

**Visual and olfactory behaviour of *Delia antiqua* (Diptera: Anthomyiidae)
in relation to time of day and ovarian development**

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**Anthomyiidae, *Delia antiqua*, onion maggot fly, activity rhythms, ovarian development, oviposition,
feeding, host-finding behaviour, monitoring**

Abstract. Visual and olfactory responses of onion maggot flies (OMF), *Delia antiqua* (Meigen), to food and oviposition resources in relation to sex, ovarian development, and time of day, were evaluated in a commercial onion field in Cloverdale, British Columbia, using horizontal coloured sticky traps baited with the oviposition attractant dipropyl-disulphide (DPDS) or feeding attractant, enzymatic yeast hydrolysate (EYH). White and blue were among the most attractive colours to both males and females, but the sex ratio was strongly male-biased (2.7 : 1). Both olfactory baits increased catches of male OMF on all coloured traps to the same extent but neither bait affected the attractiveness ranking of colours. EYH significantly increased female catches on all coloured traps, whereas DPDS only significantly increased response to white traps. The joint action of visual and olfactory stimuli appeared additive in both sexes, not synergistic. DPDS significantly increased catches of mature, gravid females, whereas EYH increased catches of immature females and unbaited traps caught equal proportions of immature and mature flies. The addition of DPDS to white sticky traps could improve monitoring programmes for OMF by attracting more ovipositing females, especially at low populations levels. Census of trap catches every 2 h established a minor flight peak between 10.00 and 12.00 h, primarily in response to food baits, and a major early evening peak (18.00–20.00 h) in response to DPDS. Daily activity patterns of males and females were not significantly different and activity patterns were independent of trap colour. Response to DPDS was low throughout the morning and only started to increase in late afternoon, which is correlated with oviposition patterns observed in laboratory studies. A general crepuscular behaviour and high early evening activity supports the view that where insecticide sprays are still used effectively, these should be applied in early evening.

INTRODUCTION

The onion maggot, *Delia antiqua* (Meigen), is a serious pest of commercially- and domestically-grown onions throughout the Northern Hemisphere (Loosjes, 1976; Judd, 1994). Onion maggot flies (OMF) have been the subject of numerous studies examining the interaction of visual and olfactory cues used during the host finding (Judd & Borden, 1988, 1989, 1991, 1992) and acceptance (Harris & Miller, 1982, 1983, 1984, 1988) phases of ovipositional host-plant selection. This information has made OMF an ideal model for studying the foraging behaviour of phytophagous insects (Miller & Strickler, 1984) and has led to novel and promising behaviourally-based control strategies (Miller & Cowles, 1990). However, in most onion-growing areas of Canada, damage from onion maggots is

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still controlled by a combination of granular and liquid insecticide formulations (Judd, 1994).

The application of liquid insecticides as soil drenches (1,000 l of water per ha) to control hatching larvae (Vernon et al., 1987), but which inadvertently kill at least a small percentage of adults (Finch et al., 1986), is based on information from OMF monitoring programmes that employ various traps and temperature-dependent emergence models alone or in combination (Eckenrode et al., 1975; Liu et al., 1982; Whitfield et al., 1985; Vernon et al., 1987, 1989). In British Columbia, where an OMF monitoring programme has probably found its greatest acceptance among onion growers anywhere in North America (Vernon et al., 1987), great care has been taken in developing an optimal trap design (Vernon et al., 1989). To date, the most effective traps for monitoring OMF have been judged to be those which capture the greatest number of flies, for the lowest cost. For this reason, unbaited vertical white sticky traps (Vernon et al., 1989) have replaced onion-baited, horizontal yellow sticky traps as the standard monitoring tool (Vernon et al., 1987).

It might be argued however, that for making control decisions or for purposes of developing accurate action thresholds, knowledge of the proportion of ovipositing females in a crop at any point in time is probably more critical than total numbers caught. Knowing when ovipositing females are most active in the crop on a seasonal and perhaps a daily basis, might enable growers to schedule insecticide sprays more precisely, making them more effective. Although many visual and olfactory stimuli have been evaluated as monitoring tools for OMF, there is almost no information on the physiological state of OMF that respond to traps or what if any resource-seeking behaviour these traps elicit. Using onion-baited yellow water traps, Finch et al. (1986) found that OMF were crepuscular in their activity, moving into onion fields in the early evening. However, the flight activity patterns reported by Finch et al. (1986) could represent oviposition activity, feeding or both. Little is known about the daily feeding patterns of OMF and how these interact with daily oviposition patterns (Havukkala & Miller, 1987), but recent investigations (Prokopy et al., 1995) have shown how hunger and egg load interact to shape foraging behaviour in phytophagous insects.

