Attractiveness of different light wavelengths, flicker frequencies and odours to the housefly (Musca domestica L.)
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Chapter 2

The attractiveness of ultraviolet, blue, green and white light to the housefly 
(Musca domestica L.)

SUMMARY

Several lamps and secondary light sources with different spectral compositions were tested for their attractiveness to houseflies (Musca domestica L.). Flies from different origin were tested: a WHO strain reared in laboratories since 1961, and two 'wild-type' strains, vanDiermen and Pesse, of which larvae had been collected in a poultry farm and piggery, respectively, and which had been cultured in the laboratory since 1995 and 1996, respectively.

Experiments in a flight chamber (210 cm long, 60 cm wide, 60 cm high) revealed differences in light response between strains and between males and females of one and the same strain. The sensitivity of the flies to light appeared to depend on the age of the flies. Flies younger than 3 days were hardly attracted to the test lamps, which coincided with a low locomotor activity. WHO females were even hardly responsive to light up to day 10. Light responses also depended on ambient illumination. In a flight chamber illuminated by a white fluorescent tube, less flies landed on the test lamps than when this flight chamber was illuminated by a red fluorescent tube emitting light invisible for flies ('dark'); on the average 9 and 31% of the flies were attracted, respectively. Overall, ultraviolet light sources attracted the highest numbers of flies. Flies also spent more time on ultraviolet light sources than on sources with emittance peaks higher than 400 nm. Within the ultraviolet region no preferences were found. It appeared that increasing the size of the luminous area of the lamps may increase their attractiveness more than increasing the lamps' intensity.

To investigate these results with a view to possible practical use in control measures, nine secondary light sources with different spectral compositions were tested for their attractiveness to mature female houseflies of the three different strains in an experimental room of 310 cm long, 200 cm wide, 240 cm high. Only small differences were found between the strains. Ultraviolet light attracted more female houseflies compared to blue, green, and white light. This was especially clear during 2-choice experiments when the room was
illuminated by a white fluorescent tube, but was also evident when the room was not illuminated except for the light emitted by the test lamps. The attractiveness of ultraviolet light was not affected by its spectral composition. The flies were attracted earlier in the dark than in an illuminated room. These results agreed with the results obtained in the flight chamber.

INTRODUCTION

Houseflies (Musca domestica L.) are a nuisance to man and animals and are potential vectors of pathogens (see Chapter 1). Electrocuting traps with fluorescent lamps emitting light in the ultraviolet range are commonly used for indoor control of these flies. Although they are considered to be promising pest-management devices (Lillie and Goddard, 1987), unfortunately, the numbers of houseflies caught by these traps are often too low to reduce the fly population to acceptable levels (Bowden, 1982; Pickens and Thimijan, 1986; Muirhead-Thomson, 1991).

It is known that the flies' sensitivity to light and phototaxis are affected by several biological and physical parameters (Skovmand and Mourier, 1986), such as ‘hunger’, kind of food, age, sex and searching activity of the flies, ambient temperature, and the presence of other visual stimuli (Cameron, 1938; Morgan and Pickens, 1968; Barker and Cohen, 1971; Meyer, 1978a, 1978b; Pickens and Thimijan, 1986; Skovmand and Mourier, 1986). This may be the reason that results of behavioural experiments with houseflies described in the literature are often contradictory. For example, Barker and Cohen (1971) observed that newly emerged houseflies are more photopositive than older ones, whereas Skovmand and Mourier (1986) reported that catches of very young flies with light traps are low. Cameron (1938) observed that females are more attracted to light than males, whereas Roberts et al. (1992) found no differences in behavioural responses to light between sexes. According to Morgan and Pickens (1968), the responses of M. domestica to various lamps (ultraviolet, blue, green, gold, pink, red) depend on ambient air temperature and differ between the sexes. Males were found to be more responsive at 19°C and 23°C and less responsive at 28°C and 32°C; females responded best at 32°C. These authors noticed no change in light response when the relative humidity varied between 20 and 60%. Finally, flies were less sensitive to light during the night than during daytime; traps with 360 nm fluorescent lamps attracted maximum numbers of houseflies between 5 and 6 p.m. (Deay and Taylor, 1962).

The behavioural responses of houseflies to light have also been found to be affected by the energy output of the lamps, their radiant area, and their flicker frequency (Cameron, 1938; Deay and Taylor, 1962; Chmurzyński, 1967, 1969, 1993; Clough, 1980; Pickens and Thimijan, 1986; Syms and Goodman, 1987; Roberts et al., 1992). The higher the energy output of ultraviolet lamps with the
same spectrum, the more attractive they were (Deay and Taylor, 1962; Pickens and Thimijan, 1986). In addition, a trap with 100 Hz (‘flickering’) ultraviolet lamps was found to catch more flies than a trap with 33 kHz (‘non-flickering’) ultraviolet lamps, even when the intensity of the 100 Hz lamps was lower than that of the 33 kHz lamps (Syms and Goodman, 1987).

In electrophysiological studies in which electroretinograms (ERGs) were recorded from *M. domestica* eyes, Mazokhin-Porshniakov (1960), Goldsmith and Fernandez (1968), and Bellingham and Anderson (1993) found ERG peaks in the ultraviolet (340-365 nm), blue-green (450-550 nm) and red (620-630 nm). Electrophysiological and optophysiological studies demonstrated that this is due to the spectral sensitivities of the eight photoreceptor or retinula cells (Hardie, 1986; Stavenga 1995; see Chapter 1). Similar spectral sensitivities were found in other Diptera, e.g., *Calliphora vicina* Meig. (Burkhardt, 1962), *Haematobia irritans* L., *Musca autumnalis* De Geer, *Stomoxys calcitrans* L. (Agee and Patterson, 1983), *Glossina morsitans morsitans* Westw. (Green and Cosens, 1983), and *Fannia canicularis* L. (Bellingham and Anderson, 1993). Behavioural studies showed that lamps emitting light between 300 and 400 nm are the most attractive to both female and male houseflies (Cameron, 1938; Deay and Taylor, 1962; Thimijan *et al*., 1973; Roberts *et al*., 1992). Within this range no preferences were found (Roberts *et al*., 1992).

