

Luring houseflies (*Musca domestica*) to traps: do cuticular hydrocarbons and visual cues increase catch?

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Abstract. Houseflies (*Musca domestica* L.) are a major pest species of livestock units and landfill sites. Insecticide resistance has resulted in an increased emphasis on lure-and-kill control methods, but the success of this approach relies on the effective attraction of houseflies with olfactory or visual stimuli. This study examined the efficacy of olfactory (cuticular hydrocarbons) or visual (colours and groups of flies) attractants in a commercial poultry unit. Despite simulating the cuticular hydrocarbon profiles of male and female houseflies, we found no significant increase in the number of individuals lured to traps and no sex-specific responses were evident. The use of target colours selected to match the three peaks in housefly visual spectral sensitivity yielded no significant increase in the catch rate of traps to which they were applied. This study also demonstrated that male and female flies possess significantly different spectral reflectance (males are brighter at 320–470 nm; females are brighter at 470–670 nm). An experiment incorporating groups of recently killed flies from which cuticular hydrocarbons were either removed by solvent or left intact also failed to show any evidence of olfactory or visual attraction for houseflies of either sex. This study concluded that variations of the most commonly applied methods of luring houseflies to traps in commercial livestock units fail to significantly increase capture rates. These results support commonly observed inconsistencies associated with using olfactory or visual stimuli in lure-and-kill systems, possibly because field conditions lessen the attractant properties observed in laboratory experiments.

Key words. Pest control, pheromones, poultry units, sexual dichromatism, spectral reflectance.

Introduction

The housefly, *Musca domestica* L. (Diptera: Muscidae), is widely regarded as an important pest species (Busvine, 1980; Chapman *et al.*, 1998a; Howard, 2001). Its habit of feeding on decaying matter, human waste and food, and concomitant close association with humans, has implicated *M. domestica* with the spread of numerous diseases including salmonella, diphtheria, tuberculosis, hepatitis and amoebic dysentery (Greenberg, 1973; Crosskey & Lane, 1993; Tan *et al.*, 1997). Problems with exces-

sive housefly populations are generally associated with livestock units and landfill sites used for domestic waste (Goulson *et al.*, 1999; Howard, 2001; Winpisinger *et al.*, 2005) and fly populations seem likely to increase with the projected warming of Earth's climate (Goulson *et al.*, 2005). The public health risks and annoyance associated with large housefly populations are therefore substantial and efforts to control the species have been the focus of considerable research for several decades (Wiesmann, 1962; Mitchell *et al.*, 1975; Carlson & Leibold, 1981; Chapman *et al.*, 1999; Hanley *et al.*, 2004).

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For many years effective control was achieved using contact insecticides applied by spraying. However, this approach has resulted in the widespread development of insecticide resistance (Chapman *et al.*, 1993; Keiding, 1999; Shono *et al.*, 2004). More recently the use of toxic baits for control of *M. domestica* has become commonplace, particularly within enclosed areas such as livestock units. These lure-and-kill systems rely on attracting houseflies to targets baited with a poison, which is then ingested by the fly (Chapman *et al.*, 1998a, 1998b). For this system to be effective, the targets must attract large numbers of flies of both sexes. Two different, but often interactive, approaches have been employed for this purpose. The principal technique has been to impregnate targets with (Z)-9-tricosene, one of many hydrocarbons associated with the cuticular layers of the housefly (Carlson *et al.*, 1971; Nelson *et al.*, 1981; Noorman & den Otter, 2001). Initial experimental inconsistencies and difficulties in understanding the role of this compound in housefly biology were reviewed by Howard & Blomquist (1982) and recent work has cast further doubt over the efficacy of (Z)-9-tricosene as an attractant, particularly over long distances and at the concentrations normally produced by wild houseflies (Chapman *et al.*, 1998b; Kelling *et al.*, 2003; Hanley *et al.*, 2004). Problems with this focused view of (Z)-9-tricosene as a sex attractant are illustrated by a field survey which failed to detect any (Z)-9-tricosene in many populations of housefly (Darbro *et al.*, 2005) and other findings of evidence that (Z)-9-tricosene production is a response to environmental stress (Noorman & den Otter, 2001, 2002). Given that blends rather than single compounds are usual in insect communication systems and hydrocarbon blends of low volatility can evoke strong behavioural responses over the short-to-medium range (Howard & Blomquist, 1982; Schiestl *et al.*, 1999, 2000), the attractant properties of other cuticular hydrocarbons from houseflies, particularly when presented in realistic ratios, need to be assessed.