Studies have shown that the sex, age and ovarian development of OMF influence their dispersal rate and long-range host-finding behaviour outside crops (Judd & Borden, 1988, 1989). Mating status, ovarian development and sex also affect the visual and olfactory behaviour of OMF foraging for ovipositional sites in onion fields (Judd & Borden, 1991, 1992). How this might affect their response to monitoring traps has not been addressed, although it is known that catches with white traps are male-biased while onion-baited traps reflect more natural 1 : 1 sex ratios (Vernon et al., 1989).

In this paper we examine the response of OMF to coloured sticky traps alone and in combination with known feeding and oviposition attractants, in an attempt to separate different resource-seeking behaviours and to establish possible stimulus interactions or synergism that could be exploited for monitoring or direct control. In this study synergism between stimuli is defined as a multiplicative increase in catches with combinations of stimuli, as opposed to simple additive increases one would expect from individual stimuli acting alone. Female response to these various baits is related to their mating status and ovarian development. Censuses of catches at timed intervals are used to establish possible daily patterns of feeding and oviposition behaviour.

MATERIAL AND METHODS

General methods

All experiments were conducted within a 6-ha commercial onion field in the muck soil growing region of the lower Fraser Valley, near Cloverdale, British Columbia, during May 1985. This period of time corresponded to peak flight of the overwintering generation of flies (Vernon et al., 1989). Coloured traps (20-by-20 cm) were constructed from white cardboard (Four-ply, Railroad Board, Domtar Fine Papers, Toronto, Ontario) that had been painted with one of the following semi-gloss enamel paints: white, blue (E871), yellow (E786), green (E785) or black. Reflectance spectra and the commercial source for these paints were described by Judd et al. (1988). Painted cardboard squares were coated with a 1-mm thick layer of Sticky Stuff® (Olson Products, Medina, Ohio) to capture alighting insects. Each sticky square was attached to a similar size horizontal wooden platform and supported 5-cm above the ground on a wooden pole. Individual traps were placed between rows of 5–10-cm high onions, cultivar Autumn Spice.

Experiments

The numbers of OMF caught on each of the 5 coloured traps alone and in combination with enzymatic yeast hydrolysate (EYH), a feeding stimulant (McLeod, 1964) and attractant (Miller & Haarer, 1981) or *n*-dipropyl-disulphide (DPDS), an oviposition stimulant (Pierce et al., 1978) and attractant (Judd & Borden, 1988, 1989) were compared. DPDS (99% pure; Kodak Chemicals, Rochester, New York) and EYH (NBC, Cleveland, Ohio) were dispensed in 25-mm-high × 60-mm-wide plastic petri dishes with lids supported 5 mm above baits on 3 nails which also held the petri dishes and sticky cards in place (Judd & Borden, 1992). DPDS was dispensed in 5 ml aliquots of a 1% (volume : volume) liquid suspension in paraffin oil and EYH was dispensed as 10 gm of powder that solidified with absorption of water moisture. Fifteen treatments (3 odour by 5 colour trap combinations) were replicated 7 times using a 3-by-5 rectangular, balanced lattice experimental design (Cochran & Cox, 1957). Each replicate lattice was spaced 25 m apart and all traps and rows within each lattice were spaced 5 m apart. This experiment was concluded after 5 days.

To determine the daily activity pattern of OMF, all flies were removed from 60 traps in 4 replicates of the above experiment every 2 h (06.00 h AM until 22.00 h PM) for 3 of the 5 days this experiment was conducted. All traps in the remaining 3 replicates were examined at the end of each day and all flies were removed. Flies were returned to the laboratory and sexed immediately. Spermathecae were dissected and examined under a compound microscope for the presence of sperm bundles as an indication of mating status. After dissection all females were fixed in Bouin's solution (Carleton & Drury, 1957) using techniques described by Theunissen (1973), and stored at 4°C for later analysis of ovarian development. Bouin's fixative preserved all ovarian structures including, ovarioles, eggs and fat bodies. Female flies were dissected under a 50× dissecting microscope and classified into one of several ovarian stages of development (Theunissen, 1973).

