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Attractiveness of different light wavelengths, flicker frequencies and odours to the housefly (*Musca domestica* L.)

Smallegange, R

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Chapter 6

General Discussion

Introduction

Despite its long association with man, the housefly (*Musca domestica* L.) remains one of the most difficult pests to control. It is a very abundant insect that can be found in human dwellings, dairies, poultry houses, horse stables, food processing factories, and other domesticated areas and buildings (Hewitt, 1910, 1912; West, 1951; Hansens, 1963; Lillie and Goddard, 1987; Kettle, 1995). Although houseflies have not been shown to cause direct losses in animal production or performance, in large numbers these flies cause annoyance and nuisance. Moreover, they are potential transmitters of human and animal pathogens. Therefore, a lot of money is spent in trying to control this insect species.

Reliance on insecticides for fly control is decreasing because of increased environmental constraints and insecticide resistance. So far, biological control with natural enemies often has disappointing results. As a consequence, there is a need for effective, target-specific, and environmentally acceptable fly control methods. Light and odour-baited traps are considered to be promising devices to control houseflies indoors, although, up to date, they are not effective enough to reduce fly populations to acceptable levels. We examined possibilities to improve the effectiveness of these types of traps. The results of our studies are described in the previous chapters and will be discussed further in this chapter, especially with a view to practical application.

Discussion of research results

Experiments to examine the responses of *Musca domestica* L. to light sources with different spectral compositions were done with flies originating from three different strains (Chapter 2): a WHO strain (Ij2) obtained from the Statens Skadedyrlaboratorium in Lyngby (Denmark) which had been reared in laboratories since 1961; a 'vanDiermen' strain which had been present in our laboratory since 1995 and had been obtained from a poultry farm in Barneveld (The Netherlands) where insecticides were still frequently used in the manure pit; and a 'Pesse' strain which had been reared in our laboratory since 1996 and which originated from a piggery in Pesse (The Netherlands). Application of chemicals at the latter farm had ended in 1995 and since then the robber fly *Ophyra aenescens* is deployed to control fly species. The strain with the most 'natural' origin, the Pesse strain, was chosen to be used in the experiments described in Chapters 3 to 5, which deal with the attractiveness of flickering ultraviolet light and with the attractiveness of several odour sources when present alone and when combined with ultraviolet light.

Differences in the amount of visual pigment were found through *in vivo* measurements on the eyes of houseflies of the various strains. A relationship with the duration of rearing in laboratories was thus revealed: wild-type and 'stable flies' (first-generation laboratory flies emerged from larvae and pupae collected in the two different stables) had considerably more visual pigment than flies which had been reared in the laboratory during several generations (Chapter 2). Although the amount of visual pigment appeared to be similar for the three laboratory strains (WHO, vanDiermen and Pesse) when it was measured, this may not have been so during the light response experiments which were done before these measurements were made; flies of different strains were tested at different periods after the beginning of their rearing in the laboratory. Differences in the amount of visual pigment between strains in the period that experiments were done may explain the differences in the light response that were found between the three strains when the attractiveness of ultraviolet lamps with different spectral compositions, and blue, green and white light was tested during 1-choice experiments in a flight chamber (210 cm long, 60 cm wide, 60 cm high; Chapter 2). However, from our results it is not clear whether this did happen and to what extent. To have been able to answer this question, the light responses and the contents of visual pigment of the Pesse and vanDiermen strains should have been examined from the moment they had been introduced in our laboratory. Also other 'strain-related' characteristics that we were not aware of may have determined the light responses of the three different strains, explaining the interactions that were found between strain and ambient illumination as well as between strain and sex of the flies.

The dramatic effect of laboratory rearing on the amount of visual pigment of houseflies indicates that, in general, care should be taken to extrapolate results obtained from laboratory insects to 'reality'. Laboratory rearing may

change several physiological characteristics. The monotonous environment and the relatively 'easy' life in the laboratory may lead to changes in sensitivity of senses and to changes in molecular mechanisms underlying them. Fundamental investigations of these mechanisms in laboratory insects may thus reveal sensitivities different from those of wild-type insects. Moreover, the behavioural responses of laboratory insects may not reflect the behaviour of the insects in nature. Therefore, we want to emphasize that the results we obtained in the laboratory may not simply be applicable in control measures in practice without first investigating their effects in the environment where fly control is needed.

