

The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand

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Abstract The phenology and sex ratios of three hover fly species on Canterbury farmland, New Zealand were recorded weekly from five yellow water-traps from October 15, 1993 to January 31, 1997. Gut fullness, egg number and pollen content were recorded weekly from September 8, 1994 to July 25, 1996. Catches of *Melanostoma fasciatum* (Macquart) and *Melangyna novaezelandiae* (Macquart) were higher during the summer months, with maximum male *M. fasciatum* catches at 0.7 per trap/day in January, 1997. Catches of female *Eristalis tenax*

L. peaked at 0.24 in August, 1994. Gut fullness and egg number in *M. novaezelandiae* and *M. fasciatum* were low from June to September, 1995, a pattern opposite to that of *E. tenax*. For all species combined, gut fullness was significantly higher in gravid females compared with non-gravid females, and males. Thirty-nine different pollen types were recorded from all hover fly classes. Male *E. tenax* (the largest of the three species) consumed the widest range of pollen in summer and autumn whereas females consumed the widest range in winter and spring, a pattern opposite to that of *M. novaezelandiae*. The value of the work in possible population enhancement programmes for hover flies in crops is discussed.

Keywords hover flies; Syrphidae; phenology; pollen; gut fullness; New Zealand

INTRODUCTION

Several European researchers have shown that aphidophagous hover fly (Diptera: Syrphidae) larvae have the ability to regulate aphid populations and therefore have potential as biological control agents (Holmes 1984; Chambers & Adams 1986; Chambers et al. 1986; Entwistle & Dixon 1990; Hickman & Wratten 1994, 1996). Adult flies require nectar for energy and pollen for maturation of their reproductive system (Schneider 1948; Chambers 1988). Therefore, manipulation of their habitats by the creation of floristically-diverse margins or within-crop strips offers a possibility for enhancing biological control.

In New Zealand, two native hover fly species, *Melanostoma fasciatum* (Macquart) and *Melangyna novaezelandiae* (Macquart), have aphidophagous larvae and are commonly found in agricultural and horticultural crops (Lövei et al. 1993; White et al. 1995; Wratten et al. 1995). Both species are abundant throughout the country, although *M. fasciatum* is more common, especially in the North Island (Miller 1921). Not only do the hover fly larvae feed

on aphids (Rohitha et al. 1985) but they also kill early-instar lepidopteran larvae, e.g., those of the white butterfly, *Artogeia rapae* (L.) and the diamondback moth, *Plutella xylostella* (L.) (Valentine 1967; Miller 1971; Ashby & Pottinger 1974).

Cowgill et al. (1993) showed that hover flies feed selectively on flowers, so effective manipulation of the habitat to enhance their numbers requires knowledge of pollen feeding. Several species of flowers are attractive to hover flies. For example, New Zealand studies show that *Phacelia tanacetifolia* Benth. (Hydrophyllaceae) is attractive to native hover fly species (Lövei et al. 1993) and when planted in strips across fields, can increase local hover fly densities (Lövei et al. 1992). White et al. (1995) showed that sowing *Phacelia* around the borders of cabbage crops significantly increased hover fly populations and decreased the numbers of aphids. At the larger scale of fields as replicates, Hickman & Wratten (1996) showed the same effect of *Phacelia* in wheat in the U.K.

Knowledge of the phenology of the insects is important to maximise their biological control potential, but this information in New Zealand is limited. Holloway (1976), for example, suggested that *M. fasciatum* fed almost exclusively on anemophilous pollen from plantain (*Plantago* spp.) and/or grass species, but no general conclusion could be valid from her small sample size. Wratten et al. (1995) reported that *M. fasciatum* and *M. novaezealandiae* produced a second generation in late summer in Canterbury, and that *Taraxacum*-type was the most frequently occurring pollen in the guts of both species. Hickman et al. (1995) found that plantain (*Plantago* sp.), *Phacelia*, coriander (*Coriandrum sativum* (L.)) and Gramineae (Poaceae) pollen was consumed in large quantities by gravid *M. fasciatum* females, and that there were differences in pollen feeding between the sexes. Both these studies took place over short periods, so the question remains whether pollen consumption changes between seasons.

In this paper we describe hover fly phenology and sex ratios over a three-year period, and gut fullness, egg number and pollen content over two years, in two aphidophagous hover fly species (*M. novaezealandiae* and *M. fasciatum*). We also observed the non-aphidophagous species *Eristalis tenax* L., because data on this species are useful in understanding the biology of flower-feeding hover flies.

METHODS

This work is part of a long-term phenology study in which hover flies have been captured from five yellow (peak trap reflectance 500 nm (Wratten et al. 1995) plastic 2 l containers (170 × 170 × 85 mm) placed 10 m apart along a fence line on the Lincoln University Mixed Cropping Farm near Christchurch, South Island. Each trap was three-quarters filled with water to which a few drops of detergent were added, together with approximately 5 g of sodium benzoate as a preservative. Hover flies were removed from the traps with forceps and transferred to 70% ethanol in plastic vials. In the laboratory, adult *M. novaezealandiae*, *M. fasciatum* and *E. tenax* were identified and sexed (in males, eyes touch dorsally; in females, eyes do not touch) using a dissecting microscope.

