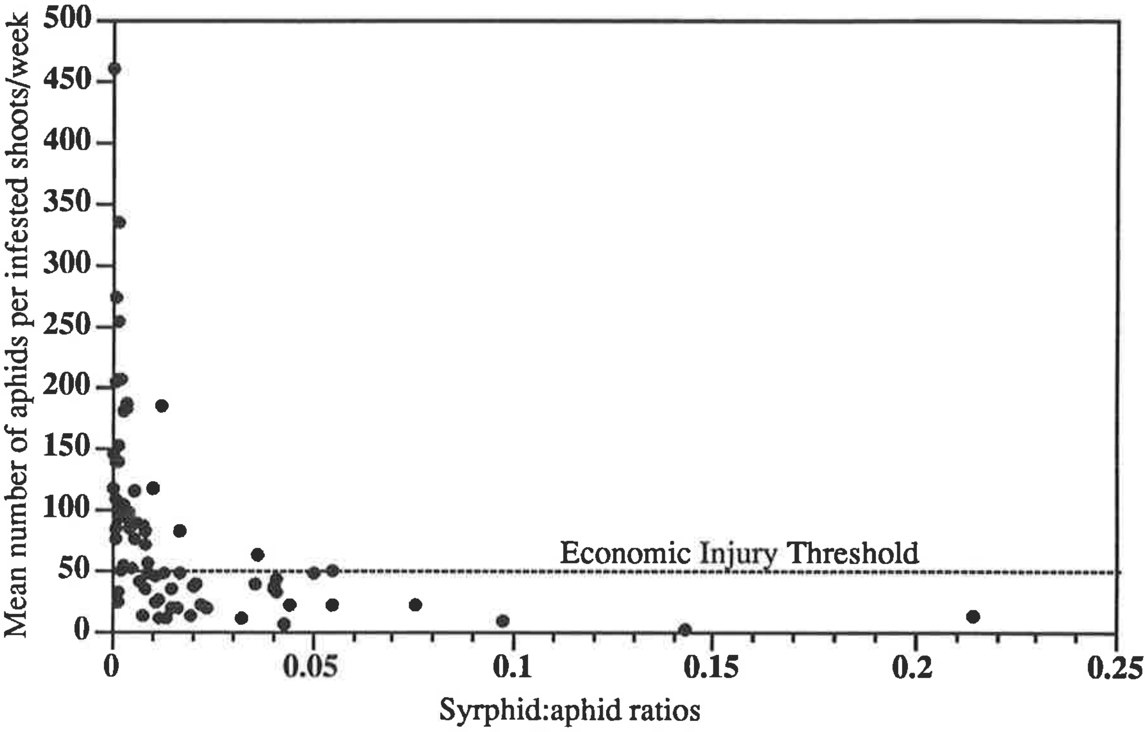

Fig. 9. 6: The relationship between the mean number of aphids per infested bud and the ratios of syrphids per 1000 aphids for *S. grandicornis* for each week during which eggs and larvae of the syrphid were found. Data of all sampling sites obtained during the two year study have been combined (n=75).

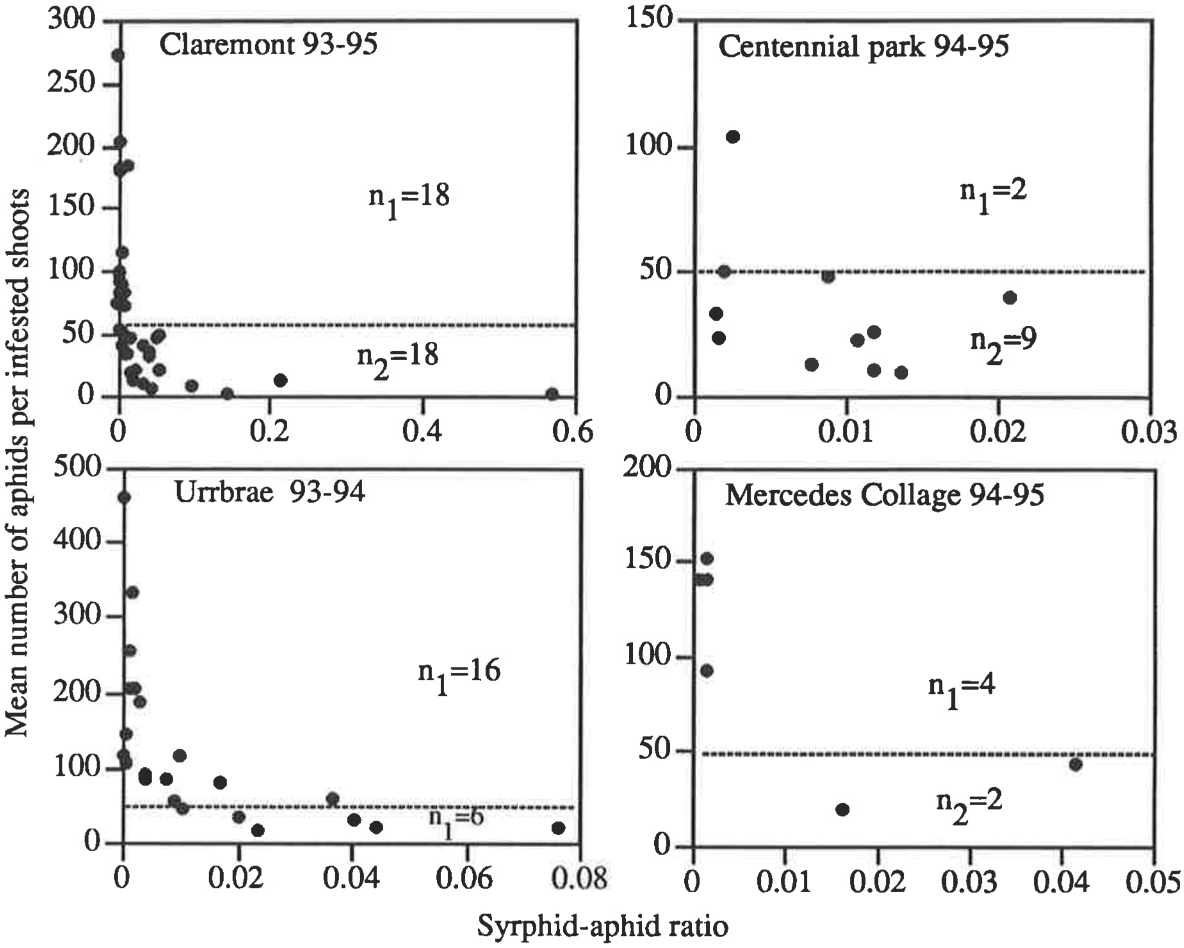

Fig. 9. 7: Relationship between the mean number of aphids per infested bud and the syrphid-aphid ratios for *S. grandicornis* to 1000 aphids in different rose gardens. The Claremont rose garden was provided with additional flowers which were attractive to hoverflies. The horizontal lines represent the proposed economic injury threshold (EIT) for rose aphids. The numbers of weeks with aphid numbers either higher (n_1) or lower (n_2) than EIT are also given.

with aphid numbers higher than the EIT than there were weeks below it ($\chi^2 = 4.56$; $p < 0.05$). In Centennial Park and Mercedes College the numbers of weeks were too small to compare.

9. 3. 4 Other predators

Table 9.6 shows the total numbers of other aphidophagous predators in different rose gardens on each occasion of sampling. The numbers of the syrphid parasitoid, *Diplazon laetatorius* are also shown in the last column. The brown lacewing *Micromus tasmaniae*, was the most abundant predator. The numbers of immature stages of this species reached a peak of 10 per sample in the Claremont rose garden. The ladybird *Harmonia conformis* was also recorded in spring and autumn.

9. 4 Discussion

The main causes of changes in numbers of rose aphids in South Australia are discussed in detail in Maelzer (1977). He (*ibid*) observed three peaks of aphids in spring-summer, with a major peak in September-October followed by two smaller peaks in December and in January-February - and another small peak in autumn. However, I observed only two peaks in each year, one in September-November and another in April-May (Fig. 9.3A, 9.4A, 9.5A). The autumn peak was higher than the spring peak (Fig. 9.3A, 9.4A, 9.5A), whereas Maelzer's data (*ibid*) showed a lower peak in autumn. The differences between the two studies are probably due to variations in weather (e.g., temperature, rain), ages of the plants, and irrigation practices which influenced the relative numbers of favourable buds and the rate of increase of the aphid population.

Maelzer (1977) ranked the native predator species in the following order of decreasing effectiveness : *Micromus tasmaniae*, *Melangyna viridiceps; Harmonia conformis*, *S. grandicornis*, and *Coccinella transversalis*. The two syrphid species *M. viridiceps and S. grandicornis* are respectively indigenous and native species in Australia (Vockeroth 1969; Maelzer 1976, 1977; Carver 1989).

Table 9.6: The numbers of other aphidophagous predators and of the parasitoid of syrphid larvae (*Diplazon laetatorius*) recorded on infested buds at different sites in 1993-95. The numbers in brackets represent the immature stages (eggs and larvae) and those without brackets show the numbers of adults.

	Dates	sample size	*Chrysopa sp.*	*Micromus tasmaniae*	*Harmonia conformis*	*Coccinella transversalis*	*Diplazon laetatorius*
Claremont	06/09/93	15		(6)	2		
	13/09/93	11		(1)			
	25/10/93	10		(10)			
	01/11/95	10		(4)			
	04/05/94	16		(2)			
	17/04/94	13		(4)			
	25/04/94	14		(2)	3		
	13/05/94	18		(2)			
	23/05/94	16		(1)			
	08/07/94	13		(4)			
	10/10/94	20		(4)			
	23/04/95	12			(1)		1
	02/05/95	23			2		1
	21/05/95	18					2
Urrbrae House	23/01/94	25		0(1)			
	30/01/94	19		0(1)			
	20/02/94	28		0(3)			
	14/03/94	29	1	(1)	1		
	27/03/94	25	2	(6)	2	1(1)	2
	17/04/94	15	3	(1)	2(1)	1	
Mercedes College	04/09/94	13		(6)			
	16/10/94	19			1(5)		

Carver (personal comm.) used these terms to distinguish between species that are restricted to Australia (indigenous), and those that are naturally occurring in Australasian in distribution (native). Both these syrphid species are mentioned as predators of aphids in various studies on the ecology and biology of aphids in Australia (Minko 1961; Hales and

Carver 1976; Maelzer 1976, 1977; Mohammad 1979; Hussein 1982; Crawford 1983; Carver and Woolcock 1986; and Völkl 1990). Furthermore, Carver (personal comm.) records that the two species prey on about one-third of the total number of aphid species occuring in Australia, but the voracity of the two species on aphids and how much they have diversified their diet to include exotic aphids are not recorded. Maelzer (1977) attributes the typical decrease in the number of rose aphids after the second peak in November to predation by *Melangyna viridiceps* and *Harmonia conformis*.

The role of *M. viridiceps*

Synchronisation between a predator and its prey is an important factor that influences the population of the prey. The adults of *M. viridiceps* start to lay eggs on roses around mid-August, depending on daily temperature. The eggs can be found during September and October and also in March, April and May in Adelaide. These periods synchronise with the peaks of aphids in South Australia (Carver 1989). However, when between 21.4 and 50% of female *M. viridiceps* were gravid in June, July and the beginning of August (Fig. 9.5C), roses had not started to grow so there were no suitable buds (Fig. 9.3C), and hence, no aphids occurred on rose plants (Figs. 9.3A, 9.4A, and 9.5A). Furthermore, not only the rose aphids but also other species of aphids are rare during winter because of low temperatures which are a limiting factor for the growth of aphid populations (Maelzer 1981). Therefore, there is no synchrony between the winter population of *M. viridiceps* and populations of aphids in general and, in particular, those of rose aphids. Additionally, when the high percentage of female *M. viridiceps* were gravid and the roses had neither buds nor aphids (Figs. 9.5C, 9.3C, 9.3A), 20% of marguerite daisy shoots were infested with *Macrosiphum euphorbiae* at a density of 150 aphids per infested bud. But no eggs were observed on the infested daisy shoots although adults of *M. viridiceps* were observed alighting on infested daisy shoots and perhaps feeding on daisy pollen or on the honeydew of *M. euphorbiae*.

At other times, when rose aphid numbers were high and adults of *M. viridiceps* were also high, the number of eggs recorded on roses were low, indicating that even when rose aphids are available they are rarely chosen as hosts. For example, in the Claremont rose garden which was provided with additional attractive flowers, the maximum ratios of *M. viridiceps* per 1000 aphids were in spring, 1993 and in spring, 1994 (Table 9.5) and were only 1.34 and 1.37 respectively. The ratios never exceeded 0.41 in other rose gardens, even in spring (Table 9.5). At Centennial Park, no eggs of *M. viridiceps* were recorded even when 80% of buds were infested with aphids at densities up to about 100 aphids per infested buds (Appendix 9. 5).