Our experiments showed that flies of all three strains were hardly or not attracted to the test lamps when they were younger than 3 days. Only older flies were positively phototactic. This means that light traps cannot be used to catch immature flies. Recordings of the locomotor activity showed that young flies were less active than older ones. The change in phototactic response at the age of three days coincides with the time that the flies become sexually mature (West, 1951; Dillwith *et al.*, 1983; Blomquist *et al.*, 1984). This seemed to confirm the suggestion of Skovmand and Mourier (1986) that young flies are hardly attracted to light because they are hardly active. However, our experiments showed that flies younger than 3 days are readily attracted to various odours (Chapter 4). This suggests that the low responsiveness of immature houseflies to light may be due to the neural processing of the visual information. *In vivo* measurements of the visual pigment did not reveal differences between flies of different age (Stavenga, pers. comm.).

Not only the origin, sex and age of the flies affect their phototactic behaviour, also environmental parameters were found to play a role. Although the flies' locomotor activity is higher in an illuminated environment than in the dark, in 5-minutes experiments in a 'dark' (illuminated by a red fluorescent tube) flight chamber (210 cm long, 60 cm wide, 60 cm high) larger numbers of mature flies were attracted to the light sources than when the flight chamber was illuminated by a white fluorescent tube (Chapter 2). This may be due to the fact that flies respond more quickly to light in the dark than in the light as was found in an experimental room (310 cm long, 200 cm wide, 240 cm high; Chapter 2). Similar to what Roberts *et al.* (1992) have found, in experiments of 2½ hours in this experimental room, catches were equally high in the dark and in the light (Chapter 2). This indicates that, during daytime, light traps can be used in dark as well as in illuminated rooms for attracting houseflies. In addition to this, from some pilot studies it appeared that the flies can also readily be caught by light traps during the night (Figure 1) although our actograph recordings showed that houseflies are hardly active during the night.