Statistical analyses

Total numbers of flies caught on each trap over the 5 day experimental period were transformed [$\log_{10}(Y+1)$] and analyzed using an analysis of variance (ANOVA) appropriate for balanced lattice designs (Cochran & Cox, 1957). Mean numbers of flies caught with each trap-type were compared using a Student-Newman-Keuls' (SNK) multiple range test (Zar, 1984). A χ^2 test was used to test the null hypothesis that sex ratios (based on total catches) were independent of trap type, and a SNK test modified for comparing frequency data (Zar, 1984), was used to test for individual sex ratio differences across trap types. χ^2 tests were also used to test for differences in the numbers of flies caught at different times of the day as a function of sex, trap colour, odour bait and ovarian development among females caught with different trap types.

RESULTS

Colour responses

Male OMF were equally responsive to unbaited white and blue traps (Table 1), both of which elicited significantly more alighting than yellow, green or black traps. Female

response to unbaited traps was slightly different than that of males, as white, yellow and green traps captured similar numbers of females (Table 1). Most surprising was the finding that yellow and green traps, colours typical of foliage, were no more attractive than black, to females. With the exception of black, all unbaited traps caught 2–3 times more males than females, with white traps producing the most male-biased catches (2.7 : 1). However, the natural population sex ratio is probably about 1 : 1, as found in catches on unbaited black traps (Table 1).

TABLE 1. Catches of adult onion maggot flies on horizontal coloured sticky traps alone (no odour) and in combination with the oviposition attractant dipropyl-disulphide (DPDS) or feeding attractant enzymatic yeast hydrolysate (EYH). (n = 7 replicates / treatment combination)

Trap colour	Mean number of flies caught / treatment combination ¹						Male / Female ratio ²		
	Males			Females					
	No odour	DPDS	EYH	No odour	DPDS	EYH	No odour	DPDS	EYH
White	8.0a	13.7a	13.1a	3.0ab	5.6a	10.9a	2.7a	2.5a	1.2a
Blue	7.9a	11.1ab	11.6a	4.0a	4.4a	10.4a	2.0a	2.5a	1.1a
Yellow	3.6b	7.4b	5.3b	1.4bc	2.3b	4.3b	2.5a	3.3a	1.2a
Green	2.4b	4.3c	4.1b	1.3bc	1.0b	6.3ab	1.9a	4.3a	0.7ab
Black	0.3c	1.7d	1.4c	0.3c	0.7b	3.6b	1.0a	2.4a	0.4b

¹ Means within a column followed by the same letter and means within a row for each sex underscored by a line are not significantly different (ANOVA $P < 0.05$ followed by SNK Test, $\alpha = 0.05$).

² Sex ratios within a column followed by the same letter or within a row underscored by a line are not significantly different [χ^2 test $P > 0.05$ followed by an SNK Test ($\alpha = 0.05$) modified for frequency data (Zar, 1984)].

Colour and odour interactions

Despite general numerical increases of about 1.7 fold to all colours combined, catches of male OMF were not increased significantly by baiting blue, white or green traps with DPDS (Table 1). DPDS had no influence on the ranking, or relative attractiveness of various colours to males. For males, the effect of combining DPDS and colour in these particular traps appears additive, as DPDS-baited white traps caught 13.7 males, which was not significantly different than 9.7, the additive catches of white (8.0) and DPDS (1.7) acting alone. DPDS-baited black traps are considered to act as olfactory traps alone because black traps alone caught so few insects and were almost invisible, at least to the human observer, when set against the near black organic soils at this study site. Given this assumption, the data suggest there is a lack of synergism between DPDS and specific visual stimuli associated with horizontal colour traps.

With the exception of white (Table 1), DPDS had little effect on the numbers of females caught on coloured traps. However, female catches with DPDS-baited white traps (5.6) were also statistically no greater than the additive catches (3.7) with each stimulus alone, suggesting that visual and olfactory stimuli from these traps were not acting synergistically as previously defined. Somewhat surprisingly, DPDS did not significantly increase catches of females on yellow or green foliage-coloured traps, above those on black traps.