Hover flies were collected every 5–9 days from October 15, 1993 to January 31, 1997 to document species and sex ratios. Hover flies collected from September 8, 1994 to July 25, 1996 were dissected to obtain egg number, gut fullness and pollen feeding. During this period, two dates approximately two weeks apart were chosen from each month every year for fly dissection.

To assess gut fullness and female gravidness, a maximum sample of five hover flies of each sex for each species was dissected on each sample date. The dissection procedure and slide preparation in outline were: the insect was removed from alcohol, placed on a glass slide in alcohol, and the abdomen separated and teased apart with mounted needles. The gut contents were spread over part of the slide, and saffranin, gelatin and phenol were added, followed by a coverslip (see Wratten et al. 1995 for more details). If there were more than 100 eggs, they were estimated to the nearest ten. Gut fullness was estimated on a semi-quantitative scale by classifying pollen number as accurately as possible, without detailed counting at the higher pollen categories, into one of seven frequency classes (0 = no pollen grains, 1 = 1–10 grains, 2 = 11–100 grains, 3 = 101–1000 grains, 4 = 1001–3000 grains, 5 = 3001–5000 grains, 6 > 5000 grains). Hickman et al. (1995) working only on *M. fasciatum*, also dissected this species for pollen type and abundance. The pollen classes used in the present work did not exactly match those used by Hickman et al. (1995) because the large pollen volumes contained in the *E. tenax* guts necessitated modified pollen-number classes.

All pollen was identified at least to family level, using 400 × magnification when necessary. The percentage of each pollen type per gut was also esti-

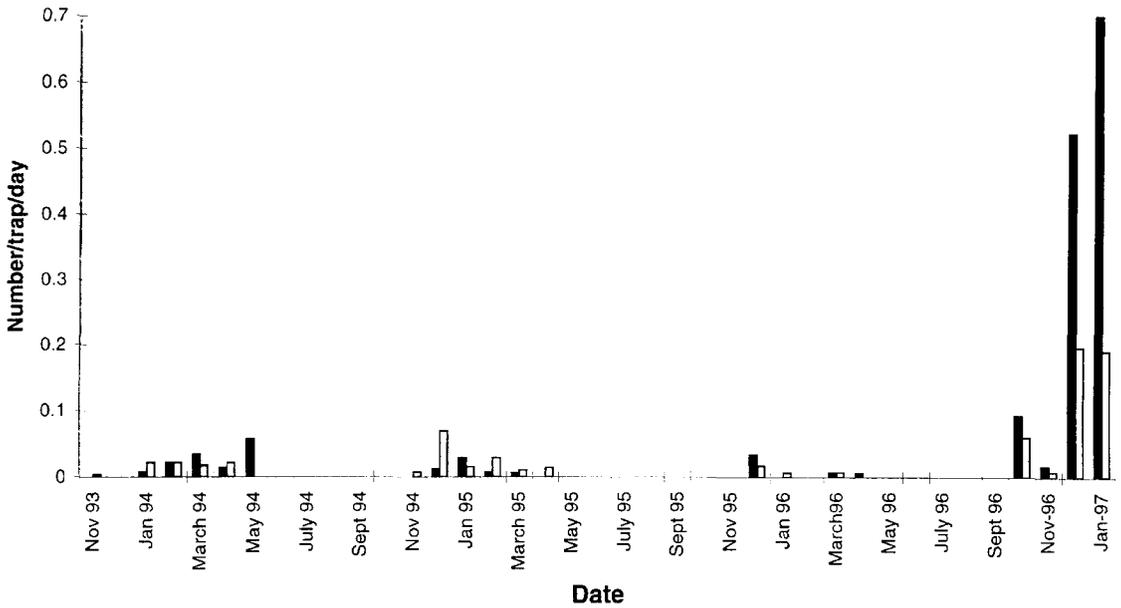


Fig. 1 Average monthly catches of male and female *M. fasciatum* from October 15, 1993 to January 31, 1997 (■ = male; □ = female).

mated from the average of counts from nine graticule quadrants. Pollen identification was aided by reference slides of pollen made from flowering plants present at the study site, and confirmed by Moore et al. (1991), Moar (1993), and from personal experience (Moar).

Differences between species, times and sex/gravidness groups were assessed for the number of flies per trap and the number of eggs using ANOVA, or for gut fullness and the number of pollen types using the Kruskal Wallis non-parametric test. The numbers of eggs were log transformed (log (x+1)) prior to ANOVA to stabilise variances. Where the ANOVA or Kruskal Wallis test indicated significant differences among groups, these were further explored using LSD or Mann-Whitney U tests respectively. The relationship between gut fullness in gravid females and the number of their eggs was assessed using Spearman’s correlation coefficient (r_s).

RESULTS

Hover fly phenology

From June to September every year no *M. fasciatum* were captured. From November to April 1994, 1995

and 1996 catches of this species were low: males reached a maximum of 0.06 individuals/trap/day and females 0.07 individuals/trap/day. However, from October 1996 to January 1997, catches of males reached a peak of 0.7, and females 0.2 individuals/trap/day (Fig. 1).

E. tenax numbers showed two obvious trends. Numbers of females reached a peak in August 1994 and 1995, whereas in 1996 the peak was in November. Secondly, no male *E. tenax* was captured from July to September 1994 and 1995. Catches of males reached a peak of 0.2 individuals/trap/day in February, 1996 (Fig. 2).