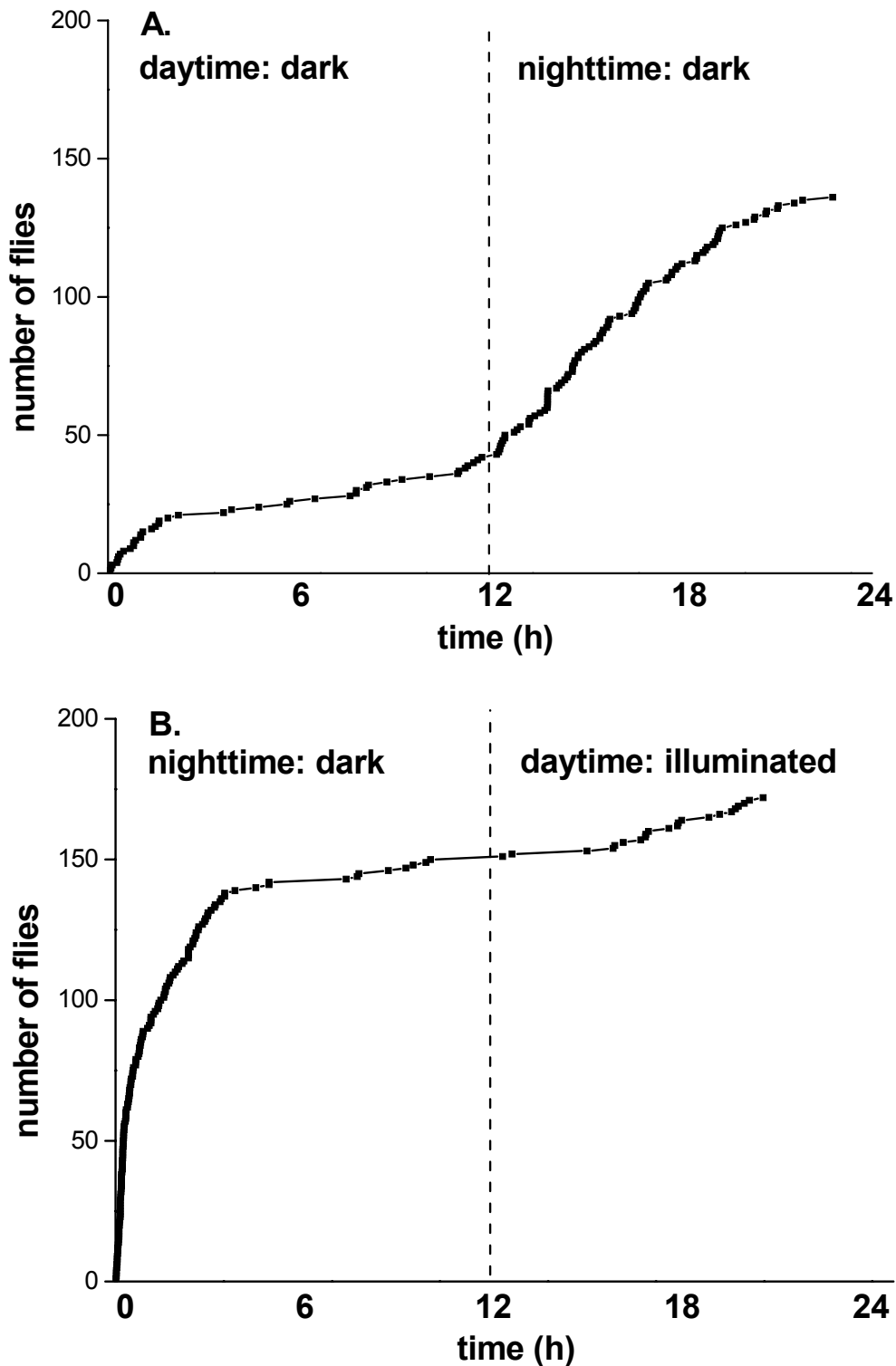


Figure 1. Examples of the catching rate of an electrocuting light trap containing an ultraviolet lamp during day and night time (about 200 flies released in each experiment; at time = 0). A: experimental room (310 cm long, 200 cm wide, 240 cm high) dark both during the day and night; B: experimental room dark during the night and illuminated during the day using a 36 Watt white fluorescent lamp (Philips TLD36W/33, 100 Hz) suspending from the centre of the ceiling.

Mazokhin-Porshniakov (1960), Goldsmith and Fernandez (1968) and Bellingham and Anderson (1993) measured a peak at 340-350 nm in the sensitivity of the eye of *M. domestica*. Goldsmith and Fernandez (1968) stated that the visual apparatus of insects such as the housefly is designed to exploit the shortest wavelengths available in the environment (because of the filtering effect of ozone in the earth's atmosphere no solar energy of wavelengths shorter than 300 nm reaches the earth's surface). This suggestion is supported by Mazokhin-Porshnyakov (1969) and Menzel (1979) who believe that the phototactic response of flying insects is an escape response in reaction to switching on a lamp and that ultraviolet light, of which the sky light is the main natural source, is the most reliable signal for this response. This could explain why for all strains all ultraviolet light sources that were tested were very attractive to both male and female flies. Obviously, in an illuminated room, the light emitted by the white, green, and blue lamps had too many wavelengths in common with the ambient light to be attractive whereas the ultraviolet lamps emitted wavelengths not present in the ambient light. The fact that ultraviolet light is highly attractive to mature houseflies can be used for the development of control measures. Considering the proportion of flies they attracted in the experimental room and their catching rate, lamps UV5 and UV9 seem to be good candidates for this purpose. These two lamps have emission peaks near to the sensitivity peak of the houseflies' eyes (at 350 and 365 nm, respectively).

Analysis of the data of the 1-choice experiments in the experimental room indicated that something in the room may have activated a group of flies at the same time. The escape response theory affords reason to expect that all flies fly to an ultraviolet light source as soon as the light is switched on. Time recordings of the catches of flies attracted to light sources (Chapter 2) showed that this is not the case. Therefore, switching on a lamp is probably not the only trigger causing an escape response. An explanation may be found in the work of Meyer (1978a) who studied the phototactic behaviour of fruitflies (*Drosophila melanogaster*). These studies revealed that as to their phototactic behaviour two different groups of flies can be distinguished. One group shows a fast phototactic response, moving quickly towards a light source, whereas the other shows a slow phototactic response and does not seem to be primarily attracted to light (Heisenberg, 1972: see Meyer, 1978a). Meyer (1978a) suggested that only relatively undisturbed insects may show slow phototaxis and that the fast phototactic reaction may be due to an escape response towards light. Both flies with fast and slow phototactic responses may have been involved in our experiments.