In this chapter the attractiveness of lamps emitting different wavelengths to free-flying *M. domestica* flies of different age and sex is reinvestigated. In addition, the responses of houseflies from different origin are compared. Initially, the experiments were done in a relatively small flight chamber (210 cm long, 60 cm wide, 60 cm high) in which the responses of the flies to the various lamps were observed for 5 minutes only. To investigate these results closer with a view to possible practical use in control measures, the attractiveness of several light sources was also studied during longer periods (2½ hours) in a room of larger dimensions (310 cm long, 200 cm wide, 240 cm high).

**MATERIALS AND METHODS**

**Insects**

*Musca domestica* L. flies were maintained in cages (30 cm wide, 30 cm deep, 40 cm high) at 24°C and R.H. 40-90% in a 12 hours light : 12 hours dark regime. They were fed a mixture of skim milk powder, sugar and yeast (5:5:1 by weight) and had access to water.

Experiments were done from July 1995 to June 1999 with three different strains: a WHO strain (Ij2) obtained from the Statens Skadedyrslaboratorium in Lyngby (Denmark) and reared in laboratories since 1961 (J.B. Jespersen, pers. comm.); a ‘vanDiermen’ strain present in our laboratory since September 1995 and obtained from a poultry farm in Barneveld (The Netherlands) where
insecticides were still frequently used in the manure pit; and a ‘Pesse’ strain, obtained in May 1996 from a piggery in Pesse (The Netherlands) where application of chemicals had ended in 1995 and, since then, the robber fly *Ophyra aenescens* was deployed to control fly species.

**Registration of locomotor activity**

Before it is possible to develop a control method for a pest insect it is necessary to know during which period of the day the target insect is active. This knowledge will give an indication when a control method should be applied and tested. For this reason the spontaneous locomotor activity of houseflies was recorded by placing them individually into actographs (Syntech, Hilversum, The Netherlands). These apparatuses are fitted with a low-power Doppler-radar motion detector. Every second, an actograph may detect displacement or any other movement of the fly which is placed inside the actograph. The detection method uses radar waves. A moving fly reflects a part of the radar waves, after which the frequency and phase shift of the reflected waves are detected by mixing with the emitted wave. In the absence of motion no output will be generated (see Knoppien *et al.* (2000) for more details of the mechanism of movement registration). The output signals of the actographs can be monitored continuously during several days and stored by a personal computer using the software ‘ACT-O-MAT’, version 2.1 (F.W. Maes, University of Groningen, The Netherlands).

To determine the circadian activity patterns of houseflies of different ages, recordings were made during several days. This was done with males and females of all three strains.

It is assumed that red light is invisible for flies. Thus, for visual observation of the behaviour of flies in the ‘dark’, it should be possible to use red light for illumination. To verify this, the activity of flies was also recorded in the dark and under red light conditions and the outputs compared.

The activity was recorded from emergence until the flies died or were 20 days old. Light was provided from 6 or 8 a.m. to 8 p.m. by xenon lamps (Osram HLX 64634 Xenophot, 15V, 150 Watt, 100 Hz) or by a red fluorescent tube (Philips TL40W/15, 40 Watt, 100 Hz) 30 cm above the actographs. Recordings were also made in continuous darkness. In the actographs a vial was present containing a 6% sucrose solution on which a cotton pad was floating. Recordings were made at 24°C. Activity was normalised to the maximum value that was measured during a recording.

**Light response experiments in a flight chamber**

To determine the appropriate light wavelengths that should be used in light traps for controlling housefly populations indoors, the attractiveness of lamps emitting different wavelengths to free-flying houseflies of different age and sex was reinvestigated under laboratory, controlled conditions. Because the origin of the flies may determine the suitability of a wavelength, flies of different
strains were tested. In addition, the effect of ambient illumination on the light responses of houseflies was examined.

Test lamps

In a first series of experiments (July 1995 - March 1996) the attractiveness of three ultraviolet lamps (UV1, UV2, UV3) which are commonly used in light traps, and of three white fluorescent lamps (W1, W2, W3) to houseflies was investigated. Details of the test lamps are given in Table 1. Since these lamps had a relatively high heat production which prevented the flies from landing on them, a second series of experiments (June 1996 - February 1997) was done with ‘secondary’ light sources. Because the heat production of these light sources was low, the flies readily landed on them.

Table 1. Characteristics of the test lamps used in the first series of experiments (see text for details). Sequence of test lamps in table and figures is based on their emittance peaks.

<table>
<thead>
<tr>
<th>test lamp</th>
<th>power (W)</th>
<th>frequency (Hz)</th>
<th>emittance peak (nm)</th>
<th>radiance (µW/cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>ultraviolet 330-385 nm</td>
<td>visible 400-1000 nm</td>
</tr>
<tr>
<td>UV1 Philips TL4W/05</td>
<td>4</td>
<td>100</td>
<td>330</td>
<td>3.5</td>
</tr>
<tr>
<td>UV2 Philips TL4W/08</td>
<td>4</td>
<td>100</td>
<td>335</td>
<td>8.3</td>
</tr>
<tr>
<td>UV3 Sylvania CFS11W BL350</td>
<td>11</td>
<td>100</td>
<td>335</td>
<td>44.0</td>
</tr>
<tr>
<td>W1 Philips TL4W/33</td>
<td>4</td>
<td>100</td>
<td>365, 405, 435, 545</td>
<td>0.3</td>
</tr>
<tr>
<td>W2 PL-S 11W 83</td>
<td>11</td>
<td>100</td>
<td>365, 405, 435, 485, 545, 610</td>
<td>1.7</td>
</tr>
<tr>
<td>W3 PL-S 11W 83</td>
<td>11</td>
<td>40.000</td>
<td>365, 405, 435, 485, 545, 610</td>
<td>2.0</td>
</tr>
</tbody>
</table>
The ‘secondary’ light sources consisted of a piece of Teflon coated with either a layer of fluorescent powder or a layer of translucent white plastic. The Teflon served as one of the vertical sides of an otherwise aluminium box (6 cm wide, 5 cm deep, 23 cm high). In the centre of the box either an ultraviolet (Philips PL-S 9W UV-C, 100 Hz) or a white (Philips PL-S 9W/830, 100 Hz) tube was plugged in. The former caused the fluorescent powder on the Teflon to fluoresce. Using different powders, different spectral compositions could be produced. Three secondary light sources (UV4, UV5, UV6) had emission peaks in the ultraviolet region and two (B and G) in the blue-green. White light (W4) containing several emission peaks was obtained with the white plastic layer combined with the white tube (Table 2).