Even with the maximum ratio (1.2) of *M. viridiceps* per 1000 aphids, the numbers of *M. viridiceps* were not sufficient to cuase a decline in the number of aphids on roses. In the laboratory, one larva of *M. viridiceps* ate about 300 medium size aphids (third instar) at 20° C. (syrphid per 1000 aphid ratio=3.33) (Chapter 8) which is 2.54 times more than the maximum ratio in the field. However, the estimation of consumption rates from laboratory data may overestimate the influence of predators in the field especially when adjacent plants in a row do not touch (Tenhumberg and Poheling 1995) and also when favourable shoots for aphids are isolated as with rose buds on rose bushes.

Similarly, no eggs or larvae of *M. viridiceps* were found in occasional samples of other plant species infested with other species of aphids during autumn and winter. For example, on 9/11/1993, when many adults were flying in an area of about 1000m^2 in Lenswood (40km from Adelaide), there were no eggs or larvae on 20 shoots of dockweed (*Rumex* sp.) which were highly infested with the aphid, *Aulacorthum solani* (Kaltenbach). Again, on 5/5/1993, in the same area, no eggs and larvae were observed on leaves of peach trees infested with *Myzus persicae* (Sulzer) at a mean density of 3.6 aphids per infested shoot. And on 24/4/94 and 12/5/94, there were no eggs and larvae of *M. viridiceps* on or near colonies of the cabbage aphid, *Brevicoryne brassicae*, on 25 randomly selected infested leaves of rapeseed planted at Lenswood.

The above observations are not consistent with Maelzer's opinion (Maelzer 1977) about the importance of *M. viridiceps* as a first ranked efficient predator of *M. rosae* in South Australia. Rather they suggest that *M. viridiceps* is neither a frequent nor an efficient predator of aphids, and that it is probably restricted mostly to prey species on native Australian trees, such as psyllids. Thus, Morgan (1984) indicates that *M. viridiceps* preys on the psyllid, *Cardiaspina retator*(Taylor.) on *Eucalyptus* trees, and was confirmed during this study using two samples of *Eucalyptus camaldulensis* (red gum) infested with the psyllid. In the first sample, on 2/11/1993, 10 eggs of *M. viridiceps* were found on 20 infested shoots (mean psyllid/ infested shoot=21.5, SE=3.8). In the second sample, on 10/7/94, 8 eggs were found on 35 shoots (mean psyllid/ infested shoot=11.4, SE=5.6). In another sample, on 11/6/94, no eggs were found on 22 infested shoots (mean psyllids/ inf. shoot=21, SE=4.69), but one egg of *M. viridiceps* was found on leaves. Carver (1989; personal comm. 1996) thinks that the original and preferred hosts of *M. viridiceps* are native Coccoidea and Psylloidea, of which Australia has a very rich fauna.

The inability of *M. viridiceps* to utilise available aphid hosts may be explained by the fact that only 135 of the 4000 described aphid species of the world are known to occur in Australia (Dixon *et al.* 1987; Maelzer 1981), and only about 20 of the 135 are indigenous (exclusively Australian) and a similar number are native species (Australasian in distribution). The Australian environment is not suitable for the radiation of aphid species (Hales 1976; Maelzer 1981) and the great majority of aphids in Australia are introduced, mostly from Europe. (Maelzer 1981). So an abundance of exotic aphids on introduced host plants have been available to this syrphid species for only a relatively short period since the migration of Europeans to Australia.

By contrast, in the northern hemisphere, predatory Syrphiniae have changed their feeding habits during evolution (Rotheray and Gilbert 1989). The genera of the Syrphinae in the Northern Hemisphere gradually have shifted from other feeding habits (detritus feeding or more likely leaf-litter arthropods feeding) to aphid feeding, and then they have narrowed their diverse range of aphid prey to fewer aphid species (Rotheray and Gilbert 1989).

There is a negative correlation between specialisation and the abundance of the syrphid species (Rotheray and Gilbert 1989). The larvae of generalists are characterised by having simple colour patterns. The larvae of *M. viridiceps* has simple patterns consistent with a lack of feeding specialisation and it has extended its feeding habits to embrace exotic aphids and has been recorded feeding on 33 different aphid species in Australia (Carver; personal communication 1996).

In conclusion, the results from the present study indicate that

(1) *M. viridiceps* is not mainly aphidophagous and it lays eggs on aphid- infested plants only facultatively, and

(2) *M. viridiceps* is not an efficient predator of rose aphids, as suggested by Maelzer (1977).

The role of *S. grandicornis*

The flight activity of *S. grandicornis* occurs from August to May (Chapter 4). Females start to lay eggs on roses from August about the same time as *M. viridiceps*. This period coincides with very low numbers of adults seeking pollen on attractive flowers (Chapter 4). As spring progresses, adult activity increases with temperature. The changes in the total numbers of immature *S. grandicornis* on infested buds in all rose gardens were similar in spring, summer and autumn during the 2 years of study and are probably representative of Adelaide and perhaps other parts of south-eastern Australia with a Mediterranean type climate. The changes in the mean density per infested bud were more complicated and will be discussed separately.

The total numbers of immature stages of *S. grandicornis* and of aphids in the Claremont garden are given in Fig. 9.4B, 9.4A. The peak in total numbers of *S. grandicornis* in spring each year in relation to the peak in total numbers of aphids showed the typical lag found in classical predator-prey interactions, with a peak in predator numbers occurring later than that of the prey (e.g. Frazer and Gilbert 1976; Niemczyk and Pruska 1986). But in autumn, there was no corresponding synchrony between the peak number of *S. grandicornis* and the peak number of aphids. The autumn peak of *S. grandicornis* in April 1994 occurred when the numbers of aphids were relatively low, and it occurred 3 to 4 weeks before the aphid peak (Fig. 9.4B, 9.4A). The numbers of *S. grandicornis* then decreased as aphid numbers increased; and when aphid numbers peaked in May, syrphid numbers were very low. A similar but more spectacular sequence occurred in autumn 1994-95 with the peak in total syrphid numbers occurring 6-8 weeks before the peak in total aphid numbers (Fig. 9.4B, 9.4A) and syrphid numbers were near zero at the time of the peak in total aphid numbers. In addition, the peak numbers of *S. grandicornis* in autumn were much lower than in spring, as is also shown by the srphid-aphid ratios in Table 5. It seems unlikely that the difference in the predator-prey interaction in the two seasons can be due to differential effects of differing temperatures at the two relevant times. It is more probable that high percentage of parasitism by *D. laetatorious* is the main reason for both the smaller peak in numbers of *S. grandicornis* in autumn and also the decrease in its numbers before the peak of aphids (see also Chapter 10).

The trends in the mean numbers of aphids and *S. grandicornis* per infested bud show the same relation between the peaks in spring and autumn as do the peaks in total numbers, in both the Claremont garden (Fig. 9.3A, 9.3B) and in the averages for all 4 gardens (Fig. 9.5A, 9.5B). However, the mean numbers of *S. grandicornis* showed another peak in January-February 1994-95 (Fig. 9.3B, 9.5B). At this time (mid summer), daily temperatures are very high and aphid numbers are very low because of a complex of factors, namely:

*the low number of favourable buds (Fig. 9.3C) and the relatively short time that a bud remains favourable for aphid increase (Maelzer 1977),

* the heavily mortality suffered by the aphid population when aphids walk off host plants and do not return (Maelzer 1981); and

* pressure of predation by *S. grandicornis*, which is illustrated by syrphid-aphid ratios at this time being the highest recorded during the study (Table 9. 7); and by data from some single buds showing very high numbers of immature stages of *S. grandicornis*

on buds with relatively few aphids (Table 9. 7). One egg and one larva were even seen on a bud with no aphids. At this time of the year, intermediate aphid colonies may be found on a few favourable buds, but the high syrphid numbers probably cause the extinction of aphids on many buds.
The same summer pattern of relatively high syrphid numbers associated with low aphid numbers was seen again in February 1995 in the mean data for all 4 gardens (Fig.9.5B, 9.4A); and again, the syrphid-aphid ratios (Table 9. 5) were higher than any recorded during spring or autumn. However, the pattern described above was not seen again in the Claremont garden (Fig. 9.5B, 9.5A) because of the zero or near zero numbers of favourable buds for many weeks in December 1994 to February 1995 (Fig. 9.3C), and consequently zero or near zero aphids and syrphids as well (Fig. 9.3A, 9.3B).

In contrast to *M. viridiceps,* the larvae of *S. grandicornis* commonly also feed on other aphid species during summer, including *M. euphorbiae* on roses, and *Hyperomyzus lactucae* on buds of *Sonchus oleraceus*, which is common around Adelaide. In rose gardens, some *S. oleraceus* grow under the shade of trees during summer and the eggs of *S. grandicornis* were laid in the presence of this aphid on the buds of *S. oleraceus*. In addition, few eggs were observed on small colonies of *Aphis gossypii* on roses in summer. But I did not find any eggs or larvae amongst colonies of *Aphis gossypii* on *Hibiscus rosa-sinensis* (Malvaceae) although the aphid has been recorded as a host of *S. grandicornis* on *Hibiscus* (Carver 1996). I did not find any on 4 infested shrubs during summer and autumn, 1993-1995.

Like *M.viridiceps, S. grandicornis* is a native species of Australia which has been recorded as preying upon 33 exotic and 5 indigenous and native species of aphids (Carver; personal comm.) ; and Maelzer (1977) ranked it fourth in effectiveness (after *M. viridiceps*) as a predator of *M. rosae* on roses in South Australia. However, its synchrony with *M. rosae* in spring, the higher numbers of eggs and larvae on buds infested with rose aphids,

Table 9. 7: The relation, during summer, between the mean numbers per infested bud of *M. rosae* and of *S. grandicornis* : the numbers on some single buds in the Claremont and Urrbrae rose gardens; and syrphid-1000 aphid ratios on individual sampling dates over all sites combined.

dates	sites	no. aphids/single bud	% infested buds	*S. grandicornis.* per bud
26/12/93	Claremont	25	4	1 eggs
"	"	47	4	3 "
"	"	0	4	1 "
31/1/94	Claremont	14	2.6	3 "
6/2/94	Claremont	26	2.5	3 "
27/2/94	Claremont	0	2	1 larva
12/2/95	Urbrrae	200	2	17 eggs and 4 larvae

and the pressure on the summer population of aphids on roses make *S. grandicornis* a much more effective predator than *M. viridiceps*. Although, the numbers of adults in spring are smaller than those of *M. viridiceps* (Chapter 4), more eggs were laid on roses infested by aphids (Fig. 9.3B, 9.4B). In addition, the more consistent association of eggs and larvae of *S. grandicornis* with other aphid species indicates that this species is more aphidophagous than *M. viridiceps*. Therefore, it seems that at least under the condition of the study, *S. grandicornis* was a more efficient biological control agent of aphids than *M. viridiceps* in South Australia. However, the number of eggs laid on roses by *S. grandicornis* compared with the number of aphids may not be enough to control rose aphids under the Economic Injury Threshold (EIT).

The ratio of the numbers of a predator to the numbers of the prey may be reasonably used to decide whether prey numbers can be kept under the EIT. The ratio of immature stages of *S. grandicornis* to 1000 aphids on roses did not exceed 2.9 in spring and autumn in those rose gardens which were not provided with attractive flowers (Table 9.5). When the ratio was at

2.9, the mean numbers of aphids per infested bud (at Centennial Park) was 83, which is higher than the EIT.

In the Claremont rose garden, which was provided with attractive flowers, the maximum syrphid-aphid ratio in spring or autumn was 9.4 and the number of aphids per infested bud reached 180, which is much higher than EIT. The same results were obtained when the weekly infestation was compared with the EIT. Even in the Claremont rose garden with attractive flowers and higher syrphid-aphid ratios, the number of weeks with the density of aphids lower than EIT was the same as those with the density of aphids higher than EIT. Thus, although I increased the numbers of *S. grandicornis* by providing additional attractive flowers, the number of aphids did not decrease to less than the EIT in spring and autumn. The only times at which the syrphid-1000 aphid ratios may have been high enough to control aphid numbers below the EIT were in summer, and then predation by syrphids was only one of a complex of variables preventing aphid increase.

Chapter 10

Natural enemies

10. 1 Introduction

The accurate measurement of insect mortality caused by parasites is of great importance to biological control, ecology, and allied fields (Day 1994). The parameter 'percent parasitism' has commonly been the measure used to present mortality by the attack of parasitoids (Van Driesche 1983) but the distinction between 'apparent' and 'real' mortality (Southwood 1966) is not often noted. Two methods most frequently used to measure insect mortality by parasites are rearing and dissection. Rearing involves host insects being fed for a sufficient time to allow immature parasites to emerge from their host, followed by maintenance of the parasites until identifiable developmental stages of the natural enemies are produced. Alternatively, dissections of insect hosts, generally under binocular microscope, usually detect parasite eggs and larvae cells, or products (Van Driesche 1983).