It is likely that the escape response also plays a role in the response to an ultraviolet lamp with a flicker frequency of 40000 Hz when in competition with an ultraviolet lamp with a frequency of 10 Hz; a frequency of 10 Hz, and probably also of 4 Hz, seems to cause an escape response in both males and females towards the higher flicker frequency (40000 Hz) (Chapter 3). Light

with a flicker frequency of 40000 Hz will appear continuous to the houseflies, like sky light (the eyes of houseflies have a flicker fusion frequency of approximately 270 Hz; Vogel, 1956). The retinula cells of the blowfly *Calliphora vicina* showed maximum responses to flickering frequencies of sinuswave light between approximately 4 and 20 Hz (Leutscher-Hazelhoff, 1973). Obviously, the low flicker frequency of 10 Hz startles the flies and leads them to flee towards sky light or a light resembling sky light (Mazokhin-Porshnyakov, 1969; Menzel, 1979; Holmquist and Srinivasan 1991; Trimarchi and Schneiderman, 1995). This suggests that ultraviolet lamps with frequencies of 4 to 10 Hz may be used in a 'push-pull system' in order to drive houseflies either outdoors or towards 'non-flickering' ultraviolet lamps in killing devices.

Male houseflies regularly chase moving conspecifics (West, 1951; Vogel, 1956; Land and Collet, 1974; Wehrhahn et al., 1982). We assumed that this chasing behaviour is induced by a visual cue, which is probably the frequency (around 175 Hz) of the wing movements of conspecifics. We expected that light flickering at the same frequency may also induce this behaviour. Indeed, in both 1- and 2-choice experiments of 2½ hours we found that test lamps flickering at 175 Hz caught males faster than lamps flickering at the other frequencies (Chapter 3). Since in 1-choice experiments 175 Hz lamps attracted considerable numbers (60-100%) of both males and females, this frequency seems a good candidate to apply in light traps. Ultraviolet lamps flickering at 40 Hz were the fastest catchers of females. This frequency attracted about 75 to 95 percent of both females and males in 2½ hours and may therefore also be interesting for practical use. However, care should be taken with application of lamps flickering below the flicker fusion frequency of humans, because this may cause emotional disturbance.

An alternative way of catching flies may be the use of attractive odours to lure them to a trap. In accordance with electrophysiological studies which showed that antennal olfactory cells of newly emerged houseflies (<1-day old) are already responsive to odours (Kelling and Den Otter, 1998; Smallegange *et al.*, 1999; Kelling, 2001), our behavioural studies revealed that young as well as mature flies not only perceive odours but may also be attracted to them (Chapter 4). Upwind flight was only observed when the airflow was loaded with (certain) odours. The physiological state of insects, for example, age, sex, reproductive development and protein deficiency, appeared to affect the behavioural responses of flies in olfactometer studies (Pospíšil, 1958; McIndoo, 1926: see Frishman and Matthyse, 1966; Baker and Cardé, 1984; Mitchell and Soucie, 1993; Ashwort and Wall, 1994; Nakagawa *et al.*, 1994; Wall and Warnes, 1994). We found no significant differences in responses to odours between young and mature houseflies, with the exception that only young flies and no mature flies were attracted to the odours of foul housefly eggs and of moist yeast. We also showed that more odour sources were attractive to the flies when they had been deprived of food (Chapter 4). This is

probably due to the fact that starved insects have lower behavioural response thresholds to food odours than fed ones (Green, 1964; Bursell, 1990; Schofield and Brady, 1996). Chicken manure, tainted chicken and tainted pig meat, fly food, and bread soaked in water or milk were attractive to well-fed as well as to food-deprived flies. Bread, marmite and fruits were only occasionally visited by food-deprived flies (Chapter 4). All these attractants are known to be suitable sources of protein and/or carbohydrates for the flies or may serve as oviposition medium and as a site to encounter mates (West, 1951; Pospíšil, 1958; Saccà, 1964; Goodman *et al.*, 1968 and Busvine, 1980: see Chapman *et al.*, 1998). This does not seem to explain why we also found that females and males (well-fed and mature) may respond differently to different odour sources: moist yeast and chicken manure were only attractive to females, whereas bread soaked in beer or vinegar attracted only males. Marmite and all types of tainted meat tested (pork, beef, and chicken) attracted both sexes (Chapter 5).