The second approach has been to attract houseflies to baited targets using visual cues. Early laboratory studies on the response of *M. domestica* to colour suggested that they preferentially settle on black or red surfaces, and avoid blue or white surfaces (Waterhouse, 1948; Pospíšil, 1962; Hecht, 1963), although work conducted in the poorly illuminated conditions of livestock units indicated that paler colours such as yellow and white may be more attractive (Mitchell *et al.*, 1975). Other studies have suggested that the degree of contrast might be far more important than colour in evoking a response (Hecht, 1970; Howard & Wall, 1998), so that, for example, black dots on a white background may be more effective. Although Richter *et al.* (1976) reported increased housefly attraction using targets painted with a regular spacing of black spots, Chapman *et al.* (1999) found that clustered groups of black spots were more effective still as they may mimic feeding groups of flies. Wiesmann (1962) first suggested that clustered groups of individuals were the principal optical cue involved in the location of food resources for houseflies.

Despite the many experimental trials of different visual attractants, there remains a great deal of uncertainty about which combinations of colour and pattern are most effective at luring houseflies to traps. This uncertainty stems in part from the contradictory results emerging from studies conducted in

comparatively well illuminated laboratory conditions, and those performed in generally poorly lit livestock units. However, none of these earlier studies considered the importance of housefly vision and spectral sensitivity in relation to target design. This is surprising given that a great deal is known about the visual system of *M. domestica*, particularly in terms of how they perceive light. The optical sensitivity of the housefly lies between 310 nm and 700 nm (Strother & Casella, 1972). In his review of the functional organization of *M. domestica* vision, Hardie (1986) describes how the photoreceptors in a housefly's compound eye have three absorbance peaks, including one at 490 nm (blue/green) and a second at 570 nm (yellow). The third (double peak) lies within the ultraviolet (UV) range; specialized UV receptors in the eye are particularly sensitive to wavelengths of 330–350 nm (Hardie, 1984). However, to date there has been no attempt to determine how houseflies react to colours of these specific wavelengths.

This paper documents the results of three separate field experiments which assessed the efficacy of olfactory and visual cues in housefly attraction. The first experiment examined the attractant properties of a combination of cuticular hydrocarbons identified from wild houseflies and specifically tested the hypothesis that male and female houseflies release olfactory signals that are attractive to other individuals, particularly those of the opposite sex. The second study examined the role of colour, using three different paints selected to match peaks in *M. domestica* spectral sensitivity (Hardie, 1986). This experiment tested the hypothesis that individuals would be more attracted to colours matching their peak spectral sensitivity than they were to a (white) target with broad spectral reflectance. Finally, the response of *M. domestica* to clusters of other houseflies was examined. Having first measured the spectral reflectance of wild male and female houseflies in the laboratory, we arranged groups of recently killed male or female flies on individual traps in the field. In order to distinguish potential interactions between olfactory and visual cues on the number of housefly landings recorded, we removed cuticular hydrocarbons from half the flies prior to the start of the experiment by solvent washing. This allowed us to test the hypotheses that houseflies are attracted to stationary individuals as a feeding cue and that visual or olfactory cues from groups of male and female flies differentially attract individuals of the opposite sex. The combination of field studies documented here therefore examines the principal methods (i.e. olfactory and visual cues) reputed to attract houseflies to commercial lure-and-kill traps and provides the first experimental review of how colours approximating the absorbance peaks in housefly vision influence trap success.

Materials and methods

Study site

All experiments were conducted in the upper level of a deep-pit, caged layer poultry unit in southern England. The unit was 100 m long and 150 m wide and contained 40 000 chickens housed in 11 rows of tiered cages. The birds were housed on the upper level and a manure pit was located on the lower level.