Catches of *M. novaezelandiae* were low in 1994, compared with September to March in 1995 and 1996 and September to January in 1997. Numbers of females and males reached peaks of 0.67 individuals/trap/day in January 1995 and 0.3 individuals/trap/day in December 1996, respectively (Fig. 3).

Egg number and gut fullness

Gut fullness and the number of eggs in *M. novaezelandiae* and *M. fasciatum* were at their lowest from June to September, 1995, as was reported for *M. fasciatum* by Hickman et al. (1995). In contrast, in *E. tenax* they were at their highest over the same period, with a peak of 108 eggs and a 5.5 gut-fullness index in August 1995 (Fig. 4, 5).

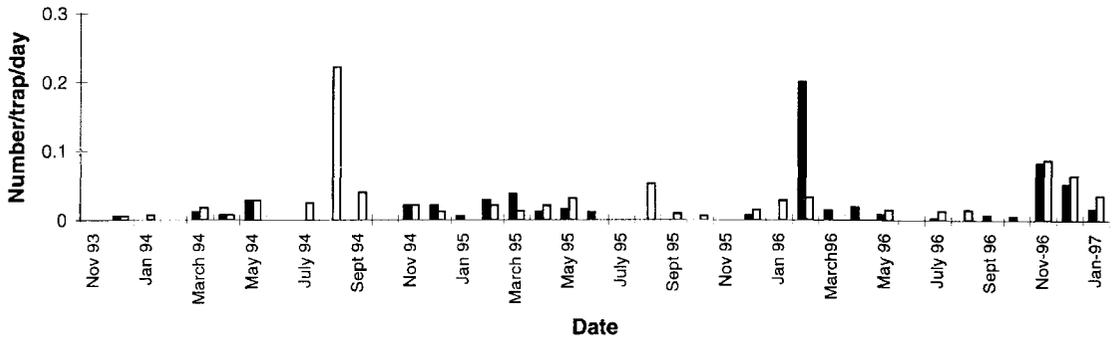


Fig. 2 Average monthly catches of male and female *E. tenax* from October 15, 1993 to January 31, 1997 (■ = male; □ = female).

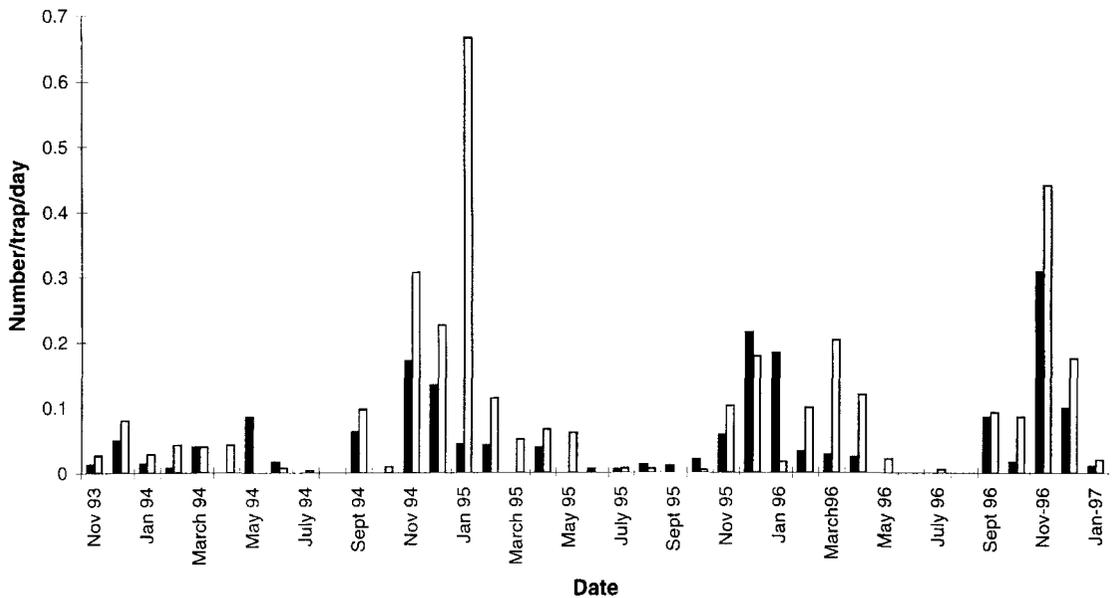


Fig. 3 Average monthly catches of male and female *M. novaezelandiae* from October 15, 1993 to January 31, 1997 (■ = male; □ = female).

Gravid and non-gravid *M. novaezelandiae* had a significantly ($U=1877.0$, $P < 0.001$) higher gut fullness (median = 5) than did males (4). Gut fullness did not significantly (*M. fasciatum*, $H=4.8$, $df=2$, $P > 0.05$; *E. tenax*, $H=3.8$, $df=2$, $P > 0.05$) differ between the sexes of the other two species. However, for all species combined, gut fullness was significantly ($U=8959.5$, $P < 0.01$) higher in gravid females (median = 5) compared with non-gravid (4.5) and male hover flies (4). There was no significant ($F=0.521$, $df=2$, 91 , $P > 0.05$) difference between the mean number of eggs per female between the three species. There was also no significant ($r_s=0.02$,

$df=122$, $P > 0.05$) relationship between gut fullness and the number of eggs in female hover flies.