The volatile compounds responsible for the attractiveness of natural products to houseflies should be identified and a synthetic mixture developed (individual synthetic odours induce hardly any response; Chapter 4). Using a standardised mixture increases the reliability of experiments and simplifies comparing data of different experiments. Tests with different concentrations of the standard mixture may reveal the best concentrations to be used for decreasing fly population densities under different circumstances. A housefly-specific attractant combined with an insecticide can be placed in a trap. A synthetic mixture with long-lasting attractiveness renders it unnecessary to frequently replace the attractant.

It is evident that the olfactory attractants to be used in control programmes have to be adapted to the environment in which they have to be applied. The volatile compounds emitted by, for example, manure are continuously present in high concentrations in the air of stables and may adversely affect the attractiveness of attractants which are placed in a trap. Although electrophysiological experiments showed that the presence of an ambient odour has no or only to a small extent an effect on the sensitivity of the antennal olfactory system of houseflies to pulses of single odour stimuli (Kelling, 2001; Kelling *et al.*, 2002), our results (Chapter 4) show that the behavioural responses of houseflies to attractive odours may be affected by ambient odours. However, food-deprived, mature females were still attracted to the odour of tainted chicken meat in the presence of a background odour of chicken manure.

The experiments described in Chapters 4 and 5 showed that in the absence of a background odour houseflies are not only attracted to tainted chicken meat but also to tainted pork and tainted beef. Humans can distinguish the smell of tainted chicken meat from the smell of tainted pork and tainted beef. Preliminary results of electrophysiological research combined with gaschromatography (GC-EAG) and analyses with mass-spectrometry (GC-

MS) revealed that tainted chicken, pork, and beef meat have several chemicals in common. The chromatograms of pork and beef extractions were much the same, whereas extractions of chicken meat appeared to contain an extra compound (F.J. Kelling, pers. comm.). Similar results were obtained when determining the chemical composition of cooked meat; many volatile compounds present in cooked pork were also reported to be present in cooked beef, and most of the compounds found in cooked chicken meat were also found in the other cooked meats, except for unsaturated aliphatic aldehydes, alcohols, and ketones which were only present in chicken meat (Mottram, 1991). GC-EAG and GC-MS also showed that chicken manure and tainted pork contain several identical compounds (Smallegange *et al.*, 1999). The volatiles common to chicken manure, tainted pork, tainted beef and tainted chicken meat may explain why all these products are attractive to houseflies. These volatiles have to be identified and a mixture of these volatiles should be tested for its attractiveness to houseflies in the presence of different background odours. Different background odours may require different (mixtures of) attractants (Chapter 4). Pickens *et al.* (1994) demonstrated that houseflies were caught by cooked chicken meat mixed with cooked rice at city dumps, where several housefly attractants are overwhelmingly present. This indicates that it may be possible to find volatiles which are attractive to houseflies and can be applied in traps even if the surrounding area is loaded with other attractive volatiles. The volatile which was only found in tainted chicken meat or one or more of the unsaturated aliphatic aldehydes, alcohols, and ketones which were only found in cooked chicken meat may be responsible for the attraction of food-deprived female houseflies in an environment loaded with the odour of chicken manure. It may be worthwhile to examine this further since these substances are likely to be effective baits in poultry farms.

We also investigated whether adding an odorous bait to a light trap may improve the attractiveness of the trap. However, it appeared that most of the odours which are individually attractive lost their attractiveness when combined with ultraviolet light (Chapter 5). As already said above attractive odours usually originate from food sources or oviposition sites which are found indoors or at dark places. If houseflies associate ultraviolet light with sky light, this may explain why no additive or synergistic effects of ultraviolet light and attractive odours were found: the flies simultaneously perceived visual and olfactory information which have opposite behavioural effects.

Practical application of the results

It is clear that indoor control of *Musca domestica* L. adults very much depends on the situation in the area where control has to be done. In short we can conclude that during daytime ultraviolet light is the best stimulus to attract flies towards killing devices in dark rooms. In illuminated rooms, odours appear to be a better option for use in traps.