Lighting (03.00–17.00 hours) was provided by 12 fluorescent strip-lights positioned at 5-m intervals along each row. Temperature was maintained at approximately 21 °C. Normal working practices were maintained throughout the duration of each experiment and, apart from the traps used in the experiments, no other housefly controls were employed during the duration of the trials. All experiments were conducted at least 8 weeks after the removal of manure, thus allowing the housefly population time to re-establish (Chapman *et al.*, 1998a). In order to standardize the relative time period between observations, all traps were set, monitored and recovered between 10.00 hours and 12.00 hours.

Experiment 1. Attractant properties of cuticular hydrocarbons

This experiment simulated the profile of principal hydrocarbons from wild male and female *M. domestica* to determine whether houseflies in the field respond to the olfactory cues provided by other flies. To prepare the experimental hydrocarbon solutions, gas chromatography (GC) and gas chromatography-mass spectroscopy (GC-MS) determined ratios and quantities of the individual hydrocarbons recovered from wild *M. domestica* obtained from the experimental locality (Table 1). Using stock solutions, tetracosane, pentacosane, hexacosane, heptacosane, nonacosane, (Z)-9-tricosene (Sigma-Aldrich Ltd, Poole, U.K.), (Z)-9-heptacosene and (Z)-9-nonacosene (Denka International BV, Barneveld, the Netherlands) were mixed and diluted to a concentration of 10 or 100 male or female fly equivalents per 100 µL aliquot. Although these mixtures were only two to three orders of magnitude more concentrated than the hydrocarbons produced by individual flies, it is known that strong background odours such as those found in commercial livestock units increase the sensitivity of the olfactory receptors in *M. domestica* (Kelling *et al.*, 2002). Consequently, the olfactory sensitivity of individuals within the population in our poultry unit is likely to be adapted to the odours produced by the chickens and their manure, and thus the flies can be expected to detect to the concentrations of cuticular hydrocarbons used here.

Table 1. Quantities (mean ± standard error [SE]) of principal cuticular hydrocarbons identified using gas chromatography-mass spectroscopy (D. Dunn, unpublished data, 2004) for male ($n = 7$) and female ($n = 8$) houseflies (*Musca domestica*) captured from a commercial poultry unit in southern England.

Cuticular hydrocarbon (µg)	Male		Female	
	Mean	SE	Mean	SE
Tetracosane	0.7	0.05	0.3	0.1
Pentacosane	78.0	18.8	14.6	3.4
Hexacosane	2.1	0.4	1.5	0.3
Heptacosane	5.8	0.7	29.7	3.2
Nonacosane	7.6	0.8	34.8	2.6
(Z)-9-tricosene	13.4	1.9	2.5	0.3
(Z)-9-heptacosene	93.9	7.7	30.0	2.0
(Z)-9-nonacosene	9.2	0.7	38.3	5.7

A 25-mm diameter filter paper (Whatman GF/B; Whatman International Ltd, Maidstone, U.K.) was fixed to the centre of a 400 × 245-mm yellow sticky trap (Agrisense-BCS Ltd, Pontypridd, U.K.) (Black & Krasfur, 1985; Hogsette *et al.*, 1993; Goulson *et al.*, 1999, 2005). A 100-µL aliquot of mixed hydrocarbon solution was applied to the centre of the filter paper using a glass pipette. Traps were then suspended 5 m apart by string from a wire running across the length of each row, with the centre of each trap positioned about 2.5 m above the ground and immediately beneath one of the fluorescent tubes illuminating the unit and casting 0.062 ± 0.005 Lux at trap height. There were six rows of traps, each with one randomly assigned, replicate sample of each of the test hydrocarbon solutions and the hexane control. Edge effects were avoided by suspending blank sticky traps at the ends of each row. The experiment was conducted over 7 days until the traps were removed. However, we quantified total fly numbers caught 1 day into the experiment, before quantifying the total number of flies and their sex ratio captured up to day 7.

Prior to statistical analysis, data were subjected to a Cochran's test for homogeneity of variance (Underwood, 1997). No transformations were required. One-way anova was used to examine variation in fly capture rates and chi-square tests were used to examine differences in the frequencies of male and female flies caught by the different hydrocarbon treatments.