Pollen feeding

M. novaezelandiae

Males consumed a higher number of different pollen types in spring compared with females, which used the highest range of different pollen types in summer and autumn (Fig. 6, 7). Twenty-eight different pollen types were found in the gut of this species in autumn, with gravid females consuming 19, non-gravid females 22 and males nine types (Fig. 7). Four different pollen types were consumed in win-

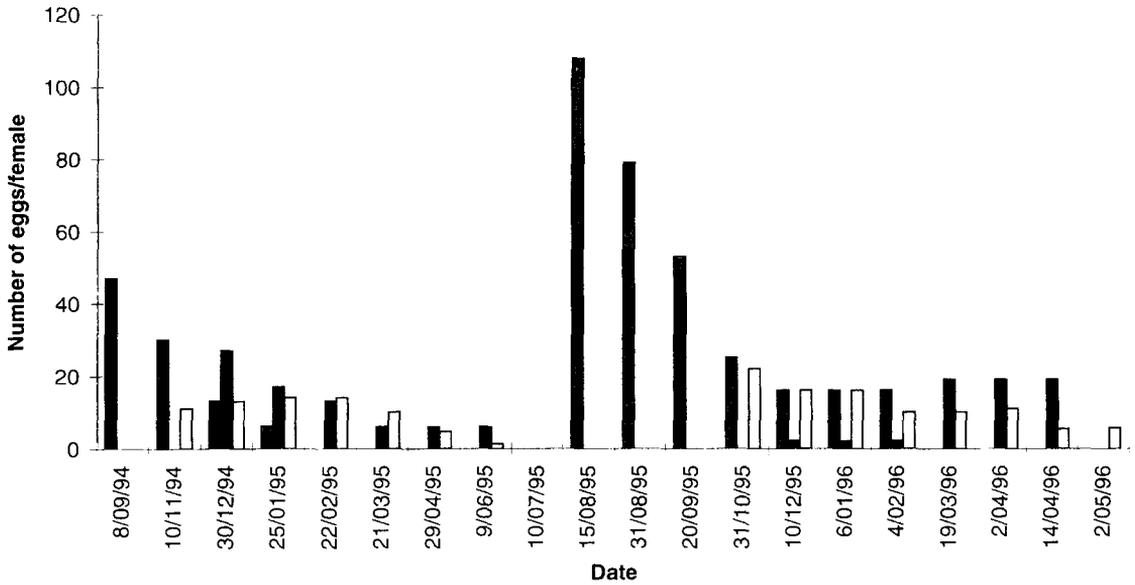


Fig. 4 Average number of eggs per female of three hover fly species, *E. tenax*, *M. fasciatum* and *M. novaezelandiae* from September 8, 1994 to May 2nd, 1996 (□ = *M. novaezelandiae*; ■ = *E. tenax*; ▒ = *M. fasciatum*).

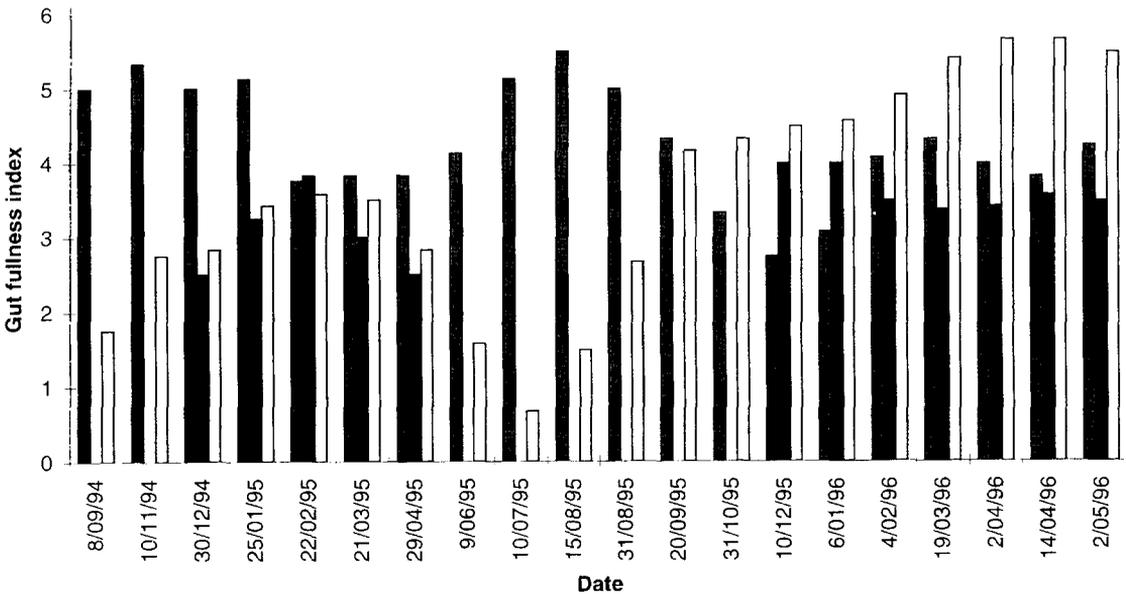


Fig. 5 Median gut fullness index for females of three hover fly species *E. tenax*, *M. fasciatum* and *M. novaezelandiae* from September 8, 1994 to May 2, 1996 (□ = *M. novaezelandiae*; ■ = *E. tenax*; ▒ = *M. fasciatum*).

ter by this species and 17 in spring (Fig. 8). Poaceae, Asteraceae, *Brassica*-type and Caryophyllaceae are used all year round by this species (Fig. 6–9), which was the only one to feed on *Geranium* spp., *Ribes* spp. and *Centaurea* spp. (Fig. 7). Male *M. novae-*

zelandiae did not consume Chenopodiaceae pollen at any time of the year (Fig. 6–9).