In cattle stables, which are usually sparsely illuminated and in restaurants, bars, kitchens, and other rooms in buildings that are not illuminated during the day ultraviolet light traps may be used. Lamps with flicker frequencies higher than the flicker fusion frequencies of humans and animals should be used at these places; for example 175 Hz. In small dark environments where no humans or animals are likely to be present, like manure pits, it may be possible to use a push-pull system: lamps flickering at 4 or 10 Hz are likely to induce an escape response in female and male houseflies to a trap with ultraviolet lamps with a flicker frequency above the flicker fusion frequency of the flies. A frequency of 40 Hz may also be attractive at these kind of places. The lamps in the light traps should preferably have emission peaks around 340-365 nm. There is no need to have the lamps operating during the whole day; catching success will approximately be the same with the lamps on during short periods and when they are burning continuously. Surprisingly, pilot studies showed that ultraviolet light can also be used to catch flies during the night (Figure 1).

Since light only attracts flies older than 2 days and odours may attract flies of all ages, odours may be used in traps in lighted rooms; houseflies do not respond to odours in the dark. Tainted meat (pork, beef, and chicken) appeared to attract young and mature, well-fed and 'hungry' males and females. However, because these products have an unpleasant smell for humans they are less desirable for use in human dwellings. In addition, it is questionable whether these substances are still attractive in rooms in which the same or other attractive odours are already present. The components in these substances which induce attraction should be identified and an effective synthetic mixture developed. It may be that these components applied in the right ratio and doses exceed the attractiveness of ambient odours and no longer pall on humans. It is likely that different application areas with different background odours require different (mixtures of) attractants.

The practicability of the traps, the number of traps that should be applied in a room and the optimum siting of the traps have to be determined. Also the effects of light or odour-baited traps on other invertebrates, humans and their domestic animals should be examined during these studies. It is also important to go into the design of the traps. Pilot studies indicated, for example, that the effectiveness of electrocutor traps is considerably improved when the distance between the wires of the grid is reduced from the commonly used 7½ mm to 5 mm (Figure 2). Eventually, attractive visual cues other than ultraviolet light may be added to a trap (e.g., colour and shape of trap, fly-sized black spots or

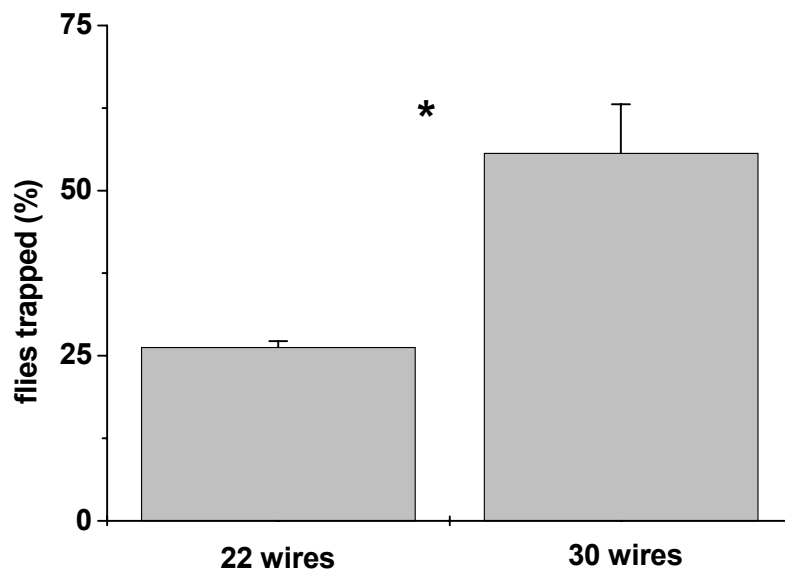


Figure 2. Mean percentages of houseflies caught during a period of 2½ hours in a dark room (310 cm long, 200 cm wide, 240 cm high) by light traps (containing an ultraviolet lamp) with electrocuting grids (15 cm wide, 15 cm high) with 22 horizontal wires at a distance of 7½ mm from each other and with 30 horizontal wires at a distance of 5 mm, respectively (three experiments with each trap; 100 flies released in each experiment). Vertical lines show standard errors of the mean. Generalized Linear Model analysis (GLM, Genstat 5, release 4.1) showed a significant effect of the design of the grid ($P < 0.001$, $df = 1$, binomial, link in logit).