Experiment 2. Attractant properties of colours

The role of colour in attracting houseflies was examined by using three paints designed to provide spectral reflectance peaks approximating the most sensitive regions of *Musca* spectral absorption (Hardie, 1986). Two of the paints were formulated from commercially available mixes (Crown Decorative Products Ltd, Preston, U.K.). A blue/green paint (Crown mixture code: 3060-B40G) and a green/yellow paint (Crown mixture code: S1050-G50Y) yielded spectral reflectance peaks at 490 nm and 565 nm, respectively (Fig. 1). A third paint (Yellow

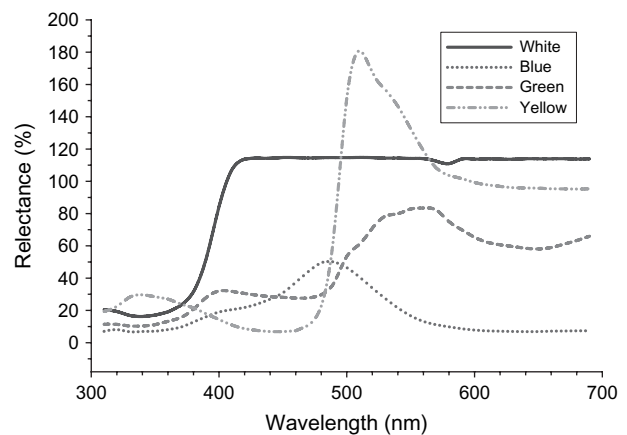


Fig. 1. The spectral reflectance of four different paints used to examine the effect of trap colour on housefly catch rates in a domestic poultry unit in southern England.

Glow B29; Plasti-kote Ltd, Cambridge, U.K.) provided two reflectance peaks at 345 nm (UV) and 512 nm (yellow). The fourth mixture was a white paint (Code BS 00 E 55, Crown Decorative Products Ltd) with a continual peak in spectral reflectance at 400–700 nm.

Two coats of paint were applied to 400 × 245-mm pieces of cardboard, such that there were 10 replicate targets of each colour. Once the paint had thoroughly dried, the targets were covered with a 1-mm thick layer of adhesive (OecoTAK A5; Oecos, Kimpton, U.K.) to trap houseflies. Spectral reflectance was checked after the glue had been applied to ensure that the adhesive did not significantly affect the paint's spectral properties. The traps were then suspended in five rows in the poultry unit as described above, with two replicates of each colour randomly assigned to each row. Traps remained in the unit for 7 days. Total fly numbers were scored on days 1 and 7. The sex ratio was scored on day 7.

Data were subjected to a Cochran's test for homogeneity of variance (Underwood, 1997); the day-7 data required square-root transformation prior to ANOVA. Because there were two replicate treatments within each row, we used nested ANOVA to examine differences in housefly catch rates among colour treatments and to test for differences between rows. Chi-square tests were used to examine differences in the frequencies of male and female flies caught using the different colour treatments.

Experiment 3. Attractant properties of housefly groups

Prior to this experiment, the spectral reflectance of 30 male and 30 female houseflies was measured to determine any visual differences between sexes. The flies were collected from the same poultry unit used in the experimental trials and were killed on the same day by freezing for 30 min, prior to measurement of their thoracic spectral reflectance. Measurements were made using a bifurcated fibre optic reflectance probe (R200-7; Ocean Optics BV, Duiven, the Netherlands) connected to a DH2000 deuterium-halogen lamp, an SD2000 dual channel spectroradiometer and a notebook computer running OOIBASE32 software (all Ocean Optics BV). Each spectrum, comprising 1125 datapoints (reflectance from 300–700 nm at 0.36-nm intervals), was standardized for brightness differences by subtracting its mean reflectance across all wavelengths. Principal components analysis (PCA) was used to transform a large number of correlated variables (in this case, reflectance at 0.36-nm intervals) into a few orthogonal variables representing spectral shape (Endler & Mielke, 2005). ANOVA was used to test for differences between male and female reflectance spectra in terms of their PC1 and PC2 scores (Cuthill *et al.*, 1999).