The emission peaks of the lamps and the secondary light sources were measured with an Oriel Corporation INSTASPEC III spectrophotometer. For measuring the radiance of the lamps a Graseby Optronics Model 371 Optical Power Meter (detector model 260) was used with a flat (400 - 1000 nm) or with an ultraviolet transmission filter (UG11; maximum transmission at 357.8 nm, half band width 55.4 nm) combined with a red filter (BG18). Radiance measurements were made in total darkness (except for the light emitted by the test lamps) at 50 cm from the light source. Because the area of the transmission curve of the flat filter has an overlap of 55% with the curve of the ultraviolet transmission filter, the total radiance of a test lamp was estimated by adding 45% of the radiance that was measured in the ultraviolet region to the radiance that was measured with the flat filter.

Table 2. Radiance of the secondary light sources (9 Watt, 100 Hz) used in the second series of experiments (see text for details). Sequence of test lamps in table and figures is based on their emittance peaks.

<table>
<thead>
<tr>
<th>test lamp</th>
<th>emittance peak (nm)</th>
<th>radiance (µW/cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ultraviolet 330-385 nm</td>
<td>visible 400-1000 nm</td>
</tr>
<tr>
<td>UV4</td>
<td>300</td>
<td>3.0</td>
</tr>
<tr>
<td>UV7</td>
<td>315</td>
<td>1.5</td>
</tr>
<tr>
<td>UV5</td>
<td>350</td>
<td>7.8</td>
</tr>
<tr>
<td>UV8</td>
<td>365</td>
<td>7.3</td>
</tr>
<tr>
<td>UV9</td>
<td>365</td>
<td>12.5</td>
</tr>
<tr>
<td>UV6</td>
<td>390</td>
<td>2.8</td>
</tr>
<tr>
<td>B</td>
<td>445</td>
<td>0.3</td>
</tr>
<tr>
<td>G</td>
<td>520</td>
<td>0.1</td>
</tr>
<tr>
<td>W4</td>
<td>405, 435, 545, 610</td>
<td>0.0</td>
</tr>
</tbody>
</table>
Figure 1. A. Schematic representation of the flight chamber used to test the attractiveness of light and odours to houseflies. Circles in the back wall represent doors through which flies could be introduced into the flight chamber. B. Top view of the first zone with a secondary light source as test lamp. C. Side view of the first zone with a secondary light source as test lamp. D. Top view of the upwind end with a control and an odour-loaded cylinder protruding through a plastic plate. E. Side view of the upwind end with an odour-loaded cylinder. F. Top view of the upwind end with a control and an odour-loaded cylinder combined with ultraviolet light. G. Side view of the upwind end with an odour-loaded cylinder combined with ultraviolet light. Arrows show the direction of the air flow.
**Experimental procedures**

The attractiveness of the test lamps to the flies was studied in a rectangular flight chamber (210 cm long, 60 cm wide, 60 cm high; Figure 1). The roof of the chamber and one side-wall, through which the flies were observed, were made of glass. The remaining walls consisted of wood coated with white plastic. On the floor of the flight chamber 9 black transverse lines, 2 cm wide, were drawn, so that 10 sections could be distinguished. Section 1 was 30 cm wide, sections 2 to 10 were each 20 cm. A test lamp was placed in the middle of section 1. The flies (groups of 5, 7 or 10) were released in section 8. Taking into account the circadian activity pattern of houseflies (see ‘Results’) the experiments were done during the day from 9 a.m. to 5 p.m. The ambient temperature was maintained at 24°C. The relative humidity (R.H.) varied between 40 and 90%.

In the first series of experiments, the attractiveness of various lamps to flies of different origin, age and sex was examined in a ‘dark’ chamber (except for the light emitted when the test lamps were switched on). During these experiments the chamber was illuminated by a 40 Watt red fluorescent tube (Philips TL40W/15, 100 Hz), hanging 30 cm above the chamber. This light did not increase the flies’ activity compared with their activity during the day in complete darkness (see ‘Results’). Flies from the WHO and vanDiermen strains were used. Females <1 to 20 days and males <1 to 14 days after emergence were tested. Because the test lamps were not always available at the same time, the total number of flies tested per test lamp varied. Responses of at least 20 WHO and 10 vanDiermen flies of the same sex and age were observed and recorded.

In the second series of experiments, the responses of males and females of all three strains to the secondary light sources were observed in a ‘dark’ and in an illuminated chamber. During the latter experiments the chamber was illuminated by a 36 Watt white fluorescent tube (Osram L36W/20 coolwhite, 100 Hz), hanging 30 cm above the chamber. This type of tube was also used to illuminate the rearing room. Taking into account the results of the first series (see ‘Results’), now only flies of 5-10 days old were used, except for WHO females which were 10-20 days old. Of each strain 50 flies of the same age and sex were tested, except for WHO females of which 100 were observed in the ‘dark’.

Before starting an experiment the flies were left for 5 minutes in the chamber with either a 15 Watt white bulb burning above section 9 (in the first series) or with the white fluorescent tube switched on (in the second series). This was done to enable the flies to ‘settle down’ and to prevent dark adaptation of the eyes. Then, the flies’ positions, either sitting or flying, were noted after which the ‘no-adaptation’ light was switched off and the test lamp switched on. After that, during 5 minutes the flies’ positions and the number of flies flying were noted every 30 seconds, using the software ‘The Observer’ (version 3.0, Noldus Information Technology B.V., Wageningen, The
Statistics
As a measure of attractiveness of a test lamp the number of flies that had landed in section 1 (in the first series) or on the test lamp (in the second series) was taken. These numbers were expressed as percentages of the total number of flies released in the flight chamber and treated as binomial observations (assuming that the behaviour of each fly was independent of the other flies that were present in the flight chamber at the same time). The percentages were transformed to logits (to get a linear function which can be used for regression analysis) and a Generalized Linear Model (GLM) was used (Genstat 5, release 4.1) to investigate the effect on the light response of age, sex and origin of the flies, of the ambient illumination, the test lamp or secondary light source in total or either the ultraviolet or visible light radiance of the test lamp or secondary light source, and all possible two-way interactions between these parameters (e.g., the light response of a fly may not only depend on the age but also on the sex of the fly). Two-sided t-probabilities were calculated to test pairwise differences of means. Effects were considered to be significant at P<0.05 (Oude Voshaar, 1994; Sokal and Rohlf, 1998).