M. fasciatum

M. fasciatum consumed fewer pollen types in summer

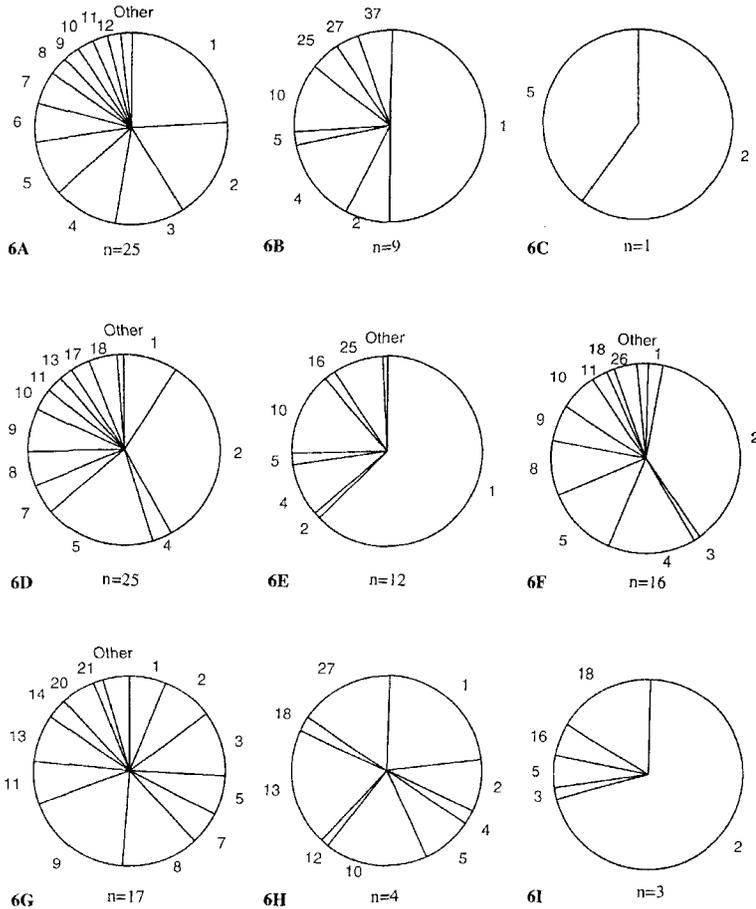


Fig. 6 Pollen types present in the guts of three hoverfly species in summer (NC = None captured, n = sample size. 1 = *Polygonum* spp.; 2 = Asteraceae; 3 = Liliaceae type; 4 = Poaceae; 5 = *Taraxacum*; 6 = unknown T; 7 = *Tilia* spp.; 8 = *Brassica* type; 9 = Rosaceae; 10 = Fabaceae; 11 = *Sedum* spp.; 12 = *Viola* spp.; 13 = Scrophulariaceae; 14 = Chenopodiaceae; 15 = Ranunculaceae; 16 = Malvaceae; 17 = Myrtaceae; 18 = Umbelliferae; 19 = Caryophyllaceae; 20 = unknown N; 21 = unknown A; 22 = Labiatae; 23 = *Pinus* spp.; 24 = unknown B; 25 = *Plantago* spp.; 26 = Ariolaceae; 27 = *Phacelia tanacetifolia*; 28 = *Geranium* spp.; 29 = *Centaurea* spp.; 30 = *Ribes* spp.; 31 = unknown D; 32 = Ericaceae; 33 = unknown Rosaceae; 34 = *Erodium* spp.; 35 = *Acacia* spp.; 36 = *Salix* spp.; 37 = *Rumex* spp.; 38 = unknown I; 39 = unknown R); **6A**. Pollen types and proportions in gravid *M. novaezelandiae* (Other = 13, 14, 15 & 16); **6B**. Pollen types and proportions in gravid *M. fasciatum*; **6C**. Pollen types and proportions in gravid *E. tenax*; **6D**. Pollen types and proportions in male *M. novaezelandiae* (Other = 12, 16 & 19); **6E**. Pollen types and proportions in male *M. fasciatum*

(median = 13) and autumn (7) than did *M. novaezelandiae* and *E. tenax* (Fig. 6, 7). There were no obvious differences between the number of pollen types consumed between sexes (Fig. 6, 7). *M. fasciatum* was the only species not to feed on *Pinus* spp. (Fig. 6, 7), although winter and spring data were not available for both years. Gravid female *M. fasciatum* was the only species to feed on *Rumex* spp. (Fig. 6), and this species fed on *Plantago* spp. and *Phacelia* in summer whereas *M. novaezelandiae* did not (Fig. 6).