Acting primarily as an attractant for males, DPDS generally skewed the sex ratio of catches towards males (Table 1), although this was statistically significant only for green traps.

The EYH feeding attractant increased male catches on all coloured traps (Table 1), but of these increases, only black showed a statistically significant increase. With the exception of green, EYH increased catches of coloured traps equivalent to DPDS. For males, the attractiveness ranking of trap colours baited with EYH was identical to their ranking with out baiting, indicating that no particular colour was synergised by this feeding bait.

In contrast to males, female responses to coloured traps were increased significantly by the addition of EYH (Table 1). However, foliage-associated colours were no more synergised by this proteinaceous bait than nonfoliage-associated colours. EYH-baited black traps caught as many females as did green traps baited with EYH (Table 1) and yellow was the only colour not showing a significant increase with addition of EYH. Catches with EYH-baited blue or white traps were greater than the additive catches of blue or white traps plus EYH acting alone (Table 1). The 1.37–1.65 fold increases above the additive increases, suggest EYH added to white or blue traps may act synergistically to increase catches of female OMF.

In contrast to males, female catches with EYH-baited traps of all colours except yellow, were significantly greater than catches with DPDS-baited traps of the same colours (Table 1). EYH produced a greater overall mean increase in female response ($\bar{x} = 5.2$) than it did in male response ($\bar{x} = 2.2$). That EYH is primarily a female attractant and DPDS a male attractant, at least for OMF foraging in onion fields, is illustrated by the changing sex ratios on black traps caused by baiting (Table 1). EYH produced a 12 fold increase in female response to black traps compared with only 4.6 in males, producing a strongly female-biased sex ratio that was significantly different from the male-biased catches on DPDS-baited black traps (Table 1).

Trap catches and ovarian development

Females could be classified into 4 distinct groups based on ovarian and fat body development. The youngest group contained females with several 1/4 to 1/2 full size developing eggs but with no visible chorion and most of the abdominal cavity was filled with bright yellow fat body tissue. These insects were typical of our dissections of recently-emerged adults (48–72 h at 22°C) from laboratory culture. The second grouping included individuals with several eggs in various stages of development 1/2 to 3/4 full size, none yet with chorions, but now the fat body tissue had almost disappeared. The third group included females with at least one, but usually several fully developed eggs having visible chorions, several younger developing eggs and little or no fat body. This group includes females in stages 8, 9 and 10 of Theunisson's (1973) classification system. The oldest group contained females with a few fully developed eggs or no eggs at all, with no fat body tissue and ovariole relics from past oviposition.

Of the 105 females dissected, 31 were caught on unbaited colour traps, 30 on DPDS-baited traps and 44 on EYH-baited traps. These sample sizes were too small to clearly establish whether there was a relationship between ovarian development and response to colour, however, pooling samples by odour bait independent of trap colour allowed determination of an odour by ovarian development relationship. The frequencies of females found in the 4 ovarian classifications varied significantly across the 3 odour baits

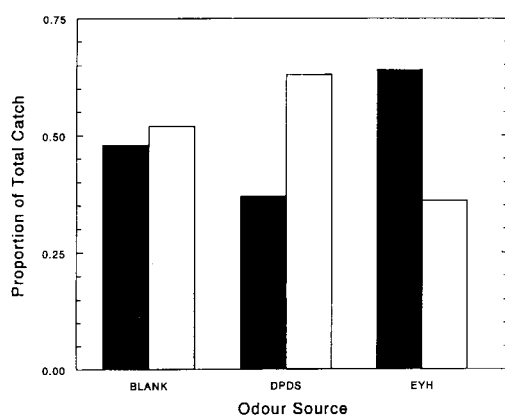


Fig. 1. Proportion of mature (white bars) and immature female OMF (black bars) caught on unbaited (BLANK), dipropyl-disulphide-baited (DPDS) or enzymatic yeast hydrolysate-baited (EYH) sticky colour traps.

any colour or odour combination, male and female catches were pooled for subsequent analysis. Pooled male and female catches during seven 2-h intervals were also independent of the five trap colours used ($\chi^2 = 30.0$, $df = 24$, $P = 0.1842$). Therefore, catches from all colours within an odour treatment were pooled and the proportions of total daily catches during each 2-h interval for the EYH-feeding and DPDS-oviposition baits were compared (Fig. 2).