Light response experiments in an experimental room
To investigate the results obtained in the flight chamber in closer relation to possible practical use, the attractiveness of several light sources was also studied during longer periods in a room of larger dimensions.

Test lamps
Nine ‘secondary’ light sources were used. Six of these had emission peaks in the ultraviolet region (UV4-9), two in the blue-green (B and G), and one emitted white light (W4). Characteristics of the light sources are given in Table 2.

Experimental procedures
The attractiveness of the secondary light sources was tested in a room (310 cm long, 200 cm wide, 240 cm high) with white walls, floor, and ceiling, at 24°C and R.H. 60-80%. To make comparison possible with the experiments done in the flight chamber, 1-choice experiments were done. The light sources were also tested in 2-choice experiments in which they were competing with an ultraviolet lamp to study the effect of a competitive attractive light source.
The experiments were done between 8 a.m. and 6 p.m. from November 1996 to June 1999.

Two light sources were placed at the ends of one of the long sides of the room at a height of 160 cm, 275 cm apart. An electrocutor trap (Insectron type I-70, Berson Milieutechniek B.V., Nuenen, The Netherlands) from which the ultraviolet lamp was removed stood in front of each light source. The electrocuting grid of a trap was 15 cm wide and 15 cm high. In order to prevent flies which had not been killed by the electrocuting grids from escaping, the catch trays at the base of each trap were filled with a shallow layer of soap water.

During the experiments the room was either dark or illuminated by a 36 Watt white fluorescent lamp (Philips TLD36W/33, 100 Hz) suspending from the centre of the ceiling. Before each experiment a cage with the flies to be tested \( n = 20 \) or \( 40 \) was placed in the room for several minutes to enable the flies to acclimatize. Taking into account the results of the experiments which were done in the flight chamber only mature females were used; WHO females were 10 to 20-days old, and vanDiermen and Pesse females 5 to 20-days old. The two traps and one (in 1-choice experiments) or both (in 2-choice experiments) light sources were switched on as soon as a group of flies had been released in the middle of the room (at a height of 50 cm), after which the experimentalist left the room. Each experiment lasted \( 2\frac{1}{2} \) hours. Initially, every 30 minutes the number of electrocuted flies was counted. Later, a personal computer using the software 'DUAL VLIEGENVAL N293' (S.J. Greven, University of Groningen, The Netherlands) recorded continuously when flies hit the electrocuting grids. In 2-choice experiments the test lamps had to compete with UV5, which has an emittance peak (350 nm) to which the compound eyes of houseflies are very sensitive (Mazokhin-Porshniakov, 1960; Goldsmith and Fernandez, 1968; Bellingham and Anderson, 1993). Each 2-choice experiment was repeated once after the two light sources had changed places in the room to rule out positional effects.

**Statistics**

As a measure of attractiveness of a light source the total number of flies electrocuted by the trap in front of it was taken as the proportion of the total number of flies released in the chamber. A Generalized Linear Model (GLM) was used to investigate possible relations between these proportions in the 1-choice experiments (with link in logit) and the various factors (strain, lamp, ambient illumination). Two-sided t-probabilities were calculated to test pairwise differences of means. Effects were considered to be significant at \( P<0.05 \) (Oude Voshaar, 1994; Sokal and Rohlf, 1998).

The catches in the 1-choice experiments can be described as an exponential function in time \( y = a + br^t; \) where \( y \) is the number of flies caught; \( t \) is the time elapsed in minutes; \( y = a + b \) at \( t = 0 \); and \( a \) is the asymptotic value at \( t \to \infty \), \( |r| < 1 \); \( r \) determines how quickly the expectation of \( y \) approaches the
asymptote). The characteristics of this function were used to predict, based on the results of the 1-choice experiments, for each combination of strain, ambient illumination and light source, the time at which 50 percent of the flies would be electrocuted \( t_{50} = \frac{\log (y_{50} - a) - \log b}{\log r} \) to get an impression of the effectiveness of each light source. Some data are missing due to electricity failures before data could be saved on the hard disk of the computer. In those cases, the total number of electrocuted flies was counted.

For the results of the 2-choice experiments the 2-tailed Fisher’s exact test of independence was used to analyse whether the distribution of catches was significantly different from a 1:1 distribution. This distribution is expected when the flies do not distinguish between two light sources with different emission peaks. A P-value less than 0.05 was assumed to show that a significant difference in attractiveness between the two light sources was found. The number of flies attracted to the secondary light source competing with UV5 as the proportion of the total number of flies attracted by the two test lamps during all 2-choice experiments was analysed with a Generalized Linear Model to investigate the effects of the ambient illumination, strains and test lamps (Oude Voshaar, 1994; Sokal and Rohlf, 1998).

**Measurements of the amount of visual pigment**

During our experiments we used houseflies which had been reared in laboratories for several generations. We assumed that these laboratory flies may differ from wild type flies in one or more characteristics. We examined one characteristic which may affect the phototaxis of flies: the amount of visual pigment in their eyes. If differences are found, this may give rise to discussion of the interpretability to practical use of research results on phototaxis obtained with laboratory flies.

*In vivo* measurements were made of the fluorescence of the visual pigment in the eyes of houseflies with a microspectrofluorometer set-up. Fly photoreceptor cells were first illuminated during 5 seconds with blue (451 nm) light, and subsequently, after a dark adaptation time of 30 seconds, for 5 seconds with red (603 nm) light. The red induced fluorescence is a measure of the visual pigment content (Stavenga, 1983).