In order to test the hypothesis that stationary (~ feeding) groups of flies attract other individuals, we fixed 10 newly freeze-killed *M. domestica* to the centre of a 400 × 245-mm yellow sticky trap (Agrisense-BCS Ltd). This treatment broadly replicated the grouping of 14 8-mm diameter black spots utilized by Chapman *et al.* (1999). Prior to being fixed to the traps, the flies were sorted into male and female groups, and

half of each sex group was washed for 60 min in hexane to remove cuticular hydrocarbons. The flies were arranged in a hexagonal array, with each insect separated by 20 mm and aligned so that their legs and ventral portion adhered to the trap surface. In addition to blank control traps, there were four treatment groups: washed male flies; washed female flies; unwashed male flies, and unwashed female flies. These treatments allowed us to investigate the role that sexual dimorphism plays in visual and olfactory cues in attracting other houseflies. The traps, with attached flies, were suspended in five rows of the poultry unit as described above, with two replicates of each treatment and control group randomly assigned to each row. Traps remained in the unit for 7 days. Total fly numbers were scored on days 1 and 7. The sex ratio was scored on day 7.

Prior to statistical analysis, data were subjected to a Cochran's test for homogeneity of variance (Underwood, 1997). No transformations were required. Variation in fly capture rates was examined by one-way nested ANOVA. Chi-square tests were used to examine differences in the frequencies of catch of male and female flies.

Results

Experiment 1. Attractant properties of cuticular hydrocarbons

There were no significant differences (day 1: $F_{4,25} = 0.04$, $P = 0.996$; day 7: $F_{4,25} = 0.08$, $P = 0.989$) between the mean number of houseflies caught by the hexane control traps and the four cuticular hydrocarbon mixtures (Fig. 2). Although there was a great deal of variability within treatments, there was remarkably little difference between the mean numbers of flies caught in the most successful (e.g. day 7 'female × 100' = 44.2 flies/trap) and least successful ('male × 100' = 36.2 flies/trap) traps. Moreover, there were no significant differences in the

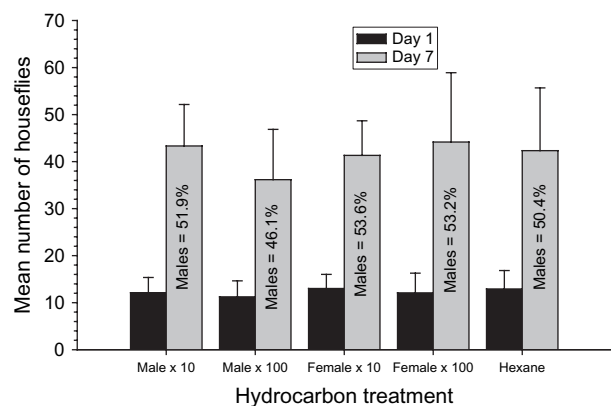


Fig. 2. The effect of hydrocarbons on mean (\pm standard error) housefly (*Musca domestica*) catch rates in a domestic poultry unit in southern England. Groups of hydrocarbons were mixed to simulate the cuticular hydrocarbon profile of male and female houseflies at 10 and 100 times the concentrations established in laboratory trials. The proportion of the total housefly catch comprised of male flies at day 7 is given.

proportions of male and female flies recorded for each treatment on day 7 ($\chi^2_4 = 0.634$, $P = 0.959$).

Experiment 2. Attractant properties of colours

Neither trap colour nor row position had a significant effect on housefly catches at day 1 (colour treatment: $F_{3,20} = 0.52$, $P = 0.676$; row effects: $F_{16,20} = 2.01$, $P = 0.070$) or day 7 (colour treatment: $F_{3,20} = 0.90$, $P = 0.463$; row effects: $F_{16,20} = 1.09$, $P = 0.423$). Moreover, there were no significant differences ($\chi^2_3 = 0.679$, $P = 0.878$) in the proportions of male and female houseflies caught by different colour treatments on day 7 of the experiment (Fig. 3).