Syrphid flies are attacked by a wide range of parasitic Hymenoptera; the most common being Ichneumonidae, Figitidae and Encyrtidae (Rotheray 1981, 1984). The subfamily Diplazontinae of the family Ichneumonidae contains 18 genera, most of which are restricted to the Holarctic region (Gauld and Fitton 1984). *Diplazon laetatorius* is a common cosmopolitan parasitoid of syrphids which occurs in Australia. Although five species of syrphid parasitoids from five genera, *Diplazon, Syrphoctonus,Woldstedtius, Syrphophagus* and *Pachyneuron* occur in Australia, there are few records of the importance of these parasitoids in populations of Australian syrphid flies. Existing host records of syrphid parasitoids suggest that they tend to be polyphagous and only four out of thirteen diplazontines showed any evidence of host preference (Rotheray 1984)

Diplazontinae are particularly harmful to syrphid populations because of their range of syrphid hosts and the marked tendency of older females to devour syrphid eggs and larvae (Rotheray 1981, Gauld and Fitton 1984) in addition to their action as parasitoids.

The behavioural process of a parasitoid wasp is divided into a series of discrete steps consisted of (i) host habitat finding, (ii) host finding, (iii) host acceptance, and (iv) host suitability (Vinson 1976). The responses to aphid odour may enable the location of aphid colonies which are the most likely places to find hosts (Rotheray 1981). However, the number of *D. laetatorius* searching on one aphid species may differ from other aphid species because of the difference in the density of available prey.

The aims of this investigation were:

(1) to identify the syrphid parasitoid fauna of Adelaide regions.

(2) to evaluate the effect of parasitoids on populations of syrphid species on rose buds in South Australia.

(3) to measure the voracity of parasitised syrphid larvae fed on rose aphids in the laboratory.

(4) to compare infested buds with uninfested buds in attracting *D. laetatorius*.

(5) to assess the attractiveness of *D. laetatorius* to different aphid species.

(6) to compare the attractiveness of the parasitoid to rose aphids with and without syrphid larvae.

10. 2 Materials and Method

10. 2. 1 Field study

Samples were collected from seven rose gardens located in Adelaide between October 1993 to March 1994 and from August 1994 to May 1995. In addition to four sample sites which described in chapters 3 and 9, samples were taken from three rose gardens located in Adelaide, Urrbrae High school, Glandore Oval, and South Terrace Park. During 1993-94 all syrphid larvae were reared to adult, but in 1994-95 parasitism was recorded by dissection.

Syrphid larvae were carried to the laboratory in small vials and dissected by a pair of fine forceps under the stereo-microscope in 0.1% methylene blue solution in which white and clear parasitoid eggs and larvae can be easily found.

The number of larvae collected on each occasion depended on the time of the year and the availability of larvae on that occasion; however, the number of *M. viridiceps* larvae on roses was too low on each occasion for useful analysis data (a total of only 21 larvae were collected during two years) but data for *S. grandicornis* were analysed. Numbers of *S. grandicornis* larvae collected on different occasions and sites per month were combined to calculate percent parasitism.

10. 2. 2 Laboratory experiments

10. 2. 2. 1 Voracity and growth of parasitised larvae

First instar larvae of *S. grandicornis* were provided with aphids from the laboratory culture (Chapter 3) and *D. laetatorious* were captured from the field by net sweeping.

Two groups each with 20 first instar larvae of *S. grandicornis* were used in this experiment. In the first group, larvae were offered one by one to the female parasitoid in a 6cm (diam.) x 1.5cm (height) plastic petri-dish. The wasp was removed from the petri-dish after the first sting to prevent super-parasitism and the stung larva was examined for the presence of the parasitoid egg through the larva's transparent cuticle under a stereo-microscope. The stung larvae with no evidence of eggs were removed from the experiment. The second group of larvae were used as a 'control' and reared under the same conditions as in the first group.

The experiment was conducted at 20±1°C and 70% humidity. Other conditions and the method of syrphid rearing are described in Chapter 8.

10. 2. 2. 2 Preference for rose buds infested with aphids

An experiment was conducted in a 2m x 2.5m x 3m glasshouse over a period of 2 days. The temperature ranged from 17 to 28°C and with day light intensities from 4000 to 70000 lux. Eight rose buds (at growth stage 4), four of which were heavily infested with *M. rosae,* were collected from the garden. Each bud was put in a small bottle filled with a 2% solution of "Flower Fresh", (Flower Fresh Products, Australia). The eight bottles were placed on the perimeter of a rotatable table (Chapter 3) spaced at 36 cm intervals and with infested buds alternating with non-infested buds. A 1% solution of honey in water was put in the middle of the table. Thirty parasitoid wasps reared in the laboratory or caught from the field were released in the glasshouse at the middle of the table at 09.00h. on 24 October 1994. The numbers of wasps on buds were recorded on 15 occasions; seven times on the first day and eight times on the second day. Each of the occasions included five counts. Before each count, the wasps alighting on the rose shoots were disturbed to make them leave the shoots and hopefully mix with the other wasps in the glasshouse compartment. 2-3 minutes after the rotation, the observer recorded the number of wasps on each bud.

Light intensity and temperature were also recorded on each occasion. The total numbers on infested versus non-infested buds on 5 rotations were used for the statistical analysis.

10. 2. 2. 3 Attraction of the parasitoid, *D. laetatorius* to different species of aphids

In this experiment three different species of aphids; *Macrosiphum rosae* on rose buds, *Hyperomyzus lactucae* on sowthistle buds and *Brachycaudus helichrysi* (Kaltenbach) on young *Prunus* shoots were placed on the perimeter of the rotatable table, as in experiment 1. Shoots of the same length and with medium infestations of aphids were collected from the field. The experiment was designed as randomised blocks with three treatments and four replicates. A block consisted of three shoots each infested with one of three species of aphids. The spaces between treatments were 18cm and between blocks were 36cm. The number of parasitoids were counted in each rotation and total numbers of wasps in 10 rotations were totalled for the ANOVA. The conditions and method of counting the parasitoids were the same as in the previous experiment.

10. 2. 2. 4 Attractiveness of infested rose buds with and without syrphid larvae

The same experiment as the first one, and under the same condition, was conducted in the glasshouse. Sixteen infested rose buds, each with 70-100 aphids, were divided into two groups. On each of the first 8 buds, two second instar larvae of *S. grandicornis* were placed on the bud in the middle of the colony of aphids (second instar larvae on the second day of life are less active than the third instar and more visible than the first instar). In the second group, the infested buds had no syrphid larvae. The two groups of buds were arranged alternatively on the edge of the round table. Again, 60 wasps were released in the glasshouse and the number of wasps on each bud was recorded on 20 occasions and 5 rotations per occasion.

10. 3 Results

10. 3. 1 Field study

In 1993-94, 308 *D. laetatorius* and 2 *Syrphophagus nigricornis* (Gravenhorst) emerged from 310 parasitised larvae of *S. grandicornis*. Five adults parasitoids which emerged from 21 *M. viridiceps* were *D. laetatorius*. The encyrtid was kindly identified by Mr John Noyes, British Museum and *D. laetatorius* was identified by the key of Gauld and Fitton 1984.

The changes in percent parasitism relative to number of *S. grandicornis* and rose aphids are shown in Fig. 10. 1. Parasitism was lowest in August before the population of *S. grandicornis* started to grow relative to the increase in the number of rose aphids. Then it peaked in March at about 80% and decreased in April, when the number of syrphids per infested bud declined also. The low infestation of rose buds has not been shown by sampling program in four rose gardens during 1994-95 (Fig. 10. 1B), but the syrphid larvae dissected during this period were not part of the regular sampling program and were collected from other rose gardens. The decrease in the number of syrphid larvae prior to the peak in the mean number of aphids in April or May (Chapter 9) coincides with the increase in parasitism by *D. laetatorius* and may indicate a causal relationship.

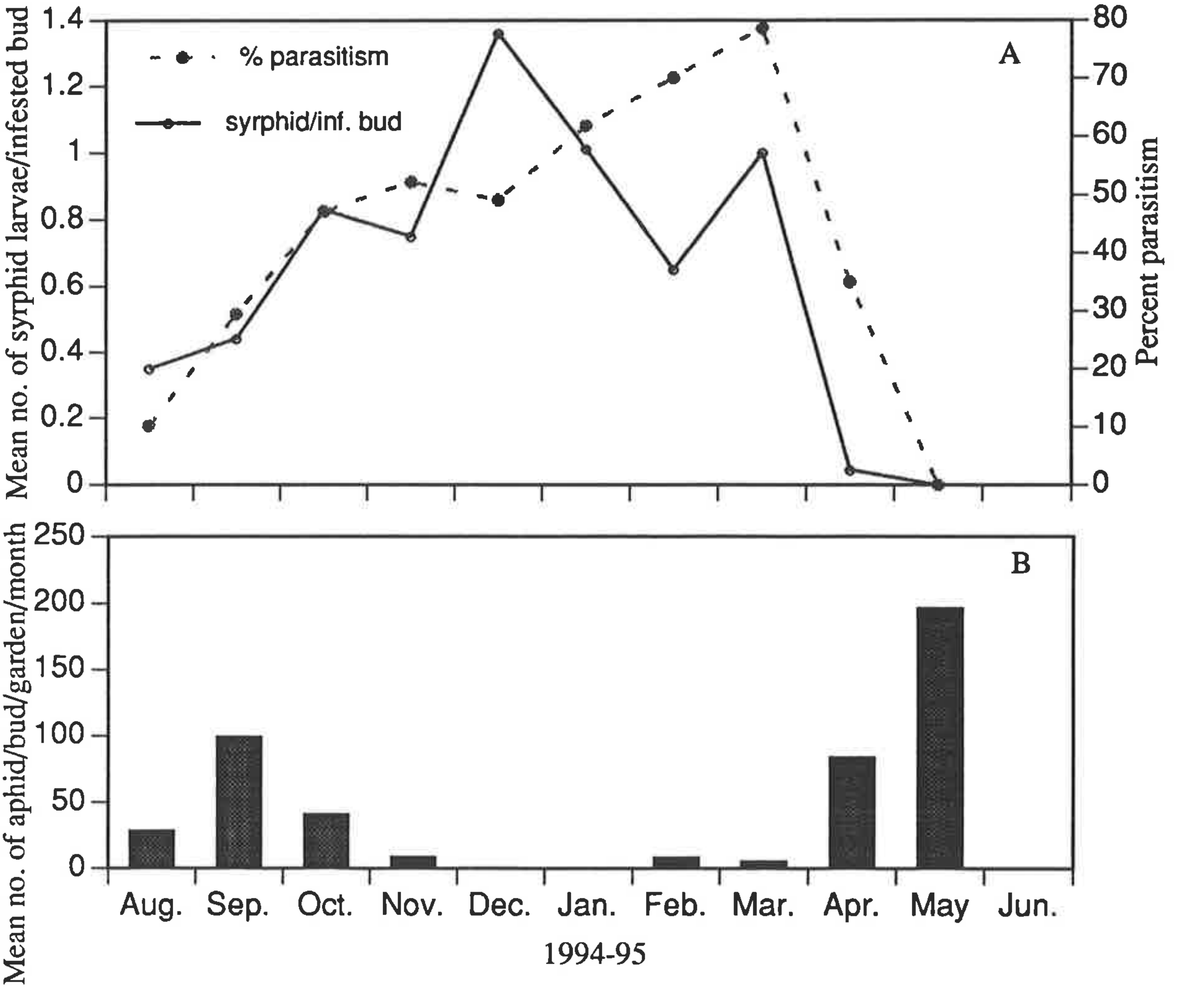

Figure 10. 1: (A). Changes in number of eggs and larvae of *S. grandicornis* /bud, and percent parasitism by *D. laetatorius* on rose gardens in Adelaide in 1994-95 (A). (B) The mean number of aphids/bud/rose garden/month and the mean number of *S. grandicornis* /bud/rose garden/month.

Both the mean numbers of *S. grandicornis* in (A) and the mean numbers of aphids in (B) are taken from Chapter 9.

10. 3. 2 Laboratory study

10. 3. 2. 1 Voracity and growth of parasitised larvae

The cumulative mean numbers of the third instar aphids eaten by parasitised and unparasitised *S. grandicornis* larvae is shown in Fig. 10. 2. Both parasitised and unparasitised larvae pupated after 10 days, but the parasitised larvae consumed significantly fewer aphids (parasitised and unparasitised larvae consumed 189.4 and 229.1 aphids respectively (x^2=3.76, p=0.05) (Fig. 10. 2). Similar numbers of aphids were consumed by parasitised and unparasitised larvae until the 7th day of development. Then the number of aphids consumed by the parasitised larvae increased less than unparasitised control.