Males and females of the three laboratory strains were examined: WHO, Pesse (14 months in the laboratory) and vanDiermen (22 months in the laboratory). In addition, the eyes of Pesse and vanDiermen flies which had been collected as larvae in stables two weeks before (‘stable flies’) and of wild-type flies caught in the field on the day of the measurements were investigated.
RESULTS

Locomotor activity
The long-term actograph recordings that were used to examine the circadian activity rhythm of houseflies (Figure 2) showed a clear diurnal pattern; the flies were hardly active during the night. Overall, the locomotor activity increased during the first 1½ day after emergence and then reached a maximum which was maintained during the rest of the flies’ life (Figure 2). During the day the activity gradually increased to a maximum which, on the average, was reached after about 4 hours (Figure 3). All strains, males and females, showed similar activity patterns.

During the day, locomotor activities of flies in complete darkness appeared to be similar to those in red fluorescent light (Figure 4). Therefore, we used the red fluorescent tube to illuminate the flight chamber for observing the responses of the flies to the test lamps in the ‘dark’. Figure 4 also shows that flies were more active in white light.

![Figure 2](image-url)

Figure 2. Actograph recordings of locomotor activity (arbitrary units; mean of 60 minutes) at 24°C of 2 individual Pesse males during 6 days, starting on the day of the flies’ emergence. Horizontal bar shows light and dark periods (L:D=12:12).
Figure 3. Locomotor activity (arbitrary units; mean of 60 minutes) at 24°C of 4 Pesse males (1-19-days old) averaged over a period of 19 days. Horizontal bar shows light and dark periods (L:D=12:12).

Figure 4. Locomotor activity (arbitrary units; mean of 15 minutes) at 24°C of 3 individual WHO flies (2-4-days old) averaged over a period of 3 days in continuous darkness (A), in red (B) or white light (C). Horizontal bars show light and dark periods (L:D=14:10).
Light responses in a flight chamber

Responses to lamps in the ‘dark’

The light response of houseflies was examined in a flight chamber to determine the possibility to use light as an attractant to houseflies. Initially, the attractiveness of fluorescent lamps of the type which is commonly used in light traps was investigated.

During control observations, with no test lamp switched on, only 5% of the flies flew in the ‘dark’ flight chamber (illuminated by a red fluorescent tube). When a test lamp was switched on, flies older than 2 days started to fly in higher numbers (29%) than newly emerged and 1 to 2-day-old flies (11%). In addition, flies older than 2 days tried to land on a test lamp quicker than younger flies; the latter responded after approximately 180 seconds after a test lamp was switched on, whereas the older flies responded immediately or within 90 seconds.

Figure 5 shows the percentages of WHO and vanDiermen flies (averaged over age) which had been in section 1 during the control observations and with various test lamps switched on. GLM analysis of all data revealed that the light response was significantly affected by strain, age, sex, and type of test lamp, as well as by the interactions age-sex, age-strain, sex-lamp, and sex-strain.

It appeared that hardly any fly landed in section 1 when the test lamp was not burning. WHO females were the least responsive to light; only 30% of all WHO females tested responded to the test lamps. WHO males were the most responsive of the four groups (49%). The mean responses of vanDiermen males and females were about the same (37 and 44%, respectively). Lamp UV3 was the most attractive to all groups. Males and vanDiermen females also showed a high preference for lamp UV2. No difference in attractiveness of the ‘flickering’ lamp W2 and the ‘non-flickering’ lamp W3 was observed.

Figure 6 shows the averaged percentages of flies attracted to the lamps as a function of the age of the flies. It appears that flies younger than 3 days were hardly or not attracted to the lamps. WHO females even hardly responded to light up to day 10. Also 20-day-old females were attracted in low numbers.

In Figure 7 the responses of ‘young’ and ‘old’ flies to the different test lamps are compared. On the average, 14% of the young flies was attracted to the lamps versus 47% of the older flies. Lamp UV3 appeared to be the most attractive to all groups of flies. Again the ‘flickering’ lamp W2 and the ‘non-flickering’ lamp W3 were equally attractive to all groups. To the WHO females these two white lamps were as attractive as lamp UV3.

Further analysis of the data showed that the light response was significantly affected by the amount of ultraviolet and visible light emitted by the test lamps. No correlation or interaction was found between the ultraviolet and visible radiance; the amounts of ultraviolet and visible light emitted by the test lamps affected the light response of the flies independently.
Figure 5. Attractiveness of various test lamps (see Table 1) in the ‘dark’ to WHO and vanDiermen female (<1-20-day-old) and male (<1-14-day-old) houseflies. Ctrl: no test lamp burning. Numbers above columns indicate numbers of flies tested. In each graph, columns marked with different letters are significantly different (least significant difference method, P<0.05). Vertical lines show standard errors of the mean.
**Figure 6.** Attractiveness of test lamps (see Table 1) in the ‘dark’ to WHO and vanDiermen houseflies of different ages. The data of all 6 lamps has been taken together. Numbers above columns indicate numbers of flies tested. Vertical lines show standard errors of the mean.
Figure 7. Attractiveness of six test lamps (see Table 1) in the ‘dark’ to ‘young’ (<3 days-old) and ‘old’ (>2 days-old) houseflies of the WHO and vanDiermen strains. 1: Ctrl; 2: UV1; 3: UV2; 4: UV3; 5: W1; 6: W2; 7: W3. Ctrl: no test lamp burning. Numbers above columns indicate numbers of flies tested. For each graph, columns marked with different letters are significantly different (least significant difference method, P<0.05). Vertical lines show standard errors of the mean.
Responses to secondary light sources in ‘darkness’ and in the light

Similar experiments were done with secondary light sources. With no secondary light source burning about 18% of the flies flew in the ‘dark’ flight chamber (illuminated by a red fluorescent tube), whereas 40% flew when the flight chamber was illuminated by a white fluorescent tube (‘in the light’). With a test lamp switched on, about 22% flew both in the ‘dark’ and in the light. The flies landed earlier on the test lamps in the ‘dark’ than in the light; within 60 and 120 seconds, respectively, after a test lamp had been switched on. Moreover, they landed sooner on an ultraviolet secondary light source than on a blue, green or white light source. It was also observed that the flies behaved differently after having landed on an ultraviolet light source than on the other light sources. On an ultraviolet light source they walked around for a long time, whereas on a blue, green or white light source they sat still or started grooming during a short period and then flew off, or they flew off almost immediately after landing.