Experiment 3. Attractant properties of housefly groups

There was a significant difference between male and female fly spectra in terms of PC1 (ANOVA on arc-sin transformed data: $F_{1,58} = 68.45$, $P < 0.001$) and PC2 (anova on arc-sin transformed data: $F_{1,58} = 6.87$, $P < 0.011$) (Fig. 4). In PCA of natural spectra, PC1 represents variation in mean reflectance (i.e. brightness) (Cuthill *et al.*, 1999). Although there are significant differences in mean reflectance between male and female houseflies, there was also a significant difference between spectral shape (colour) represented by PC2, as shown in the ordination plot (Fig. 5). The variation explained by each principal component is determined by the coefficient values at each wavelength (Fig. 6). Female housefly spectra have more negative PC1 scores (Fig. 5) and thus more of the variation in that component is explained where the coefficient values are more negative (470–670 nm; Fig. 6). Conversely, male houseflies are brighter at 320–470 nm (Fig. 5). In terms of PC2, males reflect significantly more light at 570–720 nm (red), whereas females reflect more light below 570 nm (Figs 5 and 6). Therefore, male houseflies are more 'red' in colour, whereas female houseflies reflect more short-wavelength light.

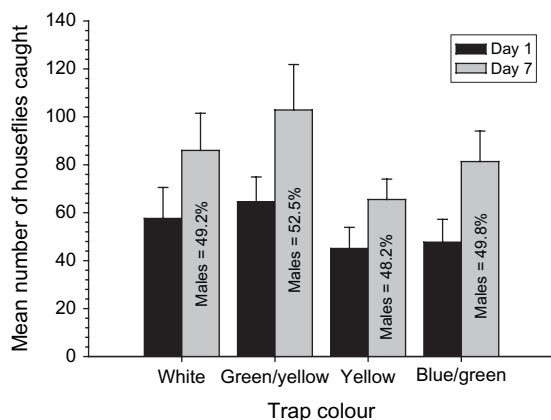


Fig. 3. The effect of trap colour on mean (\pm standard error) housefly (*Musca domestica*) catch rates in a domestic poultry unit in southern England. The proportion of the total housefly catch comprised of male flies at day 7 is given.

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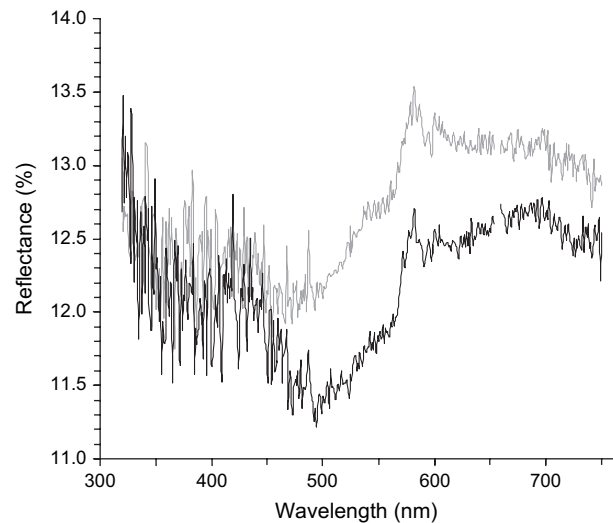


Fig. 4. Comparison of thoracic spectral reflectance for male (black, $n = 30$) and female (grey, $n = 30$) houseflies (*Musca domestica*).

Groups of houseflies had no significant effect on housefly catches at day 1 (target treatment: $F_{4,25} = 0.62$, $P = 0.665$; row effects: $F_{20,25} = 1.59$, $P = 0.136$) or day 7 (target treatment: $F_{4,25} = 1.04$, $P = 0.407$; row effects: $F_{20,25} = 1.02$, $P = 0.472$). Moreover, there were no significant differences ($\chi^2_4 = 4.314$, $P = 0.365$) in the proportion of male and female houseflies caught by different target treatments on day 7 of the experiment (Fig. 7).