beads and contrasting edges; see Chapter 1). For example, indoors, black and red materials are preferred as resting sites and more time is spent on rough surfaces (Freeborn and Berry, 1935; Hecht, 1963; Arevad, 1965), whereas yellow and white have been found to be more attractive outdoors (Hecht *et al.*, 1968; Pickens, 1995). Howard and Wall (1998) showed that contrast increases the attractiveness of coloured objects. Our experiments that are described in Chapter 2 also showed that the attractiveness of the test lamps cannot completely be explained by their emission in the ultraviolet and visible region. Other characteristics like the size of the radiant surface had an effect as well. The most attractive combination of light emission, radiant surface and possibly other characteristics of lamps has to be determined.

Light and odour-baited traps should be integrated with other housefly control measures; cultural, chemical, and biological (see also Chapter 1). Frequent sanitation and removal of possible breeding and larval feeding sites will diminish the adult population (Kettle, 1995). Closing doors and windows properly or putting gauze screens before windows and doors will reduce fly

infestation (Lillie and Goddard, 1987). Biological control agents such as parasitic wasps or predacious beetles and mites may reduce housefly populations in stables. Application of insecticides should be limited and these substances should only be used in combination with attractants in a trap. Controlling housefly populations with toxic targets, compared to large-scale spraying, has the advantage that it does not contaminate the environment and reduces the development of insecticide resistance.

Based on the present knowledge the following suggestions can be made for designing housefly traps.

Attracting houseflies indoors

To attract houseflies indoors, a cubic or pyramidal trap (Bellingham, 1994; Pickens, 1995) can be suspended from the ceiling of the room using, for example, the electrical cord of the lamp. The outsides of the trap should be made of black and rough material. In the middle of all sides electrocuting black grids are mounted of which the wires are 5 mm apart from each other. Inside the trap, either an ultraviolet (340-365 nm) lamp is placed in the centre or an odorous bait can be put on the bottom of the pyramid or cube. The lamp should be flickering at 175 or 40 Hz, depending on the application area and time. An indication lamp is switched on to show when the trap is operating. The bait should preferably be made of a mixture of chemicals and has to be 'protected' with very fine mesh (openings smaller than small flies) to prevent flies which have passed the electrocuting grids from contacting it. Candidate baits are the volatiles which are common in chicken manure, tainted pork, tainted beef and tainted chicken meat or the volatiles exclusively present in chicken meat; this depends on the ambient odours that are present in the area. Several light as well as odour-baited traps can be present simultaneously in the same room. Timers can be used to control on and off switching of the lamps and of the odour suspenders in the traps to achieve that the stimuli are operative at the desired application time. In some areas light and odour may be combined in one and the same trap. In that case moist yeast or marmite are better options as candidate odour baits.

Repelling houseflies indoors

In application areas in which no humans or animals are present, a lamp with a flicker frequency around 10 Hz can be used to chase houseflies either outdoors or otherwise towards an ultraviolet lamp flickering at a frequency higher than 270 Hz. Around this lamp electrocuting grids should be present. A white lamp will probably have the same effect as an ultraviolet lamp and has the advantage that no protection measures have to be made to prevent eye or skin injury of humans or animals. Suspenders evaporating R-limonene into the room may also be used to chase away flies and to prevent flies from entering a room. However, care should be taken, because high concentrations of this chemical may cause tumours in humans and animals.

Attracting houseflies outdoors

An odour-baited trap can be used to catch houseflies outdoors. The outside of the cubic trap should be white (Pickens, 1995). The bait should preferably be made of natural products or an attractive mixture of synthetic chemicals. These substances have to be shielded with very fine mesh to prevent flies or other animals from feeding on it or laying eggs in it. Candidate synthetic baits are the volatiles which are common in chicken manure, tainted pork, tainted beef and tainted chicken meat or the volatiles exclusively present in chicken meat; this depends on the ambient odours that are present in the area. The trap should again contain electrocuting grids. When this is not possible because humidity causes short circuits, the trap design should be adjusted in order that once flies have entered the trap they will be attracted to sky light that enters the trap from above. The flies can be captured in an outer cage. A funnel prevents that the flies will escape following the way they came in (see Pickens, 1995). The flies will die from thirst or starvation or an insecticide can be used.