E. tenax

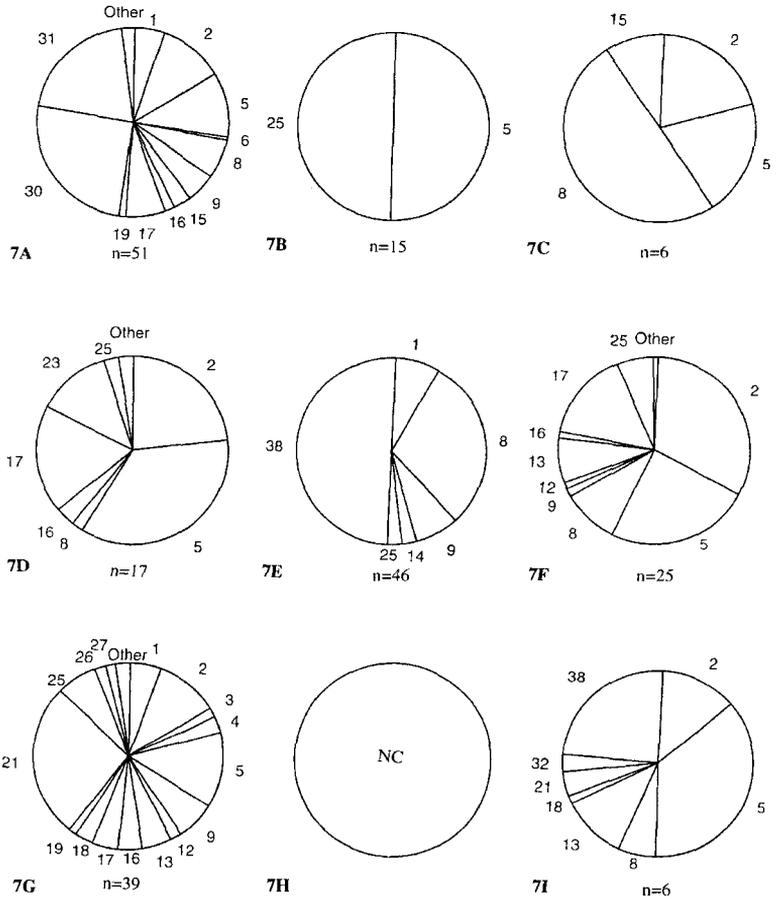
E. tenax consumed fifteen species throughout the year. The range of pollen types was wider in male flies in summer and autumn, and wider in female flies in winter and spring (Fig. 6–9) – the opposite

trend to that in *M. novaezelandiae*. *E. tenax* consumed a higher number of different pollen types in winter compared with *M. novaezelandiae*, and additionally fed on *Salix* spp., *Erica* spp. and *Pinus* spp. (Fig. 8). In contrast, *E. tenax* did not consume *P. tanacetifolia* (Fig. 6–9).

Seasonal trends

There was no significant difference between the sexes of *E. tenax* for the number of different pollen types consumed in any of the four different seasons (summer, $H=4.7$, $df=2$, $P > 0.05$; autumn, $H=2.8$, $df=2$; $P > 0.05$; winter, $H=0.3$, $df=2$, $P > 0.05$; spring, $H=1.5$, $df=2$, $P > 0.05$). Gravid *M. fasciatum* consumed a significantly ($U=25.0$, $P < 0.05$) higher number of pollen types in summer than in autumn. There were no other significant seasonal differences

Fig. 7 Pollen types present in the guts of three hoverfly species in autumn (refer Fig. 6); **7A.** Pollen types and proportions in gravid *M. novaeseelandiae* (Other = 3, 10, 14, 13, 23, 24, 25, 26, 27 & 28); **7B.** Pollen types and proportions in gravid *M. fasciatum*; **7C.** Pollen types and proportions in gravid *E. tenax*; **7D.** Pollen types and proportions in male *M. novaeseelandiae* (Other = 1 & 29); **7E.** Pollen types and proportions in male *M. fasciatum*; **7F.** Pollen types and proportions in male *E. tenax* (Other = 1); **7G.** Pollen types and proportions in non-gravid *M. novaeseelandiae* (Other = 15, 30, 31, 32, 33, 34 & 35); **7H.** Pollen types and proportions in non-gravid *M. fasciatum*; **7I.** Pollen types and proportions in non-gravid *E. tenax*.



◀ **Fig. 6 (continued)**
 (Other = 8); **6F.** Pollen types and proportions in male *E. tenax* (Other = 7, 12 & 25); **6G.** Pollen types and proportions in non-gravid *M. novaeseelandiae* (Other = 4, 6, 10, 12, 17, 22 & 23); **6H.** Pollen types and proportions in non-gravid *M. fasciatum*; **6I.** Pollen types and proportions in non-gravid *E. tenax*.

in the number of pollen types consumed by non-gravid and male *M. fasciatum*, although there were no data for winter and spring for either year. The number of different pollen types consumed by *M. novaeseelandiae* was lower in winter compared with all other seasons for all sexes. A significantly ($U=2590.0, P < 0.05$) larger number of pollen types was consumed by gravid *M. novaeseelandiae* in autumn compared with spring and summer.

DISCUSSION

Hover fly phenology

The marked increase in the number of *M. fasciatum* captured in mid-December of each year and of *M. novaeseelandiae* captured in January suggests the ap-

pearance of new generations. This contrasts with the results of Wratten et al. (1995), who found that the numbers of *M. fasciatum* peaked in mid-March in 1993. This difference was probably due to differences in climatic conditions between the years. By contrast, seasonal difference of *E. tenax* numbers were erratic. This could be due to changing seasonal attractiveness of the traps, itself possibly partly related to the varying availability of water in the vicinity of the traps, since this species lays its eggs in stagnant water.