GLM analysis showed an effect of strain, sex, type of secondary light source, and ambient illumination on the light response, as well as interaction of strain with ambient illumination. Averaged over all data (i.e. all three strains, both sexes and ambient illumination conditions) more flies landed on a secondary light source in the ‘dark’ than in the light, and more on an ultraviolet lamp than on a blue, green or white lamp. Males were more attracted to the light sources than females. No flies landed on a test lamp when it was not burning.

Figure 8 shows the percentages of flies that landed on the lamps in a ‘dark’ flight chamber. Males and females of the same strain were equally responsive to the light sources, except for the WHO strain of which the males were (again) attracted in higher numbers to the lamps than the females. It appears that WHO flies were more responsive to the lamps than Pesse and vanDiermen flies which both responded to a similar degree to the lamps. All light sources were equally attractive to both sexes of the WHO flies and to females of the Pesse strain. However, to Pesse males and to vanDiermen flies one or more of the ultraviolet lamps was significantly more attractive than the blue, green, or white light source. When averaged over all groups, the ultraviolet light sources attracted the highest numbers of flies.

When the flight chamber was illuminated by the white tube less flies landed on the light sources (Figure 9); on the average 15 and 44% of the WHO flies, 10 and 25% of the Pesse flies and 2 and 26% of the vanDiermen flies landed in the light and the ‘dark’, respectively. In the light, both sexes of the WHO and both sexes of the vanDiermen strain were on the average equally responsive to the light sources. Of the Pesse strain more males than females landed on the light sources. Again, on the average, ultraviolet light attracted more flies than blue, green, and white light. For both sexes of all three strains the number of flies attracted to the green and white light did not differ from the control.
Figure 8. Attractiveness of secondary light sources (see Table 2) in the ‘dark’ to WHO, Pesse and vanDiermen female and male houseflies. Ctrl: no light source burning. In each graph, columns marked with different letters are significantly different (least significant difference method, P<0.05). Vertical lines show standard errors of the mean.
Figure 9. Attractiveness of secondary light sources (see Table 2) to WHO, Pesse and vanDiermen houseflies in a flight chamber illuminated with a white fluorescent lamp. Ctrl: no light source burning. In each graph, columns marked with different letters are significantly different (least significant difference method, P<0.05). Vertical lines show standard errors of the mean.
Further statistical analysis showed that the attractiveness of the secondary light sources was significantly affected by the amount of ultraviolet and visible light they emitted. No correlation or interaction was found between the ultraviolet and visible radiance of the secondary light sources.

Figure 10. Percentages of vanDiermen, WHO, and Pesse female houseflies ($n = 40$ for each strain) caught in the course of 2½ hours in 1-choice experiments by nine different secondary light sources in a dark (A, C, E) and in an illuminated room (B, D, F). For every 30 minutes the cumulative numbers of electrocuted flies are shown.
Light responses in an experimental room

1-Choice experiments

1-Choice experiments were done in the experimental room to make comparison possible with the experiments done in the flight chamber. Figure 10 shows the catching rate of the electrocutor trap placed before the various light sources in the dark and in the light for WHO, Pesse and vanDiermen females. For every 30 minutes the cumulative numbers of electrocuted flies is shown. It is clear that the flies were caught faster in the dark than in the light, although, especially when the ambient light was switched on, it took quite a long time to catch 50% of the released flies with one light stimulus. Table 3 shows the $t_{50}$ for each light source, strain and ambient illumination. When the data of the strains were taken together it appeared that ultraviolet light attracted the flies most quickly; with ultraviolet light 50 percent of the flies was caught after approximately 90 minutes in the dark and 130 minutes in the light.

In the dark, the green lamp and UV9 attracted the vanDiermen flies more rapidly than the other test lamps; they attracted 50% of the flies within one hour (Table 3 and Figure 10A, B). UV7 and UV8 appeared to be slow ‘catchers’, attracting half of the released flies not before around 130 minutes had passed. The white lamp, however, was the least attractive and had only caught 40% of the flies at the end of the experimental period of 150 minutes.

In the light, only UV7, UV4 and UV9 attracted 50% of the vanDiermen flies within the test period. The flies were attracted most quickly by UV7 and UV4, each having caught half of the flies after about 90 and 120 minutes, respectively.

Similar results were found with WHO and Pesse females. WHO females were attracted most quickly with UV5 in the dark and UV9 in the light (50% caught after approximately 60 and 90 minutes, respectively), whereas UV4, UV7, and UV6 in the dark and UV5 and UV9 in the light attracted 50% of the Pesse females within 20-70 minutes (Table 3 and Figure 10C-F).

The percentages of flies of all three strains caught during 2½ hours are given in Figure 11. On the average, a single light source attracted 63% in the dark and 47% of the females in the light. However, GLM analysis of all data revealed no effect of the ambient light. VanDiermen females were less responsive than WHO and Pesse females. It also seems that the various lamps are differently attractive to flies of different strains. However, no significant differences in attractiveness were found between the lamps when the responses to them were averaged for the three strains. Neither in the dark nor in the light a correlation between the amount of ultraviolet or visible radiance and the numbers of flies attracted was found; the amounts of ultraviolet and visible light emitted by the test lamps affected the light response independently.
Table 3. The effectiveness of nine secondary light sources: predictions of the time (minutes) at which 50 percent ($t_{50}$) of the female houseflies of three strains will be caught based on results of 1-choice experiments of 2½ hours in an experimental room (see Figure 10). Sequences of test lamps in table are based on their $t_{50}$.

<table>
<thead>
<tr>
<th></th>
<th>WHO</th>
<th>Pesse</th>
<th>vanDiermen</th>
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<tr>
<td></td>
<td>light source</td>
<td>$t_{50}$ (min)</td>
<td>light source</td>
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<tr>
<td>dark</td>
<td>UV5</td>
<td>55</td>
<td>UV4</td>
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<td></td>
<td>UV4</td>
<td>66</td>
<td>UV7</td>
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<td>UV7</td>
<td>81</td>
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<td>96</td>
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<td></td>
<td>UV9</td>
<td>121</td>
<td>UV5</td>
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<td></td>
<td>W4</td>
<td>143</td>
<td>UV8</td>
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<td></td>
<td>G</td>
<td>148</td>
<td>UV9</td>
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<td>B</td>
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Figure 11. Percentages of female WHO, Pesse and vanDiermen houseflies (n = 40 for each strain) caught by different secondary light sources in 1-choice experiments during a period of 2½ hours in a dark (dark bars) and in an illuminated room (grey bars). 1: UV4; 2: UV7; 3: UV5; 4: UV8; 5: UV9; 6: UV6; 7: B; 8: G; 9: W4.