Discussion

Considerable doubt has recently been cast over the role of (*Z*)-9-tricosene as a sex-attractant in *M. domestica* (Noorman & den Otter, 2001; Kelling *et al.*, 2003; Darbro *et al.*, 2005) and thus its use as a means of luring houseflies to traps in field situations (Hanley *et al.*, 2004). Cuticular hydrocarbons such as (*Z*)-9-tricosene are of low volatility and can only influence in-

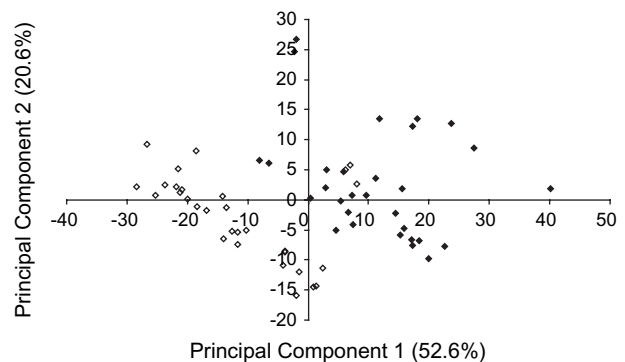


Fig. 5. Ordination plot summarizing the principal components of male (closed diamonds) and female (open diamonds) housefly (*Musca domestica*) spectral reflectance. Females have more negative PC1 and PC2 scores than males.

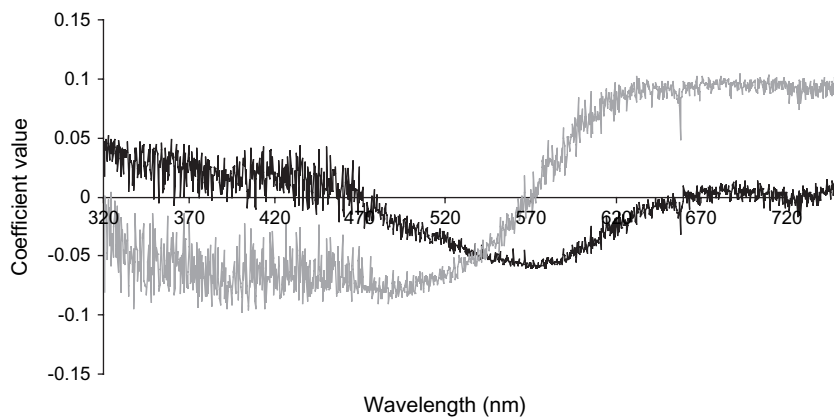


Fig. 6. Coefficient values for the principal components 1 (PC1; black line) and 2 (PC2; grey line) of housefly (*Musca domestica*) spectral reflectance. The negative PC1 and PC2 scores for females are explained by negative variation in coefficient values of 470–670 nm and below 570 nm respectively.

sect behaviour at short-to-medium range (Schiestl *et al.*, 1999, 2000; Noorman & den Otter, 2001; Kelling *et al.*, 2003). By contrast, it is widely believed that variation in trap colour and the use of strong contrast patterns to mimic aggregations of feeding houseflies significantly enhances catch rates (Mitchell *et al.*, 1975; Chapman *et al.*, 1999). It is surprising therefore that neither the use of trap colours employed to specifically match the peaks in housefly spectral sensitivity nor groups of recently killed houseflies affixed to traps resulted in significantly improved housefly attraction. Similarly, we were unable to detect any variation in male and female catch rates based on sex-specific olfactory stimuli. Although differences in cuticular hydrocarbon profiles between male and female houseflies are well known (Nelson *et al.*, 1981; Noorman & den Otter, 2001), spectral variation associated with sex has not previously been demonstrated. Here we establish a clear sexual dichromatism between male and female houseflies. Nevertheless, and despite the significant differences in cuticular hydrocar-

bon profile and spectral reflectance shown by male and female houseflies, neither factor had any significant influence on the relative proportions of male and female flies caught in this experiment. Thus, overall, none of the visual or olfactory cues we employed to lure houseflies to our traps resulted in improved catch rates of either sex above those caught on untreated control traps.