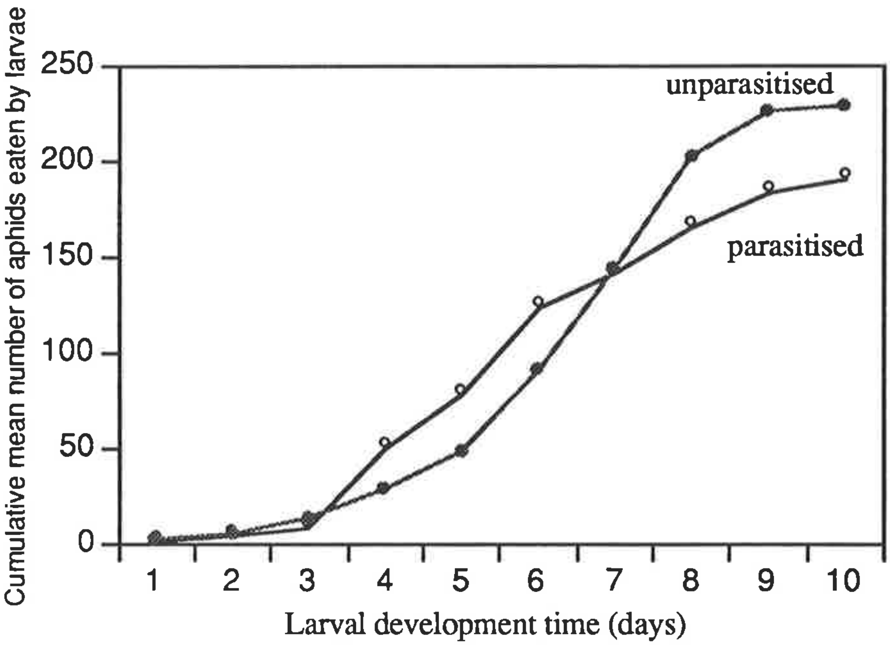

Figure 10. 2: Cumulative mean number of third instar aphids consumed by parasitised and unparasitised larvae of *S. grandicornis* at 20°C.

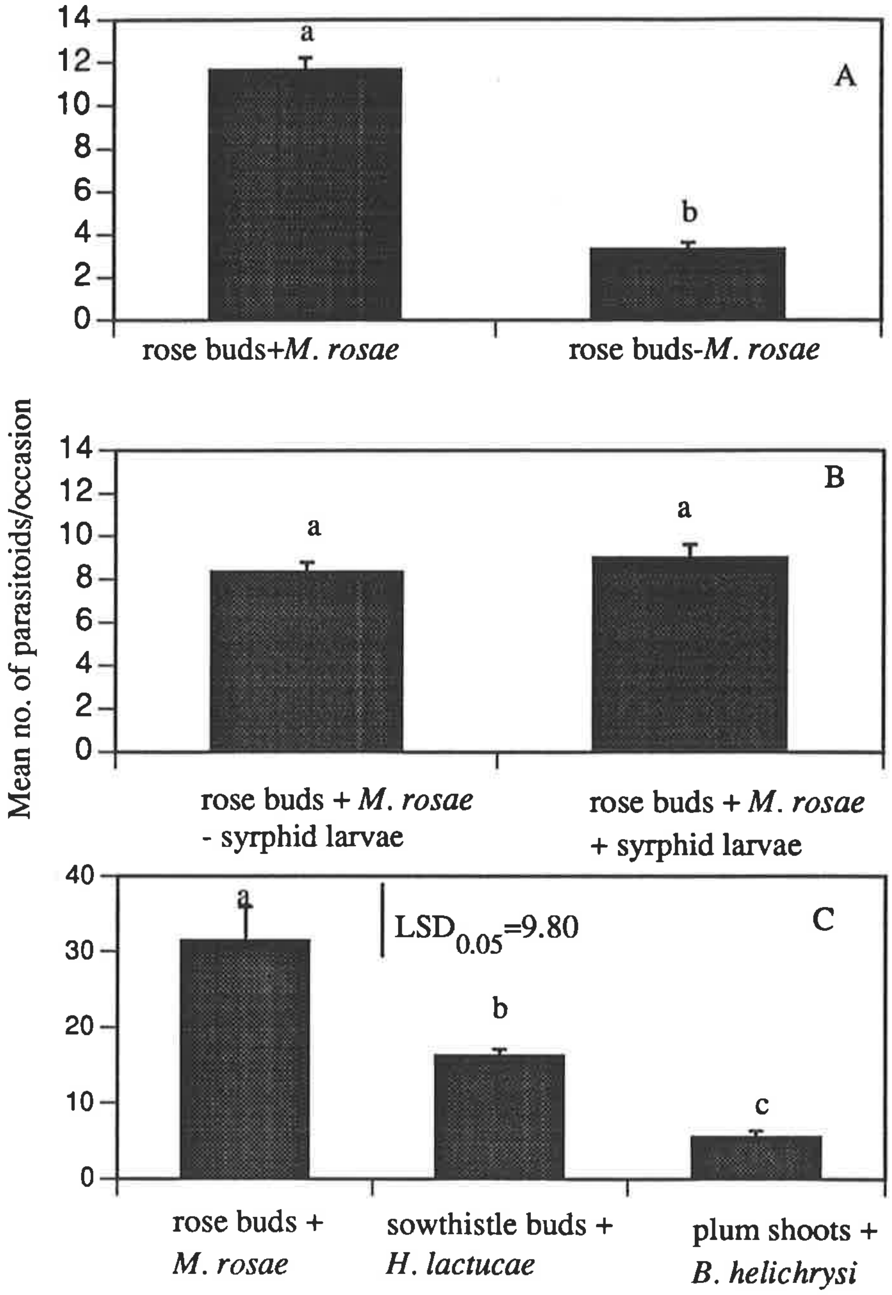

Figure 10. 3: (A) Mean numbers of the parasitoid, *D. laetatorius* alighting on rose buds, infested and uninfested with *M. rosae*, (B): comparison between the numbers of *D. laetatorius* on rose buds infested with *M. rosae* with and without syrphid larvae, (C): numbers of parasitoids on shoots infested with different aphids. Vertical bars show standard errors of the means.

1 0. 3. 2. 2 Attractiveness of infested buds with and without syrphid larvae

The total number of wasps on buds infested with rose aphids was significantly higher than on uninfested buds (p=0.001, df=28, t=13.12) (Fig.10.3 A), indicating an attraction to rose aphids. Parasitoids were not attracted by the presence of syrphid larvae, since no differences were detected between the numbers of wasps on infested buds with and without syrphid larvae (t=-0.85, df=38, p=0.4,) (10.3 B). The parasites showed a preference between aphid species; of the three types of buds and aphids presented to *D. laetatorius* the highest number was attracted to infested rose buds and the number of parasitoids attracted to sowthistle buds infested with *Hyperomyzus lactucae* was higher than those on young *Prunus* shoots infested with *Brachycaudus* sp. (Fig 10. 3 C). An ANOVA indicated that the differences between aphid species were highly significant (F=21.28, p= 0.002, $LSD_{0.05}$=9.80).

10. 3. 2. 3 Other natural enemies

In addition to *D. laetatorius* and *S. nigricornis* which were parasitoids of larvae, a nematode species parasitising adults was also recorded during this study. During dissection of adults (Chapter 6) two out of 105 *S. grandicornis* were infested with this nematode. However, no nematodes were seen in dissections of 305 *M. viridiceps*. This suggests that the infection rate by nematodes is naturally low. Samples were identified by Dr. Kerrie A. Davies, Department of Crop Protection, Waite Institute as *Syrphonema sp.* (Davies and Lloyd 1996).

Adult hoverflies may also be attacked by flower spiders. I observed a flower-spider, *Diaea* sp (Thomisidae) attacking adult *M. viridiceps* feeding on marguerite daisy, but no attempt has been made to obtain data on spider predation during this study.

10. 4 Discussion

Two parasitoid species emerged from *M. viridiceps* and *S. grandicornis* pupae; an ichneumonid, *D. laetatorius* (99.4% of parasitised larvae) and a polyembryonic encyrtid, *Symosyrphus nigricornis* (G) (0.6% of parasitised larvae). These data were collected only from Adelaide rose gardens. and it may be that levels of parasitism varied with host plants, since it was shown that *D. laetatorius* preferred to land on infested roses compared to other infested plants.

S. grandicornis are heavily parasitised by the originally holarctic, now almost cosmopolitan ichneumonid, *Diplazon laetatorius* which, in Australia, is thelytokous (Carver pers. communication). Like the introduction of aphids to Australia (Maelzer 1976, Carver 1989), the present distribution of *D. laetatorius* is a result of human activity (Gauld and Fitton 1984). The importance of *Diplazon* spp. (Diplazontinae) in suppressing populations of syrphids has been reported in some parts of the world; Patel and Patel (1969) and Rao and Salyanarayana (1981) from India; Barabas, L. (1981) from Slovakia; Krotova (1993) from Russia. *D. laetatorius* overwinters as adults in South Australia. It seems that they are less active in winter than spring, summer and autumn.

While parasitoids of some phytophagous insects which are attracted to a kairomone produced by the feeding activity of the host larvae (Nealis 1986) the parasitoid of syrphids appear to be attracted to aphids not to its direct host. Since greater numbers of *D. laetatorius* were attracted to rose shoots infested with aphids than uninfested shoots, while no differences were detected between infested shoots with syrphid larvae and infested shoots without larvae. This result confirms Rotheray's (1981) conclusion that syrphid parasitoids search aphid colonies. It is possible that some parasitoids respond to aphids as a source of adult food rather than as a potential site for hosts (Rotheray 1984). Some female syrphid parasitoids are even reported to respond to aphid odours which bring them to the region of an aphid colony (Rotheray 1979).

Different species of parasitoids vary in their pattern of resource exploitation. *D. laetatorius* feeds on honeydew of aphids, but some aphid species are more attractive to the parasitoid than others. Rose aphids on rose shoots attracted the highest numbers of *D. laetatorius* and *Brachycaudus helichrysi* attracted the lowest number. Field observations confirmed that *Prunus* trees highly infested with *Brachycaudus helichrysi* (Kaltenbach.) did not attract the parasitoid and no eggs of syrphids were found on the colonies of this aphid species. In contrast, sowthistle aphids often occur on sowthistle near rose gardens and *S. grandicornis* lays eggs on colonies of this species in summer when the population of rose aphids decreases.

This aphid is also attractive to, so sowthistles may be an oversummering site for both *S. grandicornis* and *D. laetatorius*. Since the parasitoid responds variously to different aphid species so the syrphid effect may change according to aphid species. In other words, adult syrphids and the *D. laetatorius* appear to use the same cues in habitat selection and host location.

Although parasitation of the first instar larvae of *S. grandicornis* reduces the voracity of unparasitised up to 17.3 %, the main influence of the parasitoid on populations of *S. grandicornis* is on the next generations when it drastically reduces the population of syrphids.

Chapter 11

Summary and Discussion

The aims of the research undertaken for this thesis were to:

(1) observe the influence of the two common syrphid species on populations of rose aphids in rose gardens in Adelaide,

(2) measure the effect of providing attractive flowers on the suppressive effect of syrphids on rose aphids,

(3) observe some ecological and biological aspects of the two syrphid species in a Mediterranean climate.

The results of the research are summarised as follows:

Seasonal occurrence of adult hoverflies

The flight activity of adult *M. viridiceps* in Adelaide increases in autumn (April), peaks in late winter (July and August) and is much reduced in December. *S. grandicornis* adults increase activity in spring (August) and continue activity until late autumn. Adults of both species are probably present throughout the year, but in low numbers during some months (4. 3. 2).

M. viridiceps is a cold-loving and *S. grandicornis* is a warm loving species. However, *M. viridiceps* probably oversummers as adults and *S. grandicornis* overwinters as adults (4. 3. 2 and 4. 3. 3).

Mark-recapture studies of *M. viridiceps* indicate that this species is highly mobile with respect to the 1.5 ha study area (4. 3. 5).

Diurnal flight activity of *M. viridiceps* and *S. grandicornis*

1- In winter, the flight activity threshold of *M. viridiceps* was 13°C and activity around African daisy started about two hours after sunrise (0900 CST), peaked mostly around five hours after sunrise (1200CST) and declined rapidly in the afternoon (5. 3. 1. 1 and 5. 3. 1. 2).

2- In summer, when both species were present, adult *M. viridiceps* started activity earlier than *S. grandicornis* in the morning. During the day, both species were active around weeds. Later in the day, *M. viridiceps* moved to marguerite daisy but *S. grandicornis* remained on weeds (5. 3. 2. 1).

3- In summer both species moved to shady areas, apparently to avoid the direct effects of the sun(5. 3. 2. 2).

Pollen and flower selectivity by *Melangyna viridiceps* and *Simosyrphus grandicornis*

1- In the laboratory, both species were attracted to yellow colour, while in the field, yellow and white flowers were the most visited ones (6. 3. 1).

2- Both species selected flowers from herbs, shrub and tree strata. *M. viridiceps* preferred pollen from herbs while *S. grandicornis* was highly attracted to wild radish (*Raphanus raphanistrum*), and *Eucalyptus* and *Acacia* trees in flowers (6. 3. 2). A maximum of six pollen types was found in specimens dissected. However, females had more pollen types in their guts than did males (6. 3. 3).

3- Both species fed from African and marguerite daisies. These were not the top-ranking plants as hoverfly food sources, but their growth characteristics make them useful plants for that purpose (6. 3. 2. 2).

4- *M. viridiceps* mostly feeds on pollen whereas *S. grandicornis* feeds on nectar and honeydew. No difference was found between the amounts of gut-pollen content of males and females of either species. (6. 3. 3).