Catches were made throughout the daylight hours except before 06.00 h or after 20.00 h

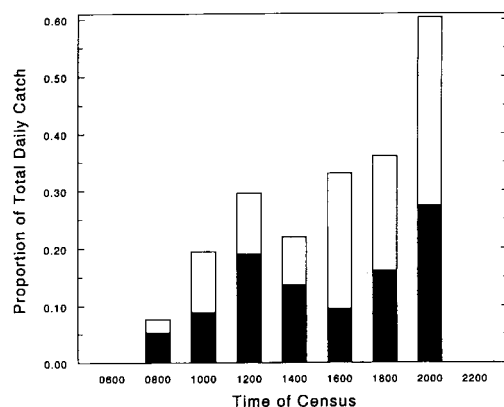


Fig. 2. Comparison of the proportion of OMF (males and females) caught on coloured sticky traps baited with the oviposition attractant dipropyl-disulphide (white bars) and feeding attractant enzymatic yeast hydrolysate (black bars) during 2-h intervals (06.00–22.00 h).

($\chi^2 = 21.6$, $df = 6$, $P = 0.0014$). Fig. 1 shows the proportions of females classified as immature (groups 1 + 2) or mature (groups 3 + 4) for each odour bait. Similar frequencies of immature and mature females were caught on unbaited traps, but DPDS increased catches of mature, gravid females, and EYH increased catches of immature females (Fig. 1). The percentages of mated females across the three odour baits, 86, 89, and 74%, respectively, were similar.

Trap catches in relation to time of day

As the numbers of insects caught were small and χ^2 tests indicated that daily flight activity of male and female OMF was not significantly different for any colour or odour combination, male and female catches were pooled for subsequent analysis. Pooled male and female catches during seven 2-h intervals were also independent of the five trap colours used ($\chi^2 = 30.0$, $df = 24$, $P = 0.1842$). Therefore, catches from all colours within an odour treatment were pooled and the proportions of total daily catches during each 2-h interval for the EYH-feeding and DPDS-oviposition baits were compared (Fig. 2). There were two peaks in daily activity (Fig. 2), a minor peak occurring between 10.00 h and 12.00 h, and a major peak between 18.00 and 20.00 h. Most of the morning activity, particularly the minor peak at 12.00 h (Fig. 2), was in response to EYH-baited traps, whereas the major evening peak was comprised of responses to both baits. Response to DPDS appeared to be lower through the early part of the day (Fig. 2) but started to increase in early afternoon between 14.00 and 16.00 h peaking at 20.00 h. However, the activity patterns were not significantly different ($\chi^2 = 14.5$, $df = 12$, $P = 0.2678$) across baited and unbaited traps. Therefore, the best measure of daily flight

activity is probably based on pooling catches across sexes, colours and odour baits as shown by the stacked bars in Fig. 2.

DISCUSSION

The response of male OMF to various unbaited horizontal colour traps was identical to their response to vertical traps having the same spectral characteristics (Judd et al., 1988). Female OMF, however, did not discriminate between colours presented as horizontal squares in exactly the same way they were discriminated when presented as vertical rectangles (Vernon & Bartel, 1985; Judd et al., 1988). These findings support the hypothesis (Judd & Borden, 1991) that spectral discrimination by female OMF depends on the shape and orientation of the visual stimulus fitting a particular template. Differences in the angle at which males and females approach traps or the heights at which each sex flies relative to the crop or traps could influence spectral discrimination of traps. Females apparently fly closer to the ground than males (Vernon et al., 1989). Viewing horizontal traps through the ventral region of the eye, which often has fewer classes of photoreceptor and potential sexual differences in the arrangement and numbers of photoreceptors across the ommatidia (Hardie, 1986), may reduce the potential for spectral discrimination of horizontal traps compared with vertical ones.