The majority of studies showing strong visual (Hecht, 1963; Richter *et al.*, 1976; Howard & Wall, 1998) or olfactory (Silhacek *et al.*, 1972; Carlson *et al.*, 1974; Cosse & Baker, 1996) stimulation in houseflies have been conducted in laboratory conditions where light and air quality are high and easily controlled. Trials conducted in field conditions have, by contrast, often yielded results contradictory to those of laboratory experiments (Howard & Wall, 1998; Chapman *et al.*, 1999; Hanley *et al.*, 2004). The relatively poorly aerated and dimly lit conditions associated with commercial livestock units would foster competing odour sources and may be particularly effective at reducing the attractant properties of otherwise strong olfactory or visual stimuli, although in some cases pale-coloured targets (white or yellow) impregnated with (*Z*)-9-tricosene have proved to be highly effective lures for houseflies in poultry units (Mitchell *et al.*, 1975; Burg & Axtell, 1984; Chapman *et al.*, 1998b). The use of male and female cuticular hydrocarbons (experiment 1), and relatively pale visual cues (yellow, fluorescent yellow or white targets in experiment 2) had no significant effect on *M. domestica* catch rates in this study, suggesting that when these olfactory and visual cues are used in isolation, they are ineffective. However, it must be remembered that the hydrocarbons used in experiment 1 were applied to yellow-coloured traps, with no clear synergistic effect. Moreover, experiment 3 combined the widely reported visual stimulation provided by clustered individuals (Richter *et al.*, 1976; Chapman *et al.*, 1999) with potential olfactory stimulation arising from groups of freshly killed male or female houseflies, without yielding increased rates of fly capture.

The lack of observed differences in housefly catch rates for treated traps might also be ascribed to the generally high *M. domestica* populations present in the poultry unit during our experiments. Although our catch rates were lower than those reported in similar studies (Black & Krasfur, 1985; Hogsette

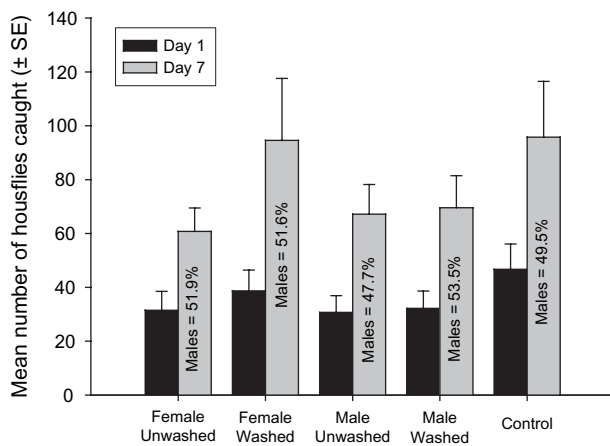


Fig. 7. The effect of clusters of male and female houseflies on mean (\pm standard error) housefly (*Musca domestica*) catch rates in a domestic poultry unit in southern England. Flies were either washed in hexane to remove their cuticular hydrocarbons or presented unwashed. The proportion of the total housefly catch at day 7 comprised of male flies is given.

et al., 1993), after only 7 days most traps had caught well in excess of 50 individuals (equivalent to > 510 flies/m²/week). Moreover, the random capture of flies on any given trap might in itself lead to increased landings simply because of the attractant effect that groups of houseflies appear to exert on other individuals (Richter *et al.*, 1976; Chapman *et al.*, 1999) (although no such effect was apparent in experiment 3). Such high rates of capture could potentially mask the attractant effects of visual or olfactory stimuli examined in this study. However, the fact that there was no effect of visual or olfactory stimulation on houseflies after only 1 day, presumably while olfactory cues were still most contrasting before the targets became heavily loaded with flies, suggests that the high *M. domestica* density in the poultry unit had little influence over the lack of significant differences between treatments. Moreover, effective control is most needed when fly populations are high and the data in this study suggest that these approaches are not effective at attracting flies under these conditions.

Given the projected increases in housefly populations and incidence of vector-borne disease associated with global warming (Goulson *et al.*, 2005; Haines *et al.*, 2006), the need for effective housefly control may become increasingly important. From this point of view, the failure, in this study, to lure houseflies to traps using various olfactory or visual cues suggests that lure and trap systems alone may not represent the most effective control measure for this pest species. Given the inherently large housefly populations associated with commercial livestock units, higher concentrations of cuticular hydrocarbons than those employed in this study may increase individual capture rates. However, the economic costs associated with this approach reduce its feasibility, even if it is successful. Other options, such as methods that use biological control with fungal pathogens (Kaufman *et al.*, 2005; Lecuona *et al.*, 2005), parasitoids (Skovgard & Nachman, 2004) or autosterilization (Howard & Wall, 1996a, 1996b), may be required as part of an integrated control strategy for houseflies in the future.

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