Oviposition of adults and feeding behaviour of larvae

1- The pre-oviposition period is 4-11 and 3-9 days for *M. viridiceps* and *S. grandicornis*, respectively. The longest oviposition periods of females were 26 and 22 days, and the highest numbers of eggs laid were 476 and 407 eggs for *M. viridiceps* and *S. grandicornis* respectively. The mean longevity of females was 32.9 days for *M. viridiceps* and 19.9 for *S. grandicornis* (7. 3. 1).

2- In the laboratory, the number of eggs laid by *S. grandicornis* increased with aphid density up to 100/bud, and then decreased. The largest numbers of eggs were laid on buds with 71-100 aphids/infested bud. *S. grandicornis* laid fewer eggs on buds with exuviae than those without exuviae (7. 3. 2. 1).

3- In the field, both species laid eggs singly on infested buds. No relationship was found between the number of aphids per bud and the number of *S. grandicornis* eggs per bud on different sampling occasions. Eggs were laid with equal frequency on buds with aphid densities above and below the mean number of aphid per infested bud (MNAI). However, once a bud was selected, females laid more eggs on buds which were infested with numbers of aphids higher than the MNAI (7. 3. 2. 2).

4- Small larvae of both syrphid species tend to capture small-sized aphids while large larvae (2nd and 3rd instars) tend to capture medium-sized and large aphids (7. 3. 2).

5- The first instar larvae of *M. viridiceps* may shift to phytophagy if starved of aphids longer than 5-6 hours (7. 4. 3).

Temperature-dependent development in eggs, larvae and pupae of *M. viridiceps* and *S. grandicornis* and the voracity of larvae in the laboratory

1- *M. viridiceps* larvae consumed 351.5, 310 and 296.1 third instar equivalents (TIEs) of rose aphids at 10°C, 15°C and 20°C respectively and *S. grandicornis* larvae ate 373.4, 357.5 and 224.3 TIEs (8. 3. 1).

2- 89.1% and 80.5% of aphids were consumed during the third larval instar of *M. viridiceps* and *S. grandicornis* respectively, which accounted for 55.5 and 56.7% of the total larval development time at 20°C. *S. grandicornis* required fewer aphids for a weight gain of one milligram. (8. 3. 1).

3- By using records of daily maximum-minimum temperatures and data on development at different temperatures as inputs in computer simulation models, it was estimated that a maximum of 11-13 and 10 generations of *M. virdiceps* and *S. grandicornis* respectively, were possible. However, the number of generations is likely to be reduced if prey is in short supply, or if quiescence or aestivation occur in one of more stages.

Seasonal occurrence of immature stages of *M. viridiceps* and *S. grandicornis* and their synchronisation with rose aphids

1- Both *M. viridiceps* and rose aphids had population peaks in spring and autumn but the absolute numbers of eggs and larvae of *M. viridiceps* were low, even at their peaks (9. 3. 2).

2- The spring and autumn ratio of *M. viridiceps* egg to aphids was higher in the rose garden with attractive flowers than in those without flowers.

3- When high percentages of female *M. viridiceps* were gravid in the field in late winter, roses were still dormant and aphid populations had not started to increase (9. 3. 2).

4- *S. grandicornis* laid more eggs than did *M. viridiceps* on roses during spring to late autumn. The egg:aphid ratio of *S. grandicornis* was mostly greater in the garden with attractive flowers than in gardens without flowers (9. 3. 3).

5- No functional response by *S. grandicornis* to increasing aphid density could be demonstrated; the peak number of immature stages of *S. grandicornis* occurred before the peak of rose aphids in autumn (9. 3. 3).

Natural enemies

The ichneumonid *Diplazon laetatorius* was reared from both species of hoverflies. It is probable that the parasitisation rates of up to 80% in autumn could be a major factor in preventing *S. grandicornis* controlling autumn populations of rose aphids.

Discussion

M. viridiceps is indigenous (restricted to Australia) and *S. grandicornis* is native to Australia (naturally occurring in Australia but also occurs elsewhere) (Carver 1996 personal communication). At least one of the two syrphid species is active in South Australia throughout the year, in contrast to species in some temperate parts of Europe which are active during spring to autumn. *M. viridiceps* is a cold-loving species which was not detected during the heat of summer to early autumn, while *S. grandicornis* is active during this period. In contrast, the latter was not detected in late autumn and winter when *M. viridiceps* is active. In addition, the activities of both species overlap in spring and autumn coinciding with the spring and autumn peaks of aphids in South Australia (Carver 1989).

The rose aphid, *Macrosiphum rosae* was selected as a model to study the impact of the two syrphid species. Rose aphid was probably introduced to Australia by European settlers (Maelzer 1977; Carver 1989). *M. rosae* is present on rose buds for about nine months of the year in South Australia, with 1-2 peaks in spring-summer and one peak in autumn. This aphid species is available as prey throughout the year except in June-July (winter) and January-February (summer) when the number of aphids per infested buds and the percentage of buds infested with aphids decreases. However, at these critical times very low number of bud infestation can be seen in some rose gardens.

Under the Mediterranean climatic conditions of Adelaide, neither *M. viridiceps* nor *S. grandicornis* can effectively control rose aphids below the level at which they damage the flowers. The reasons for their low efficacy were found to be:
-poor synchronisation with aphid prey
-lack of functional response to increasing aphid density
-high percentage of parasitism
- *M. viridiceps* has not evolved towards specialization

Supplementing pollen sources by planting attractive flowers near to roses increased the overall numbers of adults and eggs of *M. viridiceps* and *S. grandicornis* on roses but did not improve aphid control. During the three year study, the numbers of aphids did not decline to a density lower than economic injury level in the rose garden supplied with attractive flowers.

Selectivity studies showed that while *M. viridiceps* preferred the native species of plants available, *S. grandicornis* preferred introduced pollen-producing plants. Although not the most preferred plants, African daisy and marguerite daisy were found to be useful supplementary food supplies and could be used in agricultural systems because they (a) were attractive to both *M. viridiceps* and *S. grandicornis*, (b) they were perennial (c) they had long flowering periods, (d) they were hardy and did not require much care and (e) they were unlikely to become weeds in crops.

It is concluded that provision of supplementary food sources for *M. viridiceps* and *S. grandicornis* did not, under the weather conditions in this study, practically improve control of rose aphids. It is possible, that with different aphid species and cropping systems, this technique may have been more successful. However, in southern Australia, most aphid pests in crop plants have similar dynamics to those of rose aphids.

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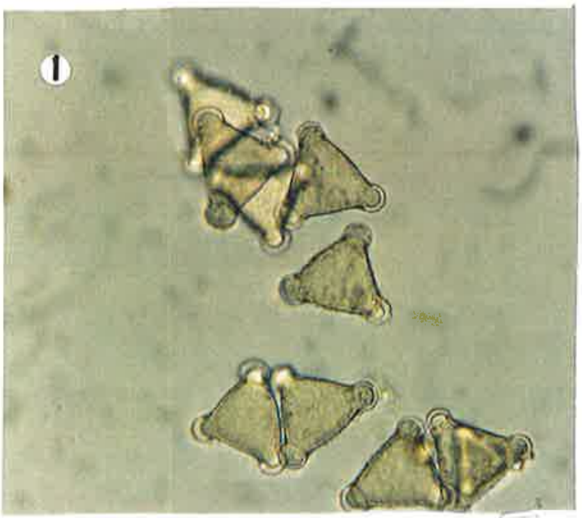
Appendix 4. 1: The actual dates of sampling and the designated dates of sampling denoted as weeks within months for census-walk at the Claremont rose garden in 1995.

designated sampling date week	Month	actual sample date	Mean no. M. viridiceps/sampl. day mar. daisy	Af. daisy	Mean no. S. granicornis/sampl.day mar. daisy	Af. daisy
1		5-Mar	0	0	0	0
2	Mar.	12-Mar	0	0	0	0
3		19,25-Mar	0	0	0	0
4		31-Mar	0	0	0	0
1		9-Apr	0	0	0	0
2	Apr.	16-Apr	0	0	0	0
3		21,23,24-Apr.	1.3	1.3	0	0
4		26,28-Apr.	3	7	0	0
1		3-May	1	2	0	0
2	May	10,15-May	2	4	0	0
3		17,18,19,21-May	1	9	0	0
4		28,29,30-May	1	0.3	0	0
1		1-Jun.	1	3	0	0
2	Jun	12,13,15-Jun.	3	2.3	0	0
3		17,18,19-Jun.	5	6.3	1	0
4		22,23,26,28-Jun.	12.5	12.5	0	0
1		8-Jul	84	24	0	0
2	Jul	9-Jul.	124	34	0	0
3		19,20,21-Jul.	66.7	15.3	0	0
4		25,31-Jul.	266	16	0	0
1		8-Aug.	25	1	3	0
2	Aug.	9,11,14-Aug.	35	11.3	3	0
3		16,18,20-Aug.	30.3	7.7	4	0
4		25,27,31-Aug.	92	4	4	0
1		3-Sep.	80	5	3	0
2	Sep	11,14-Sep.	138.5	12	3	0.5
3		17,18-Sep.	66.5	7.5	4	2
4		29-Sep.	70	12	6	4
1		1,3,6-Oct.	31.3	10	5	3
2	Oct	8,9-Oct.	20	6.5	17	4
3		11,12,13,14,16-oct.	20.2	5.8	12	8
4		27,29,30-Oct.	16.7	6.7	8	8
1		1,3-Nov.	4	0	8	4
2	Nov	9-Nov.	0	0	0	6
3		15-Nov.	0	0	0	0
4		27-Nov.	0	0	0	0

Appendix 6. 1: Pollen grains; native species planted at the Claremont rose garden, (1) *Grevillaria crithmifolia*, x957,(2) *G. glabrata*, x957, (3) *Callistemun sp*.x2392, (4) *Goodenia ovata*, x2392 (5) *Helychrysum sp*. x2392, (6) Olearia oxillaris, x2392.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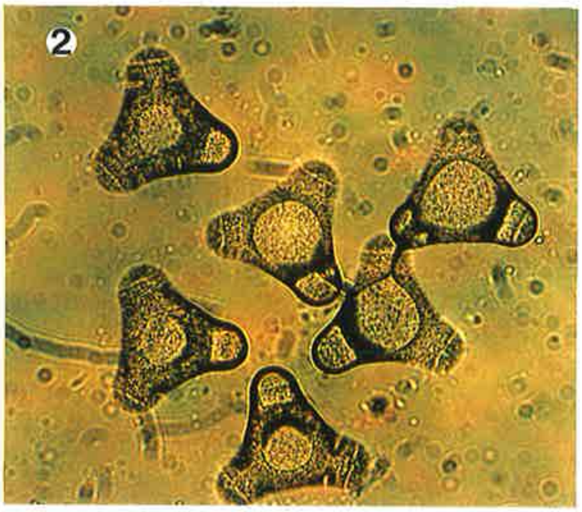
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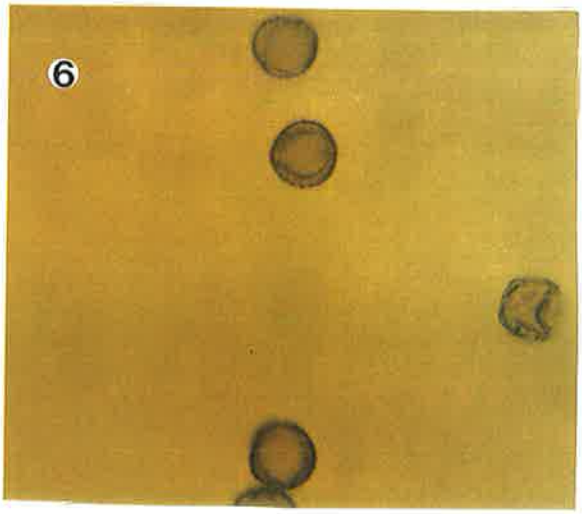
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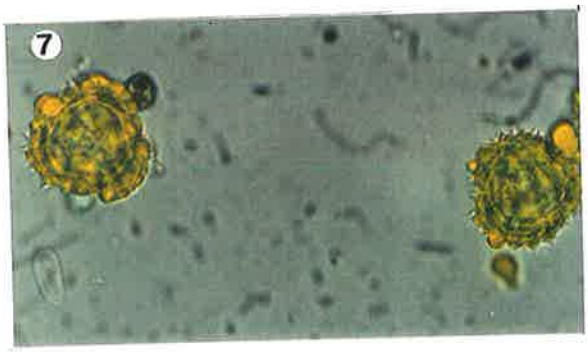
Appendix 6. 1: (cont.): Pollen grains; some common exotic species at the Claremont rose garden, (7) *Euryops pectinatus* (African daisy), x957, (8) *Chrysanthemum frutescens* (marguerite daisy), x2392, (9) *Polygonum sp.*, 2392 (10), *Lepidium africanum...*, x2392, (11) *Capsicum-bursa pastoris* , x2392, (12)*Poa annua*, x2392, (13) *Fumaria densiflora.*, x2392, (14) *Anagalis sp.*, x2392.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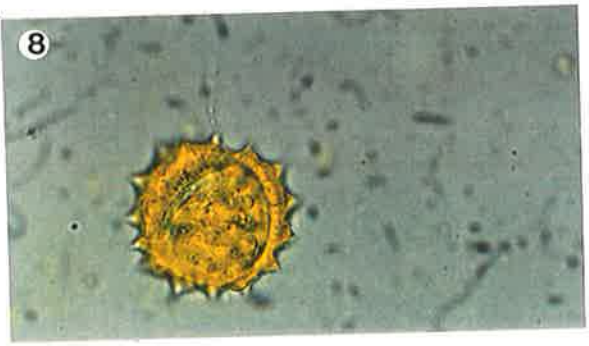
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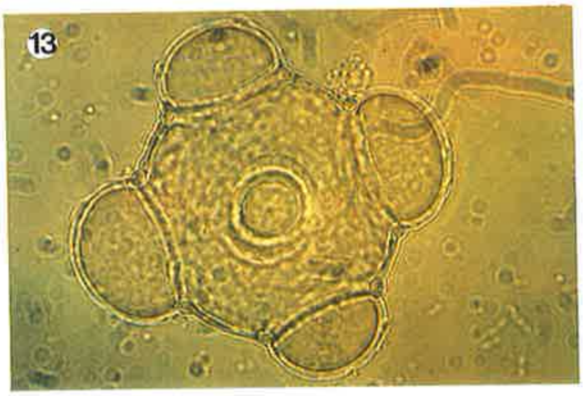
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Appendix 6.2: Johnson's (1980) method for analysing differences between availability and usage of pollen.
Converted availability (first column) is the product of two correction factors and availability. Also given is the ranked converted availability (second column) ; and the %s of pollen found in the guts (estimates of usage) of each of 6 flies