2-Choice experiments

The effect of a competitive attractive light source (UV5) was studied in 2-choice experiments. Figure 12 shows the results of these experiments. On the average, 76% of the released flies was caught in the dark and 63% when the room was illuminated. In most cases no significant differences were found in attractiveness between the six ultraviolet light sources and UV5, both in a dark and in an illuminated room. However, in an illuminated room UV6 attracted significantly less WHO and vanDiermen females than UV5, whereas UV9 attracted significantly more vanDiermen females. In both a dark and an illuminated room the green and white lights were less attractive than UV5. Blue was also less attractive than UV5 in the light, but in the dark both these light sources were about equally attractive.

GLM analysis of the proportions (see ‘Statistics’) showed no differences between the strains or ambient light conditions. The proportion was significantly lower when the competing light source emitted green or white light than when an ultraviolet light source was tested. Blue light attracted a smaller proportion of flies than UV5 and UV9. On the average, UV9 caught more flies than UV6.

Figure 13 shows typical examples of catches in the course of time in 2-choice experiments with UV5 and an ultraviolet light (UV7) (A, B) and green light (C, D), respectively. Again, the cumulative number of electrocuted flies is shown for every 30 minutes. It appears from the figure that ultraviolet light sources continued to catch flies throughout the experiment (Figure 13A and B), whereas green light only caught flies during the first 30 minutes of the experiment (Figure 13C and D).
Figure 12. Percentages of female WHO, Pesse and vanDiermen houseflies ($n = 40$ for each strain) attracted to different secondary light sources and a competing lamp (UV5; 2-choice experiment) during a period of 2½ hours in a dark and in an illuminated room. Asterisks indicate that the attractiveness of a light source is significantly different from UV5 (2-tailed Fisher’s exact test of independence, $P<0.05$). The black bars represent the attractiveness of UV5, the grey bars represent the attractiveness of the test lamps; 1: UV4; 2: UV7; 3: UV5; 4: UV8; 5: UV9; 6: UV6; 7: B; 8: G; 9: W4. Vertical lines show standard errors of the mean.
Figure 13. Examples of the catching rate of traps combined with a secondary light source in 2-choice experiments (UV5 vs UV7; UV5 vs Green) in a period of 2½ hours in a dark and in an illuminated room. The numbers of electrocuted Pesse females ($n = 40$) are summated for every 30 minutes. Asterisks indicate that the attractiveness of the two competing light sources is significantly different (2-tailed Fisher’s exact test of independence, $P<0.05$).
Amount of visual pigment
The in vivo measurements of fluorescence of the visual pigment rhodopsin showed that the fluorescence signals of the eyes of wild-type and first generation laboratory Pesse and vanDiermen flies ('stable flies') were considerably higher than those of the eyes of the WHO flies and of the Pesse and vanDiermen flies which had been reared in the laboratory for 14 and 22 months, respectively ('laboratory flies'). This means that wild-type and stable flies had considerably more visual pigment than flies which had been reared in the laboratory during several generations. Similar patterns were found for both females and males.

DISCUSSION

Amount of visual pigment
Wild-type and first generation laboratory flies were found to have considerably more visual pigment than flies which had been reared in the laboratory during several generations. This strongly suggests that the amount of visual pigment decreases during rearing in the laboratory. This decrease may have affected the flies' responses to light during the experiments and may thus explain the differences that were found in the responses to light between the strains. The light response of the different laboratory strains was tested during different periods after the beginning of rearing in a laboratory. Although the amount of visual pigment appeared to be about the same for the three laboratory strains when it was measured, this may not have been so during the light response experiments. This may explain why, on average, WHO flies were more responsive to the lamps than Pesse and vanDiermen flies. The amount of visual pigment of these flies was already low when the experiments started and this may have lowered their power to distinguish between the different lamps, making the lamps equally attractive to them (see Figures 6, 9 and 10).

Before conclusions can be drawn about the effect of the amount of visual pigment on the light responses of houseflies, comparison should be made between the light responses of wild-type flies caught in a stable and of flies of the same strain which have been reared in the laboratory for several generations, and the relation with the amount of visual pigment should be examined.

It is possible that the food that was offered to the flies in our laboratory lacked vitamin A (they were fed a mixture of skim milk powder, sugar and yeast). Vitamin A is necessary for the production of the visual pigment, rhodopsin. Flies reared on a vitamin A-deprived diet have a low visual sensitivity due to a low concentration of visual pigment (Goldsmith et al., 1964; see Stavenga, 1995). In addition, the sensitivity of the photoreceptor cells of flies reared on a vitamin A-deprived diet is much depressed in the ultraviolet
relative to the peak in the blue-green (Stark et al., 1977; see Stavenga et al., 2000).

Rearing in laboratories during many generations may also have affected other characteristics of the flies’ eyes, for example, differences in calcium concentrations. Illumination of fly photoreceptors induces migration of pigment granules towards the rhabdomere, due to a so-called pupil mechanism. The ‘pupil’ controls the magnitude of the light flux in the photoreceptor and, in addition, improves visual acuity. Calcium has been found to play an important role in this pigment migration (see Stavenga, 1995). However, not only characteristics which are related to the visual system may have changed due to long-term rearing under unnatural situations. Noorman (2001), for example, showed that the amount of the female sex pheromone (muscalure) that can be found on the cuticle could hardly be detected on first generation vanDiermen and Pesse flies, but increased considerably after some generations in the laboratory. This gives rise to the question how representative results are that have been obtained with laboratory insects.