The fact that blue traps were significantly more attractive than yellow traps to both sexes contradicts previous findings with horizontal traps (Vernon & Borden, 1983; Ishikawa et al., 1985). Differences between studies using horizontal traps are likely due to differences in the spectral qualities of the horizontal traps used in the respective studies, as the present data (Table 1) are supported by studies where the identical colours were used on vertical traps (Vernon & Bartel, 1985; Vernon, 1986; Judd et al., 1988). In any event, the present study argues against the importance of yellow colouration as an important cue used to locate potential adult food plants such as the common yellow dandelion, *Taraxacum officinale* L. (Baker & Stewart, 1928; Vernon & Borden, 1983; Finch et al., 1986). There was no significant relationship between ovarian development and colour, no interaction between feeding attractants and colour and no significant increase in catches on yellow traps baited with EYH. Dapsis & Ferro (1983) also found no correlation between ovarian development and catches of *D. radicum* L. on coloured stakes, leading one to question whether there is any correlation between spectral preferences in *Delia* sp. and adult food plants (Vernon & Borden, 1983).

It could be argued that OMF caught in onion fields are unresponsive to yellow traps typical of flowering plants because they are foraging for oviposition hosts and are only responsive to cues from food plants when they leave the crop for bordering areas (Finch et al., 1986). This seems unlikely however, as volatiles from the EYH feeding attractant were as, or more attractive, than the DPDS oviposition attractant, at least in an onion field. The fact that EYH increased male and female responses to all colours, suggests that responses to volatiles from protein sources are probably not associated with any particular visual stimulus, unless it were derived by associative learning. This general response might be expected from an insect that is thought to have evolved from a general plant feeder and one which is often seen feeding on a wide variety of decaying plant material in onion fields (unpublished data). In addition, despite observations of OMF feeding on dandelions surrounding onion fields (Baker & Stewart, 1928; Finch et al., 1986), analysis of several

hundred OMF collected from commercial onion fields in British Columbia failed to find any pollen grains on or in adults (unpublished data). Flowering plants may not be important in the feeding ecology of OMF in this area of the world.

Results from this study also support previous conclusions (Judd & Borden, 1991) that for male OMF foraging within an onion crop, certain visual stimuli are more attractive than certain olfactory stimuli. Unbaited white traps were about 27 times more attractive than unbaited black traps, whereas EYH and DPDS only increased attraction to black traps by about 5–6 times. It would appear that white traps provide a simple and effective method of monitoring male OMF activity that is improved little by adding these particular volatiles. Part of the reason white traps, that may mimic white flowers, are more effective than other coloured traps, could be the fact that OMF are very active near dusk (Fig. 2), when trap luminosity and background contrast may become important features of trap visibility. As yet there are no published studies of the importance of contrast in visual responses of OMF.

Although white traps are useful for monitoring activity of male OMF their use for commercially monitoring female OMF activity is open to question. White horizontal traps produced a male-biased sex ratio (2.7 : 1) which was almost identical to that found on vertical white traps (2.4 : 1) by Vernon et al. (1989). These authors suggested placement of traps closer to the ground might bring the ratio closer to 1 : 1, but this clearly did not happen in this study. Although white traps were considered an improvement over onion-baited yellow traps for commercial monitoring programmes because of their cost efficiency (Vernon et al., 1989), many more females are attracted to onion-baited traps (Vernon et al., 1989), particularly ovipositing females (Judd & Borden, 1992), making them more sensitive to low populations and fluctuating physiological states among females. White traps caught similar proportions of immature and mature female OMF so this should be taken into account when comparing thresholds from different traps (Vernon et al., 1989).

While food baits like EYH significantly increased catches of females on white traps and brought sex ratios near 1 : 1, they primarily attracted immature females (Fig. 1). In addition, while it was attractive during this early season study, EYH decreases in attractiveness over time (Miller & Haarer, 1981), and may significantly underestimate populations of ovipositing females later in the season. For this reason EYH should probably be avoided in commercial monitoring programmes.

In comparison, traps baited with DPDS generally caught more mature females than unbaited or EYH-baited traps of similar colour. Use of DPDS-baited white traps in an OMF monitoring programme might be preferred over their unbaited counterpart (Vernon et al., 1989) for three reasons: (1) DPDS-baited traps will be somewhat more sensitive to low OMF populations because DPDS significantly increased catches of females over unbaited white traps (Table 1), and therefore, provide an earlier warning of damaging populations, (2) DPDS increases the response of gravid females (Fig. 1) and therefore, trap catches will more accurately reflect populations of ovipositing females in a crop, and (3) the inclusion of DPDS may increase the specificity of traps by deterring closely related and difficult to separate species like the cabbage maggot, *D. radicum*. Of course the additional cost and difficulty in using baited traps must be weighed against any benefits.