plant group	converted * availability	ranked convered availability	% of pollen in gut (usage) of fly number :					
			1	2	3	4	5	6
Acacia	3.00	16	4.3	0.0	4.2	0.0	0.0	0.0
Myrtaceae	5.40	18	87.6	0.0	0.0	0.0	0.0	0.0
Eucalyptus pectinatus	5.50	19	0.0	10.6	70.1	0.0	7.7	5.3
Chrysanthemum frutescens	3.20	17	0.0	6.9	0.0	18.5	41.6	55.7
Fumaria	1.80	13	0.0	0.0	0.0	0.0	0.0	0.0
Lamium	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Sonchus	1.00	12	8.1	0.0	24.3	21.6	0.0	10.6
Veronica	0.90	11	0.0	0.0	0.0	0.0	0.0	0.0
Polygonum	2.00	14	0.0	82.5	1.4	6.8	1.9	28.4
Plantago	2.80	15	0.0	0.0	0.0	14.3	22.9	0.0
R. raphanestrum	0.80	10	0.0	0.0	0.0	15.6	25.9	0.0
Anagalis	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Oxallis	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Poa	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Lepidium	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Solanum nigrum	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Atriplex	0.70	9	0.0	0.0	0.0	0.0	0.0	0.0
Ind. Asteraceae	0.00	4.50	0.0	0.0	0.0	0.0	0.0	0.0
Proteaceae	0.00	4.50	0.0	0.0	0.0	23.2	0.0	0.0

Appendix 6. 3: Ranking of the usage data in Appendix Table 1, ranked converted availability (also from Table 1), and calculation of the difference between mean ranked usage and ranked converted availability.

plant group	ranked usage by fly number :						mean ranked usage	ranked converted availability	difference in ranks
	1	2	3	4	5	6			
Acacia	17.0	8.5	17.0	7.0	7.5	8.0	10.83	16.00	5.17
Myrtaceae	19.0	8.5	8.0	7.0	7.5	8.0	9.67	18.00	8.33
Eucalyptus pectir	8.5	18.0	19.0	7.0	16.0	16.0	14.08	19.00	4.92
Chrysanthemum :	8.5	17.0	8.0	17.0	19.0	19.0	14.75	17.00	2.25
Fumaria	8.5	8.5	8.0	7.0	7.5	8.0	7.92	13.00	5.08
Lamium	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Sonchus	18.0	8.5	18.0	18.0	7.5	17.0	14.50	12.00	-2.50
Veronica	8.5	8.5	8.0	7.0	7.5	8.0	7.92	11.00	3.08
Polygonum	8.5	19.0	16.0	14.0	15.0	18.0	15.08	14.00	-1.08
Plantago	8.5	8.5	8.0	15.0	17.0	8.0	10.83	15.00	4.17
Raphanus	8.5	8.5	8.0	16.0	18.0	8.0	11.17	10.00	-1.17
Anagalis	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Oxallis	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Poa	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Lepidium	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Solanum	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Atriplex	8.5	8.5	8.0	7.0	7.5	8.0	7.92	9.00	1.08
Ind. Asteraceae	8.5	8.5	8.0	7.0	7.5	8.0	7.92	4.50	-3.42
Proteaceae	8.5	8.5	8.0	19.0	7.5	8.0	9.92	4.50	-5.42

Apendix 6. 4 : Calculation 'F' in Johonson's method analysis

$$F = \frac{J(J-I+1)}{(J-1)(I-1)} \sum_{i=1}^{I-1} \sum_{k=1}^{I-1} \bar{t}_i \bar{t}_k u_{ik}$$

I =numberof plant species

J =number of individuals

u_{ik} =is the designated element of the inverse matrix of V and $U = \left[u_{ik}\right] = V^{-1}$ is distributed under null hypothesis as Snedecor's F with $I-1$ and $J-I+1$ degree of freedom.

For comparison between components (plant groups) see text.

Appendix 6. 5 : Percentage of different pollen grains in guts of M. viridiceps at the Claremont rose garden in 1995

Date	Sex	*Polygonum*	Myrtaceae	*Acacia*	*Chr.frutescens*	*E. pectinatus*	*Plantago*	Proteaceae	*R. raphanestrum*	*Veronica*	*Anagalis*	*Solanum nigrum*	*Rumex*	*Fumaria*	*Synapis*	*Lamium*	*Sonchus*	*Poa*	Indeterminated	Ind. Asteraceae	No. of types
8/5/95	m	0.0	87.6	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.1	0.0	0.0	0.0	3
	m	82.5	0.0	0.0	6.9	10.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
	m	1.4	0.0	4.2	0.0	70.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.3	0.0	0.0	0.0	4
10/5/95	f	6.8	0.0	0.0	18.5	0.0	14.3	23.2	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.6	0.0	0.0	0.0	6
	f	1.9	0.0	0.0	41.6	7.7	22.9	0.0	25.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6
	m	28.4	0.0	0.0	55.7	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0.0	0.0	0.0	3
16/6/95	f	0.0	0.0	0.0	3.8	92.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
	f	0.0	0.0	0.0	0.0	84.6	0.0	15.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.6	8.8	61.2	0.0	10.9	0.0	18.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4
	m	0.0	0.0	0.0	9.1	90.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	20.6	55.1	20.6	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.5	0.0	0.0	0.0	5
	f	0.0	0.0	0.0	1.6	98.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
19/6/95	f	0.0	0.0	0.0	30.7	64.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	4.5	0.0	0.0	0.0	4
	m	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
	f	0.0	0.0	0.0	22.5	77.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	f	0.0	0.0	0.0	70.0	21.8	0.0	0.0	0.0	0.0	8.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
	f	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
	f	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
	f	0.0	0.0	0.0	0.6	60.7	0.0	0.0	0.0	0.0	32.6	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
22/6/95	m							only nectar													
	m							only nectar													
	m	0.0	0.0	0.0	34.6	65.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	18.0	72.9	0.0	0.0	0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
	f	0.0	0.0	0.0	12.8	49.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.6	0.0	0.0	0.0	0.0	3

Appendix6. 5 (cont.) : Percentage of different pollen grains in guts of M. viridiceps at the Claremont in 1995

Date	sex	*Polygonum*	Myrtaceae	*Acacia*	*Chr.frutescens*	*E. pectinatus*	*Plantago*	Proteaceae	*R. raphanestrum*	*Veronica*	*Anagalis*	*Solanum nigrum*	*Salsola*	*Fumaria*	*Synapis*	*Lamium*	*Sonchus*	*Poa*	Indetermined	Ind. Asteraceae	No. of pollen types
23/6/95	m	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
4/7/95	m	0.0	0.0	0.0	65.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.0	0.0	10.0	0.0	4
	m	0.0	0.0	0.0	8.0	4.0	0.0	0.0	0.0	42.5	0.0	0.0	0.0	0.0	0.0	0.0	45.5	0.0	0.0	0.0	4
	m	0.0	0.0	0.0	70.0	0.0	0.0	0.0	0.0	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
	m	0.0	0.0	0.0	70.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	4
19/7/95	f	0.0	0.0	0.0	8.5	23.9	0.0	0.0	0.0	42.6	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	4
	f	0.0	0.0	0.0	20.5	1.2	0.0	0.0	65.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	9.7	5
	m	0.0	0.0	0.0	51.4	25.7	0.0	0.0	17.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	4
	m	0.0	0.0	0.0	1.8	9.2	0.0	0.0	85.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	4
	f	0.0	0.0	0.0	50.0	7.1	0.0	0.0	33.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.9	4
	m	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
25/7/95	m	0.0	0.0	0.0	14.8	69.5	0.0	0.0	15.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
	m	0.0	0.0	0.0	0.0	61.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30.3	0.0	0.0	8.0	0.0	0.0	0.0	3
	m	0.0	0.0	0.0	15.5	67.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.1	0.0	0.0	0.0	0.0	0.0	2.8	4
	m	0.0	0.0	0.0	30.1	35.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34.1	0.0	0.0	0.0	0.0	0.0	0.0	3
	m	0.0	0.0	0.0	0.0	80.6	0.0	19.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	96.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	0.0	0.0	2
	m	0.0	0.0	0.0	23.6	0.0	0.0	0.0	72.8	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	14.3	7.1	0.0	0.0	73.2	0.0	0.0	0.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4
28/7/95	m	0.0	0.0	0.0	32.3	29.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	38.3	0.0	0.0	0.0	0.0	0.0	0.0	3
	f	0.0	0.0	0.0	2.5	80.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	15.0	0.0	0.0	0.0	4
	f	0.0	0.0	0.0	15.4	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	69.6	0.0	0.0	12.0	0.0	0.0	0.0	4
	f	0.0	0.0	0.0	63.6	9.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	27.3	0.0	0.0	0.0	0.0	0.0	0.0	3
	f	0.0	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	87.5	0.0	2
	f	0.0	0.0	0.0	50.0	21.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.6	3

Appendix 6. 5 (cont.): Percentage of different pollen grains in guts of *M. viridiceps* at the Claremont rose garden in 1995

Date	Sex	*Polygonum*	Myrtaceae	*Acacia*	*Chr.frutescens*	*E. pectinatus*	*Plantago*	Proteaceae	Wild raddish	*Veronica*	*Anagalis*	*Solanum nigrum*	Torshak	*Fumaria*	*Synapis*	*Lamium*	*Sonchus*	*Poa*	Indetermined	Ind. Asteraceae	No. of pollen types
7/8/95	f	0.0	0.0	0.0	22.9	54.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9	0.0	10.4	0.0	5.7	0.0	5
	f	0.0	0.0	0.0	96.3	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	46.2	23.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.3	3
	m	0.0	1.5	0.0	16.7	51.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.7	0.0	0.0	7.6	0.0	5
	f	0.0	0.0	0.0	2.6	4.3	0.0	0.0	93.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
24/8/95	f	0.0	0.0	0.0	7.1	5.2	0.0	0.0	79.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.7	0.0	0.0	0.0	4
	f	0.0	0.0	0.0	2.9	48.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	45.7	4
	f	0.0	0.0	0.0	2.3	11.6	0.0	0.0	14.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	72.1	4
	m	0.0	0.0	0.0	4.2	4.3	0.0	0.0	81.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	4
	m	0.0	0.0	0.0	21.8		0.0	0.0	78.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	66.7	29.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	0.0	3
	m	0.0	0.0	0.0		73.1	0.0	0.0	26.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	6.5	93.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	14.9	66.0	0.0	0.0	19.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
	m	0.0	0.0	0.0		7.7	0.0	0.0	65.4	0.0	0.0	0.0	0.0	0.0	26.9	0.0	0.0	0.0	0.0	0.0	3
13/9/95	m	0.0	0.0	0.0	83.2	16.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m				only nectar																
	m				only nectar																
	m	0.0	0.0	0.0	60.5	39.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	58.6	41.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m	0.0	0.0	0.0	80.5	19.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
	m				only nectar																
	m				only nectar																
	m	0.0	0.0	0.0	36.9	44.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.2	0.0	0.0	0.0	3
	m	0.0	0.0	0.0	11.3	88.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2
17/9/95	f	0.0	0.0	0.0	56.5	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	26.2	4
	f	0.0	0.0	0.0	21.6	10.8	0.0	0.0	59.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.2	4

Appendix 6. 6 : Pollen quantities (ranks) in the gut of *M. viridiceps*. Rank 0 is empty and rank 3 is full.

pollen ranks (males) n=123					pollen ranks (females) n=30
1	2	1	2	3	0
3	2	1	2	3	0
0	2	1	2	1	3
0	2	0	2		1
3	2	0	2		2
1	2	0	2		2
3	2	0	2		2
1	2	0	2		3
1	2	0	2		3
1	2	0	1		0
1	1	0	1		2
1	1	0	1		1
1	1	0	0		2
1	1	1	1		2
1	1	1	1		2
2	1	1	1		2
3	1	1	0		1
0	1	1	1		1
3	1	1	1		1
2	1	1	0		1
3	1	1	0		0
1	1	1	1		1
1	1	1	1		3
0	1	1	3		1
1	1	2	3		0
1	1	2	3		1
2	1	2	3		2
1	1	2	2		0
1	1	2	2		0
2	1	2	1		3

Appendix 6. 7: Numbers of *Melangyna viridiceps* and *S. grandicornis* attracted to 3 species of flowers in the glasshouse.

syrphid species	no. of occasions	***Eucalyptus.***						***Acacia***						**African daisy**					
		replications					mean	replications					mean	replications					mean
M. .viridiceps	**29**	**2**	**2**	**1**	**6**	**1**	**2.4**	**1**	**1**	**1**	**0**	**0**	**0.6**	**30**	**26**	**28**	**37**	**31**	**30.4**
S. grandicornis	**24**	**6**	**4**	**5**	**3**	**3**	**4.2**	**7**	**3**	**8**	**4**	**5**	**5.4**	**20**	**16**	**20**	**21**	**18**	**19**

Appendix 6. 8: Analysis of Variance for comparison between the attractiveness of *Eucalyptus*, *Acacia* and African daisy flowers to *M. viridiceps*.. Data from Appendix 6. 6 transformed to ln (x+1).