The relatively low number of aphidophagous hover flies captured before December may suggest that predation on aphids by hover fly larvae may be limited early in the season. However, evidence from European field and modelling studies suggests that very low larval densities can still bring about large declines in aphid populations (Chambers & Adams

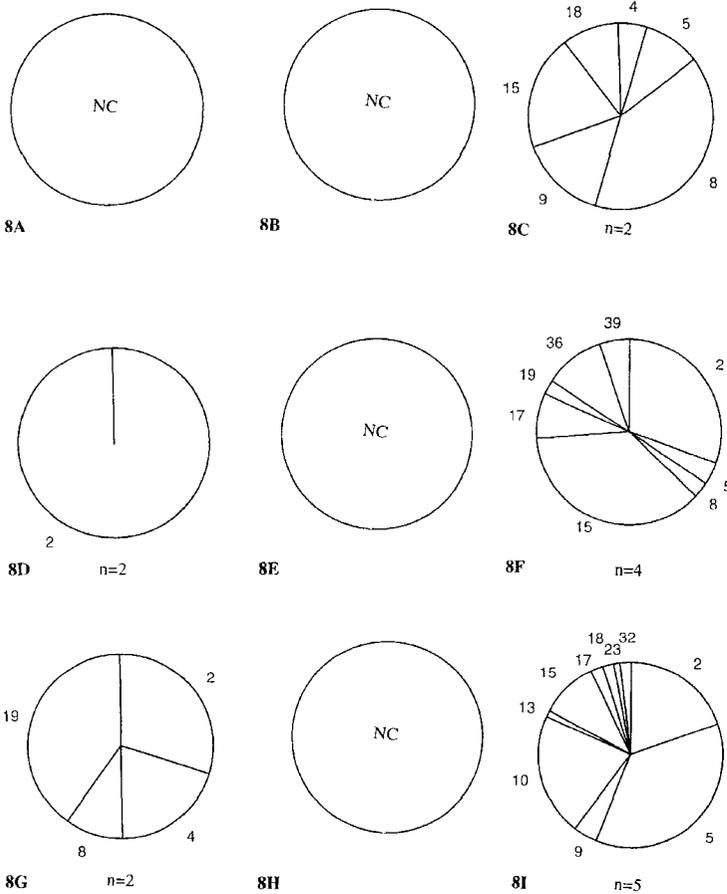


Fig. 8 Pollen types present in the guts of three hoverfly species in winter (refer Fig. 6); **8A.** Pollen types and proportions in gravid *M. novaezelandiae*; **8B.** Pollen types and proportions in gravid *M. fasciatum*; **8C.** Pollen types and proportions in gravid *E. tenax*; **8D.** Pollen types and proportions in male *M. novaezelandiae*; **8E.** Pollen types and proportions in male *M. fasciatum*; **8F.** Pollen types and proportions in male *E. tenax*; **8G.** Pollen types and proportions in non-gravid *M. novaezelandiae*; **8H.** Pollen types and proportions in non-gravid *M. fasciatum*; **8I.** Pollen types and proportions in non-gravid *E. tenax*.

1986; Entwistle & Dixon 1990; Winder et al. 1994). Very little information is available on the role of New Zealand hover flies in the regulation of aphid numbers, but White et al. (1995) found that aphid predation rates in early summer could be enhanced with the provision of floral resources adjacent to a *Brassica* crop, and that this led to lower aphid populations.