Even with these improvements, however, the use of DPDS is not ideal because it can lose attractiveness later in the season which does not appear to happen with cut onion baits (Vernon et al., 1989). Ideally the inclusion of volatiles from decaying onion might be the

best addition to white traps because these natural volatiles are even more attractive than DPDS to ovipositing females (Judd & Borden, 1992). Perhaps the reason for this is that decaying onion identifies a potential feeding site (personal observations), as well as oviposition site. A combination of the EYH feeding attractant and DPDS oviposition attractant might have produced catches greater than either bait alone and a sex ratio similar to onion-baited traps (Vernon et al., 1989), but even this combination would probably not produce catches equivalent to aged onion on white traps (Judd & Borden, 1992). At the present time there is no synthetic replacement for the onion-baited trap developed by Vernon et al. (1987) because despite years of research, the volatiles responsible for the attraction of aging onions are unknown. Identification of these volatiles could still benefit monitoring programmes and potentially lead to attract-and-kill or mass-trapping methods of direct control, particularly for non-commercial onion growers.

Flight activity of both male and female onion flies was seen in the late afternoon (Fig. 2). Increases in flight activity later in the day have been seen often enough with different traps (Loosjes, 1976; Whitfield, 1981; Finch et al., 1986) to suggest it is a natural pattern. Havukkala & Miller (1987) found a correlation between late afternoon and early evening flight activity and laboratory oviposition behaviour. Our observation of increased catches of gravid females on DPDS-baited traps during late afternoon and early evening would support this correlation, but with general flight activity and response to feeding baits also occurring at this time, such a correlation may be coincidental. This study has also suggested that OMF may partition their daily feeding and oviposition activities according to different times of the day. Response to DPDS was low throughout the early part of the day, when most flies were caught on EYH-baited traps and presumably searching for food (Fig. 2). Finch et al. (1986) also observed onion flies feeding in the morning hours. Response to protein baits inside an onion field indicates that OMF do not restrict their feeding activities to field borders (Finch et al., 1986). Whether OMF move in and out of onion fields more than once a day in British Columbia, or move into the field to oviposit at night and remain there until the next morning when they might feed before flying to field borders, is unclear from this study.

Patterns of daily flight activity in OMF appear to be affected by climatic differences. In this cool coastal area of British Columbia, the pattern of OMF activity was similar to that found under similar climatic conditions in The Netherlands (Loosjes, 1976), except in that study the morning peak occurred 2 h earlier. During hot dry conditions in Michigan (Whitfield, 1981) and New York (Finch et al., 1986), OMF were active in the crop before 08.00 and after 18.00 h and almost non-existent during midday. We saw some fly activity nearly all day long (Fig. 2). Under extreme heat conditions, OMF may seek shelter in headland areas or spend more time feeding there, because ephemeral food resources like cull onions and other decaying plant material would probably disappear from these fields more quickly, relative to fields with the cool, showery conditions under which OMF usually emerges in British Columbia. If more food is available in the crop and temperature and humidity conditions are not extreme, then OMF may spend a greater proportion of the day foraging in the crop (Fig. 2).

A general increase in fly activity during early evening, particularly oviposition, suggests this would be an ideal time to apply liquid insecticides against OMF (Havukkala & Miller, 1987; Finch et al. 1986), at least in areas where they are still effective because of a lack of resistance (Vernon et al., 1987; Judd, 1994). Finch et al. (1986) have challenged the utility

of adulticide sprays because their data indicated that at any one time only a small fraction of the population was affected by them, flies were seen to move out of the rows as tractor sprayers passed, and little spray was deposited on the onion leaf and much of that evaporated under high heat. For reasons stated above, weather conditions found in British Columbia may increase the proportion of flies found in the crop at any one time, and applying insecticides as a soil drench (1,000 l of water per ha), as they do in British Columbia (Judd, 1994), causes spray material to run down the sides of the onion bulb entering soil cracks where OMF are often found ovipositing. Actively ovipositing OMF are usually very sedentary and difficult to disturb (personal observations), so they probably do not fly away as tractors pass and consequently will be exposed to drench sprays for a longer time than a standard foliar spray. Although the efficacy of sprays for control of onion maggots has been questioned, onion pest managers in many areas of Canada, in particular British Columbia, are still recommending sprays with good success.

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