Source	DF	Sum squares	Mean squares	F-test	p value
Blocks	4	0.387	0.097	0.137	0.997
Treatment	2	25.117	12.559	77.158	0.0001
Residual	8	1.302	0.163		
Total	14	26.806			

Appendix 6. 9: Analysis of Variance for comparison between the attractiveness of *Eucalyptus*, *Acacia* and African daisy flowers to *S. grandicornis*. Data transformed to ln (x).

Source	DF	Sum squares	Mean squares	F-test	p value
Blocks	4	0.644	0.161	0.219	0.922
Treatment	2	6.939	3.469		
Residual	8	0.426	0.053	65.11	0.0001
Total	14	8.01			

Appendix 6. 10. Numbers of *Melangyna viridiceps* and *S. grandicornis* attracted to 3 species of flowers in the glasshouse.

	Sowthistle						Wild radish						African daisy					
syrphid species	replications					mean	replications					mean	replications					mean
M. viridiceps	7	2	5	9	3	5.20	5	10	5	6	1	5.40	11	16	8	7	10	10.40
S. grandicornis	13	20	17	15	10	15.00	20	25	20	21	22	27.00	11	14	11	9	16	12.20

Appendix 6.11: Analysis of Variance for comparison the attractiveness of sowthistle, wild radish and African daisy flowers to *M. viridiceps* .

Source	DF	Sum squares	Mean squares	F-test	p value
Blocks (Rep.)	4	39.733	9.933	0.571	0.69
Treatment	2	100.933	50.467	5.526	0.031
Residual	8	73.067	9.133		
Total	14	213.733			

Appendix 6.12: Analysis of Variance for comparison between the attractiveness of sowthistle, wild radish and African daisy flowers to *S. grandicornis*.

Source	DF	Sum squares	Mean squares	F-test	p value
Blocks (Rep.)	4	47.6	11.9	0.408	0.799
Treatment	2	232.933	116.467		
Residual	8	58.4	7.3	15.954	0.002
Total	14	338.933			

Appendix 8. 1: Details of the ANOVA to test the hypothesis that the number of TIEs eaten over all by the larvae of *M. viridiceps* at 10, 15 and 20°C can be described as a linear function of temperature.

Source of Variation	d.f.	S.S.	M. S.	F
Total	59	192084.2		
Among group	2	34246.6		
Linear regression	1	31899.9		
Deviation from linearity	1	2346.7	2346.7	<1.0*
Within groups	57	157837.6	2769.1	

*p> 0.25; do not reject hypothesis of linearity of regression. The fitted equation was Y=403.6-5.648x

Appendix 8. 2: Details of the ANOVA to test the hypothesis that the number of TIEs eaten over all by the larvae of *S. grandicornis*at 10, 15 and 20°C can be described as a linear function of temperature.

Source of Variation	d.f.	S.S.	M. S.	F
Total	59	551875		
Among group	2	268276		
Linear regression	1	222502		
Deviation from linearity	1	45774	45774	9.20*
Within groups	57	283599	4975.4	

*p< 0.01; reject hypothesis of linearity of regression.

Appendix 8. 3: Median development time (days) of the eggs of *M. viridiceps* and *S. grandicornis* held at constant temperature

Syrphid species	Temperature °C	n	median (days)	mean (days)	range
S. grandicornis.	4	30	13	13.3	12-16
	8	28	9	8.3	6-10
	10	29	4	3.9	3-4
	15	27	3	3.5	3-4
	20	29	2	1.5	1-3
	25	29	1	1.5	1-2
	30	30	1	1.2	1-2
M. viridiceps	4	35	died		
	8	23	10.3	10.4	10.3-11.3
	10	20	6.3	6.3	-
	15	20	2.8	2.9	2.8-2.9
	20	20	1.9	1.8	0.8-1.9
	25	39	1.9	1.9	0.8-2.5
	30	37	2.3	2	1.2-2.3

Appendix 8. 4A: Development time (days) of 3 different instars of the larvae of *S. grandicornis* separately at constant temperatures.

	temperature °c	n	median	mean	range
1st instar	8	50	16	16.5	13-21
	10	50	10.5	11	9-15
	15	48	6	6.6	3-12
	20	47	3	3.2	2-6
	25	33	1	1.5	1-3
2nd instar	8	48	10	10.6	9-15
	10	50	4	4.7	3-9
	15	48	3	3.8	1-7
	20	47	2	2.1	1-6
	25	33	1	1.6	1-3
3rd instar	8	47	14	14.5	11-19
	10	50	13	13.3	9-18
	15	48	8	8.1	6-11
	20	47	7	7.4	3-12
	25	33	4	4.6	6-9

Appendix 8. 4B: Developmental time (days) of the 3 larval instars of *M. viridiceps* at constant temperatures.

larval instars	temperature C°	n	median	mean	range
1st instar	10	22	4.1	4.5	1-6
	15	25	3.5	3.4	2-5
	20	30	2.4	2.3	1-4
	25	35	2.2	2.2	1-3
	30	31	2.8	3.1	2-5
2nd instar	10	25	7.1	7.0	5-9
	15	27	1.8	2.2	1-4
	20	36	2.1	3.0	1-5
	25	32	2.2	1.9	1-3
	30	27	2.2	2.5	1-4
3rd instar	10	25	10	10.5	8-13
	15	22	5.6	6.5	4-9
	20	25	6.3	5	2-8
	25	26	5	4.7	2-8
	30	25	6.9	7.3	5-10

Appendix 8. 5: Development time (days) of pupae of *S. grandicornis*. and *M. viridiceps* held at constant temperature.

species	Temperature C°	n	median	mean	range
	8	25	27	27.4	20-35
S. grandicornis	10	30	24	24.4	19-31
	15	30	17.5	17.3	8-20
	20	25	8	7.7	5-11
	25	25	8	8.2	6-9
M. viridiceps	10	22	20	23.1	17-26
	15	18	14.3	17.2	12-19
	20	21	8.3	8.5	7-10
	25	25	7.1	7.5	5-10

Appendix 8. 6A: Estimates of parameters in 3 non linear curves, Stinner, Exponential and Exponential T_b fitted to describe the relationship between temperature and the median developmental rate (1/day) of different life stages of *S. grandicornis*..

Life stage	models	temp. °c	c	k_1	k_2	T_{opt}	ψ	ρ	T_b	adj. coeff.
egg	Stinner	4-30	13.8	5.8	-0.13	27.58	-	-	-	0.99
inst. 1	Stinner	8-25	54.8	9.1	-0.21	-	-	-	-	0.99
inst. 2	Exp.	8-25	-	-	-	-	0.12	0.13	-	0.98
inst. 3	Exp.	8-25	-	-	-	-	0.06	0.08	-	0.85
overall larvae	Exp.	8-25	-	-	-	-	0.02	0.10	-	0.97
pupae	linear	8-25	-	-	-	-		0.006	3.60	0.75

Appendix 8. 6B: Estimates of parameters in 3 models Stinner, LoganTb and Exponential and linear fitted to describe the relationship between temperature and the median developmental rate (1/day) of different life stages of *M. viridiceps* .

Life stage	models	temp. °c	c	k_1	k_2	T_{opt}	ψ	ρ	Δt	T_b	adj. coeff.
egg	Stinner	4-30	0.57	4.05	-0.31	23.5	-	-		-	0.98
inst. 1	Stinner	10-30	3.4	3.14	-0.06	24.1	-	-	-	-	0.92
inst. 2	Log Tb	10-30	-	-	-	-	0.42	0.06	1.2	9.5	0.99
inst. 3	Exp.	10-25	-	-	-	-	0.03	0.12	-	-	0.95
overall larvae	Linear	10-30	-	-	-	-	-1.07	0.003	-	-	0.63
pupae	Linear	10-25	-	-	-	-	2.66	0.006	-	-	0.93

Appendix 9.1: Data from Claremont Rose Garden (1993-1994).

weeks	month & year	favour. buds per plant	total favour. buds	total infested buds	% infested buds	N	MEAN PER INFESTED BUD aphids	MEAN PER INFESTED BUD syrphid S.g	MEAN PER INFESTED BUD syrphid M.v.	TOTAL ON 70 PLANTS aphids	TOTAL ON 70 PLANTS syrphid S.g	TOTAL ON 70 PLANTS syrphid M.v.	CV aphids	CV syrphid S.g	CV syrphid M.v.
1	Aug-93														
2															
3		3.5	245	123	50.0	11	12.1	0	0.50	1482	0	61	136		240
4		7.7	539	376	69.8	11	91.8	0.36	0.20	34042	133	74	120	139	315
1	Sep	4.5	315	268	84.0	15	75.1	0.40	0.27	19871	106	71	115	228	311
2		7.3	511	410	79.0	11	96.2	0.40	0.45	39634	161	182	100	130	182
3		6.3	441	358	80.0	12	50.3	0	0.08	17728	0	28	80		363
4		4.3	301	287	94.0	7	181.7	0.63	0.29	51410	177	82	71	192	169
1	Oct	6.5	452	386	85.3	13	115.4	0.64	0	44444	246	0	93	141	
2		6.1	430	328	75.8	10	151.2	0	0	49259	0	0	100		
3		6.7	469	419	89.0	10	72.3	0.50	0	29840	206	0	42	194	
4		7.4	518	462	89.0	10	72.6	0.60	0	33094	274	0	93	180	
1	Nov	5.2	364	255	69.0	10	47.2	2.40	0	11855	603	0	51	74	
2		7.2	504	470	92.0	10	22.1	0.50	0	10247	232	0	86	140	
3		7.4	518	326	62.0	8	12.9	0	0	4143	0	0	99		
4		13.9	973	107	10.0	21	8.8	0.43	0	937	42	0	138	188	
5		8.3	581	11	1.8	3	2.3	0.33	0	24	3	0	100	176	
1	Dec	8.1	568	0	0		0	0	0	0	0	0			
2		4.3	301	18	5.8	4	3.3	0	0	57	0	0	117		
3		5.3	371	0	0		0	0	0	0	0	0			
4		3.6	252	10	3.9	14	3.5	0.29	0	34	3	0	43	286	
1	Feb-94	3.6	252	0	0	17	0	0.13	0	0	0	0		400	
2		5.3	371	35	9.3	7	40.1	1.43	0	1384	49	0	72	127	
3		1.4	98	14	14.2	4	2.3	0	0.00	32	0	0	73		
4		3.5	245	41	17.8	10	9.2	0.90	0	401	39	0	124	110	
5		2.0	137	4	2.5	14	14.0	3.00	0	48	10	0		0	
1	Mar	3.4	236	10	2.3	2	11.0	0	0	60	0	0	20		
2		7.3	511	7	1.4	4	188.0	2.25	0	1316	16	0	9	116	
3		8.4	588	60	10.2	8	36.8	1.13	0	2207	67	0	92	129	
4		4.5	315	82	25.5	8	11.6	0.50	0	934	40	0	136	214	
1	Apr	5.1	354	66	18.6	12	53.6	0.13	0	3562	9	0	119	262	
2		5.1	357	27	7.5	9	44.8	0	0	1200	0	0	66		
3		2.4	168	31	17.9	5	21.8	1.20	0.40	656	36	12	46	70	223
4		4.5	312	102	32.6	14	33.6	0.54	0	3432	55	0	158	163	
1	May	6.1	424	271	73.4	20	34.6	0.29	0	10755	90	0	85	197	
2		5.2	361	247	67.0	20	52.3	0.25	0	12620	60	0	167	208	
3		4.3	301	222	71.0	19	75.3	0.05	0	16092	11	0	166	460	
4		4.0	280	202	71.2	14	98.6	0.20	0	19856	40	0	70	290	
1	Jun	5.6	392	164	85.7	16	274.3	0.18	0	92149	60	0	18	300	
2		4.1	284	210	74.0	18	65.0	0	0	13636	0	0	116		
3		2.8	193	160	83.6	16	138.5	0	0	22289	0	0	95		
4		1.9	130	114	89.2	15	69.9	0	0.30	8074	0	35	137		
1	Jul										0	0			
2		2.7	189	106	55.5	11	55.5	0		5816	0	0	71		
3											0	0			
4											0	0			
1	Aug	1.1	77		95.0	13	88.5		0.47	6474	0	34	89		57
	Mean	5.2	362	166	46.7		58.0	0.46	0.07	13595	82	13	92	189	232
	S.D.	2.4	167	151	35.9		59.6	0.69	0.15	19287	111	34	39	98	98

n=numbers of samples (buds); Favour.=favourable buds;
S. g=Simosyrphus grandicornis; M.v=Melangyna viridiceps;
CV=Coefficient of variance

Appendix 9.2: Data from Claremont Rose Garden (1994-1995).