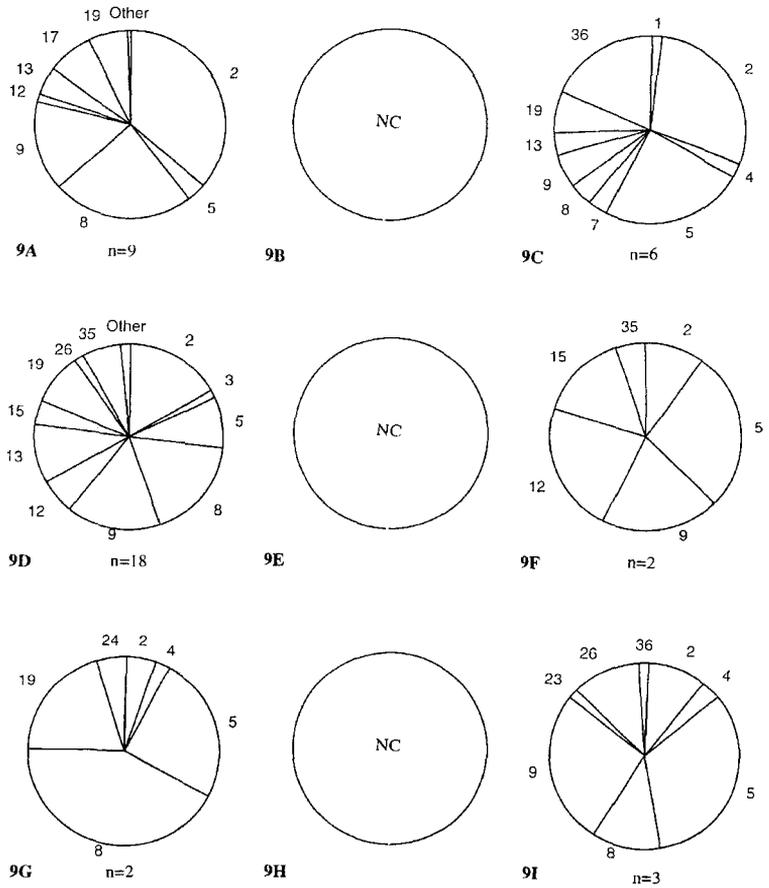
Egg number and gut fullness

The trend of egg number in *M. novaezelandiae* and *M. fasciatum* throughout the year followed that of gut fullness (Fig. 4, 5). This is consistent with the idea that pollen is important for sexual maturation in hover flies (Schneider 1948; Chambers 1988), and suggests that providing enhanced pollen resources in early spring can increase the proportion of gravid flies in the population. In contrast to *M. novaezelandiae* and *M. fasciatum*, gut fullness in *E. tenax*

was highest during winter (Fig. 4, 5). Egg number in *E. tenax* was also high during the winter period so this, like gut fullness, probably reflects the fact that this species lays its eggs in stagnant water, which would be more available during the winter months (Miall 1895). Peak numbers in traps were also in winter, spring or early summer, depending on the year (see above).

For all species combined, gut fullness was higher in gravid females than in non-gravid females and males, and was higher in non-gravid females compared with males. This is consistent with the results of Hickman et al. (1995), and supports the idea that females need pollen during summer/autumn to mature their eggs, whereas males need nectar to provide energy for mate seeking. Immature females had less pollen than did gravid females, perhaps because newly emerged females may take nectar for energy for mate seeking instead of consuming pollen

Fig. 9 Pollen types present in the guts of three hoverfly species in spring (refer Fig. 6); **9A.** Pollen types and proportions in gravid *M. novaezelandiae* (Other = 25); **9B.** Pollen types and proportions in gravid *M. fasciatum*; **9C.** Pollen types and proportions in gravid *E. tenax*; **9D.** Pollen types and proportions in male *M. novaezelandiae* (Other = 4, 23 & 36); **9E.** Pollen types and proportions in male *M. fasciatum*; **9F.** Pollen types and proportions in male *E. tenax*; **9G.** Pollen types and proportions in non-gravid *M. novaezelandiae*; **9H.** Pollen types and proportions in non-gravid *M. fasciatum*; **9I.** Pollen types and proportions in non-gravid *E. tenax*.



(Hickman et al. 1995). The absence of a difference between the sexes of *M. fasciatum* in terms of gut fullness was probably a statistical consequence of low numbers captured (Fig. 1).

Pollen feeding and seasonal trends

Thirty-nine different pollen types were recorded in hover fly guts in this study, including sixteen in *M. fasciatum* alone. By contrast, Holloway (1976) suggested, from a few museum specimens, that *M. fasciatum* fed almost exclusively on anemophilous pollen (from *Plantago* spp. and grasses). That conclusion is clearly not supported by the current large data set.

Female *M. novaezelandiae* consumed a higher number of pollen types in summer and autumn. This suggests that oogenesis is most intense during the summer and autumn, and that female hover flies require a larger range of pollen types during this pe-

riod to obtain the range of amino acids needed for egg maturation. By contrast, males consumed most pollens in the spring (Fig. 6, 7, 9). If spermatogenesis is most intense during the spring, the pollen requirements of males would be higher then. The pollen frequency trend in *E. tenax* was opposite to that of *M. novaezelandiae*, in that females consumed a larger range of pollen types in winter and spring, while males took most in summer and autumn (Fig. 6–9). This is consistent with their egg maturation and gut fullness trends, which were also the opposite of those of *M. fasciatum* and *M. novaezelandiae* (Fig. 4, 5). Inter-specific differences in tongue-length may also explain why some flies took pollens not recorded in the guts of others (Gilbert 1981; Hickman et al. 1995). However, the only three pollen genera taken by *E. tenax* but not by the other two species were from *Salix*, *Erica* and *Pinus* spp. These plants flower mainly in winter and spring, the period of

highest abundance of *E. tenax*, so seasonal availability of pollen is clearly an important phenological factor. Pollen types taken by *M. fasciatum* and *M. novaezelandiae* also differed to some extent, but these differences could not be explained by the flies' tongue length or by phenology.

This research suggests that pollen is essential for sexual maturation of hover fly eggs, so the provision of floral resources may enhance hover fly numbers in agricultural and horticultural landscapes with a depauperate flora. *M. novaezelandiae* consumed *Taraxacum*-type, *Brassica*-type, Rosaceae and Asteraceae in the spring; therefore, sowing or leaving these and/or other pollen sources around crop margins or in a central strip (by avoiding herbicide use) may be a management option for early enhancement of hover fly populations, with a consequent reduction in crop damage by aphids. The dominance of these four types may reflect their abundance at the site as well as 'preference'. Provision of non-prey resources in this way is more likely to have practical value in environments such as the Canterbury Plain, New Zealand, where this work was carried out, as native vegetation is virtually absent, herbicide use in field margins is very common, and hedgerows and their associated herbaceous vegetation, typical of North-West Europe (Wratten & van Emden 1995; Wratten et al. 1998) are virtually absent (Keesing & Wratten 1997). Sowing plants of value to hover flies, but of low weed status and of little value as pests' hosts, is probably the ideal habitat management option – see Gurr et al. (1998).

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