							MEAN PER INFESTED BUD			TOTAL ON 70 PLANTS			CV		
weeks	month & year	Favour. buds per plant	total favour. buds	total infested buds	% infested shoots	n	aphids	Syrphids S.G	Syrphids M. V	aphids	Syrphids S.G	Syrphids M. V	aphids	S.g	M.v
1	Aug-94														
2															
3		5.41	379	133	35	12	33.1	0	0	4387	0	0	82		
4		5.8	406	53	13.1	15	24.36	0	0	1296	0	0	154		
1		5.6	392	98	25	15	83.7	0.07	0.462	8203	7	45	113	371	301
2		4.6	322	171	53	15	16.2	0.6	0	2765	102	0	79	117	
3	Sep	5.4	378	2	0.66	21	108.05	0.52	0	270	1	0	118	224	
4		4.95	347	259	74.7	19	113.05	0.53	0	29261	137	0	78	159	
1		4.9	343	276	80.6	15	82.1	0.67	0.07	22697	185	19	64	166	371
2		5.35	375	228	61	20	19.65	0.3	0.05	4489	69	11	71	219	448
3	Oct	8.25	578	352	61	21	32.43	1.33	0.24	11424	469	85	65	120	274
4		9.19	643	429	66.7	20	47.25	0.8	0	20274	343	0	162	119	
5		10.59	741	354	47.7	18	40.28	0.29	0	14243	103	0	137	203	
1		9.267	649	102	15.8	25	12.2	0.24	0	1250	25	0	88	249	
2		13	910	129	14.2	25	7.36	0.32	0	951	41	0	96	174	
3	Nov	11.7	819	20	2.5	6	3.22	0	0	66	0	0	99		
4		18.38	1287	10	0.8	2	1	0	0	10	0	0			
1															
2															
3	Dec														
4															
1															
2															
3	Jan-95	0.65	46	0	0	20	0	0	0	0	0	0			
4															
1															
2															
3	Feb	4.88	342	0	0		0	0	0	0	0	0			
4		6.46	452	0	0		0	0	0	0	0	0			
1		5.01	351	0	0		0	0	0	0	0	0			
2		4.875	341	0	0		0	0	0	0	0	0			
3	Mar	3.437	241	0	0	1	10	3	0	0	0	0			
4		6.368	446	37	8.33	4	50	2.75	0	1857	102	0	72	62	
5		3.04	213	15	6.94	5	46.8	0.6	0	691	9	0	73	149	
1		1.89	132	11	8.62	5	49.2	0	0	561	0	0	171		
2		1.68	118	22	18.37	15	31.93	0	0	690	0	0	147		
3	Apr	3.55	249	150	60.4	12	121.4	0.08	0.17	18221	12	26	116	363	341
1		3.81	267	114	42.7	23	203.1	0.174	0	23129	20	0	103	391	
2		4.43	310	9	2.8	18	380.4	0	0	3303	0	0	81		
3	May	3.92	274	274	100	17	511.3	0	0	140301	0	0	79		
4												0			
1												0			
2		1.1	77	77	100	15	176.5	0	0	13591	0	0	44		
3	Jun	1.2	84	84	100	8	132.9	0	0	11164	0	0	73		
4												0			
1		1.5	105		80	7	16.4	0	0	1378	0	0	59		
2												0			
3	Jul	0	0		0		0	0	0	0	0	0			
mean		5.46021	5		32.725	15	71.33	0.37194	0.03006	10196	49	5	97	206	347
stdev.		3.88091	4		34.731	7	111.41	0.71812	0.09313	24800	105	16	35	100	68

n=numbers of samples (buds); Favour.=favourable buds;
S. g=Simosyrphus grandicornis; M.v=Melangyna viridiceps;
CV=Coefficient of variance

Appendix 9.3: Data from Urrbrae House Rose Garden (1993-1994).

weeks	months & year	% infested buds	n	MEAN PER INFESTED BUD			CV		
				aphids	S. g	M. v	aphids	S.g	M.v
1									
2			13	12.2		0.08	104		338
3	Aug-93		20	25.6		0.1	79		448
4			20	32	0.1	0	45	447	
1			20	123	0.15	0	107	447	
2			20	180.6	0.2	0	125	447	
3	Sep-93		17	206.9	0.24	0.35	60	233	174
4			24	206	0.38	0	46	211	
1			10	187.7	0.6	0	35	117	
2			20	255.5			115		
3	Oct-93		27	56.9	0.52	0	53	135	
1			13	333.4	0.46	0	34	67	
2			12	87.9	0.67	0	141	101	
3	Nov-93		34	118	1.3	0	131	27	
4			31	81.7	1.38	0	161	225	
1									
2									
3	Dec-93								
4									
1									
2		45.6	26	46.6	0.5	0	120	228	
3	Jan-94	34.7	25	34.8	1.4	0	83	221	
4		16.4	19	62.7	2.26	0	133	124	
5		23.5	20	18.9	0.45	0	157	184	
1		21.6	16	21.1	0.94	0	126	163	
2		16.4	10	22.3	1.7	0	87	104	
3	Feb-94	56.1	28	37.1	0.75	0	463	120	
4		43.7	13	93.5	0.36	0	163	258	
1		62.9	17	85.2	0.35	0	101	223	
2		70.7	29	108.7	0.07	0	167	371	
3	Mar-94	82	28	150.6	0.07	0	176	371	
4		100	25	461.5	0.16	0.32	77	231	234
1		59.4	22	66.4	0	0	236		
2		62	29	117.5	0.03	0	138	633	
3	Apr-94	41	15	66.2	0	0	236		
4		10.4	5	63.4	0	0	143		
mean		46.65	20.3	112.13	0.56	0.029310345	128	237	299
stdev		25.71	7.09	101.87	0.59	0.087909492	82	147	120

n=numbers of samples (buds); M.v=Melangyna viridiceps; S. g=Simosyrphus grandicornis

ppendix 9. 4: Data from Mercedes College

							MEAN PER INFESTED BUD			TOTAL ON 70 PLANTS			CV		
weeks	month & year	favour. buds per plant	total favour. buds	total infested buds	% infested buds	n	aphids	Syrphid S. g	Syrphid M.v	Aphids	Syrphid S. g	Syrphid M. v	aphids	S.G	M.v
1	Aug-94														
2															
3															
4		4	280	90	32	19	35.2	0	0	3154	0	0	76		
1	Sep	6.2	434	263	60.5	13	231.4	0.23	0	60759	60	0	147	361	
2		8.4	588	359	61.1	19	121.8	0.26	0	43759	93	0	36	215	
3															
4		9.4	658	477	72.5	19	95.5	0.16	0.05	45558	76	24	43	231	460
1	Oct	11.1	777	754	97	22	151.5	0.23	0	114184	173	0	97	187	
2		14.83	1038.1	474	45.7	19	19.2	0.05	0	9109	24	0	116	460	
3		15	1050	735	70	17	22.7	0.29	0	16685	213	0	79	172	
4		12.25	857.5	429	50	16	27.1	0.13	0	11619	56	0	112	262	
1	Nov	10.5	735	118	16	18	29.5	0.17	0	3469	20	0	173	224	
2		5	350	35	10	19	17.8	0	0	623	0	0	159		
3															
4		11.1	777	36	4.6	2	4.5	0	0	161	0	0	16		
1	Dec														
2															
3															
4															
1	Jan-95														
2															
3															
4															
1	Feb	3	210	22	10.5			0			0	0			
2		5.47	382.9	39	10.1	8	43.5	1.8	0	1682	70	0	113	228	
3		1.86	130.2	0	0	39	2	0	0	0	0	0			
4		1.5	105	0	0	40	0	0	0	0	0	0			
1	Mar	1.07	74.9	0	0	30	0	0	0	0	0	0			
2						29									
3		3.92	274.4	30	11.1	12	9	0	0	274	0	0	51		
4					1.66										
1	Apr	5.2	364	151	41.4	31	140	0.19	0	21097	29	0	113	316	
2		4.21	294.7	151	51.3	27	93.1	0.15	0.04	14075	23	6	128	200	475
3		2.8	196	25	12.9	21	140.17	0.1	0	3544	3	0	110	300	
4															
1	May	1.25	87.5	88	100	20	264.6	0	0.046	23153	0	4	78		438
2															
3		0.846	59.22	59	100	20	452.65	0	0	26806	0	0	68		
4		0.125	8.75	9	100	8	192.4	0	0	1684	0	0			
1	Jun														
2															
3		0.05	3.5	3	80	5	54.8	0	0	153	0	0	21		
4												0			
	mean	5.795	405.65	181	41.53	19.71	93.40957	0.156667	0.006	15738	35	1	91	263	458
	Stdev	4.6629	326.4	232	35.98	9.553	110.5058	0.36421	0.01592	12978	57	5	45	83	18.9

n=numbers of samples (buds); Favour.=favourable buds;
M. v=Melangyna viridiceps; S. g= Simosyrphus; CV=coefficient of variance

Appendix 9. 5: Data from Centennial Park

							MEAN PER INFESTED BUD			TOTAL ON 70 PLANTS			CV	
Week	month & year	Favour. buds per plant	total favour. buds	total infested shoot	% infested shoot	n	aphids	Syrphid S. g	Syrphid M. v	aphids	S. g	M. v	aphids	S. g
1	Aug-94													
2														
3														
4		5.1	357	76	21.2	14	10.57	0	0	800	0	0	83	
1	Sep	5.7	399	166	41.7	20	50.35	0.1	0	8377	17	0	144	310
2		8.7	609	244	40	20	47.6	0.4	0	11595	97	0	131	170
3											0			
4		9.61	673	320	47.5	19	103.6	0.26	0	33104	83	0	152	250
1	Oct	14.72	1030	556	54	25	23.32	0.04	0	12976	22	0	119	500
2		16.25	1138	497	43.7	16	22.75	0.244	0	11309	121	0	111	123
3		14.1	987	740	75	20	25.5	0.3	0	18876	222	0	112	217
4		8.1	567	340	60	25	16.28	0.32	0	5538	109		133	322
5		4.5	315	126	40	20	13.05	0.1	0	1644	13	0	178	310
1	Nov	3.58	251	32	12.9	8	10.5	0.125	0	341	4	0	85	283
2		5.87	411	153	37.2	15	9.73	0.133	0	1479	20	0	65	388
3											0			
4		10.11	708	0	0	9	0	0.07	0	0	0	0		
1	Dec													
2														
3														
4														
1	Jan-95													
2														
3														
4														
1	Feb													
2		4.12	288	0	0	17	0	0	0	0	0	0		
3		2.81	197	0	0	18	0	0	0	0	0	0		
4		2	140	0	0		0	0	0	0	0	0		
1	Mar	3.72	260	0	0	29	0	0	0	0	0	0		
2		3	210	0	0	17	0	0	0	0	0	0		
3		2.67	187	0	0		0	0	0	0	0	0		
4		-			0		0	0	0	0		0		
1	Apr	3.05	214	26	12	6	39.8	0.83	0	981	21	0	100	160
2		0.72	50	19	38	20	58	0	0	1117	0	0	216	
3		2.96	207	121	58.5	19	33.26	0.05	0	4017	6	0	91	460
4														
1	May	2.5	175	73	41.86	20	83.55	0	0	6120	0	0	141	
2														
3		0.632	44	44	100	25	61.64	0.04	0	2725	2	0	101	500
4		0.4	28	10	35.3	12	34.5	0	0	1771	0	0	161	
1	Jun													
2														
3		0.5	35	12	35.3	8	17	0	0	205	0	0	119	
mean		5.4169	379	142	30.545	17	25.4231	0.1158	0	4730	27	0	125	312
Stdev.		4.5293	317	201	27.013	6	27.9331	0.188	0	7679	53	0	37	122

n=numbers of samples (buds); Favour.=favourable buds; S. g=Simosyrphus grandicornis; M.v=Melangyna viridiceps; CV=Coefficient of variance