**Locomotor activity and light responses in a flight chamber**

Young flies were found to be hardly active (Figure 2). This may explain their poor response to light, as was also suggested by Skovmand and Mourier (1986). 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). In males and females of the blowfly *Calliphora vicina* an increased flight activity in the rearing cage and a steep increase in light response was observed on the second day after emergence, a day before maturation (Meyer, 1978a). The reason why WHO females were even less responsive to light up to day 10 is unclear. Our results also indicate that the sensitivity to light gradually decreases with age when the males are older than about 10 days and when the females are older than about 17 days. These results suggest that phototactic behaviour as well as locomotor activity of houseflies is affected by their physiological state. However, in addition, environmental parameters are important. Although the locomotor activity in the actographs as well as in the flight chamber was higher in the light than in the dark, in the ‘dark’ flight chamber larger numbers of mature flies were attracted to the light sources than when the flight chamber was illuminated by a white tube. Hence, phototactic orientation of houseflies operates better in the dark than in the light. This agrees with the results of Pickens and Thimijan (1986) who found that ambient luminance affects attractiveness to light adversely. However, Roberts et al. (1992) found no differences in attractiveness of ultraviolet and longer wavelengths with the room lights on or off. Although the emission of visible light and total energy output was much higher, the white lamps W2 and W3 were less attractive than the UV3 lamp, which emitted the highest amount of energy in the ultraviolet (Table 1 and Figure 14A). This is also true for the secondary light source W4 compared to UV5
Figure 14. A. Mean percentages of flies attracted in the flight chamber to six test lamps and the amount of ultraviolet, visible, and total light emitted by the test lamps. B. Mean percentages of flies attracted to six secondary light sources in the ‘dark’ as well as in an illuminated flight chamber and the amount of ultraviolet, visible, and total light emitted by the light sources.
(Table 2 and Figure 14B). This indicates that the emission of light between 400 and 1000 nm and the total radiance of a lamp are less important for its attractiveness than the amount of radiance in the ultraviolet region, which is confirmed by regression analysis of the data. Within the ultraviolet region no spectral preferences were found. The fact that flies spend more time on ultraviolet light sources may be important for the development of trapping devices.

Statistical analysis showed that the amounts of ultraviolet and visible light emitted by the test lamps affected the light response independently. This means that it may be possible to increase the attractiveness of light sources by combining the optimal emission in the ultraviolet region with the optimal amount of visible radiance. However, the statistical analysis also showed that these two variables cannot explain the attractiveness of the test lamps completely. This indicates that more characteristics of the lamps were involved. Figure 14 shows that about the same maximum light response to a test lamp and a secondary light source (49% and 41%, respectively) can be expected when the amounts of ultraviolet and visible light of a test lamp are 6 to 15 and 2 to 3 times higher, respectively, than those of a secondary light source. This difference between the test lamps and the secondary light sources suggests that increasing the size of the luminous area may have more effect than increasing the intensity of the lamps; the radiant surface of a test lamp which can be seen from one point of view is much smaller than of a secondary light source. Pilot studies done in our laboratory showed that the larger the radiant surface of a lamp, the more attractive it is to houseflies (unpublished data).

No differences in attractiveness were observed between white lamps with flicker frequencies of 100 Hz and 40 kHz (W2 and W3). Electrophysiological studies (Leutscher-Hazelhoff, 1973; Mastebroek et al., 1980) suggested, however, that the attractiveness of ultraviolet light to flies may be affected by using flicker frequencies between 4 and 20 Hz: movement detecting neurons in the third optic ganglion of the visual system of the blowfly C. vicina were found to respond maximally at a contrast frequency of about 4 Hz (Zaagman et al., 1978; Mastebroek et al., 1980). In addition, a flickering sine wave light stimulus was found to yield a response of retinula cells of this fly up to 240 Hz, with a peak between 4 and 20 Hz (Leutscher-Hazelhoff, 1973). Experiments in which the attractiveness of ultraviolet lamps with different flicker frequencies was examined are described in Chapter 3.

**Light responses in a room**

GLM analysis of the 1-choice experiments showed a high so-called dispersion parameter (i.e. the variance is higher than can be expected in a binomial distribution). This raises the question whether the movements of the first flies responding may induce light responses of the other flies in the room. It can be argued that another source in the room may have activated flies at the same
time. This ‘activator’ could have been the sudden appearance of light when the test lamp(s) were switched on. Perhaps, as a reaction to this, several flies may have flown at the same moment towards the light source(s). This may explain why in the 1-choice experiments no differences were found in attractiveness between the lamps and also, because this is likely to go together with each other, no correlation was evident between the amount of ultraviolet or visible radiance and the numbers of flies attracted. This may especially be due to the fact that a test lamp was the only stimulus present in the room. However, the results presented in Figure 10 seem to exclude the switching on of the test lamp as the trigger of the light response of the flies.

In contrast to the results in the flight chamber, no significant effects of ambient illumination on the total number of electrocutions in both 1- and 2-choice experiments were found. Also Roberts et al. (1992), who tested the attractiveness of lamps with peak emission of 313 to 585 nm in 2-choice experiments of 24 hours in a white-walled room (280 cm long, 280 cm wide, 400 cm high), did not find differences in the relative efficacies (the number of flies caught by the test trap as a percentage of the total number of flies caught by the test and standard trap together) of ultraviolet and longer wavelengths either with the room lights on or off. This means that, during daytime, light traps can be used in dark as well as in illuminated rooms to attract houseflies. However, we found that the flies were caught earlier in the dark than in an illuminated room. This may explain why during 5 minutes experiments in the flight chamber higher numbers of flies were attracted to the secondary light sources in the ‘dark’ than in the light.

Especially when the room was illuminated but also in some cases in the dark, in the 2-choice experiments the traps standing before blue, green or white lights caught only a few flies compared to the traps standing in front of UV5 (Figure 12). In 1-choice experiments the same tendency could be seen when these lights are in competition with ambient light, whereas they attracted considerable numbers of flies on their own in the dark (55% in the dark, 22.5% in the light) (Figure 11). These findings agree with the results of experiments done with secondary light sources in the flight chamber. Similar to our results, Roberts et al. (1992) found that M. domestica is more attracted to ultraviolet light than to violet-blue or orange-yellow light. We found no significant differences in attractiveness between the six ultraviolet light sources UV4-UV9. This is also in agreement with the results of the experiments which were done in the flight chamber and with those of Roberts et al. (1992). Nevertheless, the amount of ultraviolet radiance seems to be one of the factors contributing to the attractiveness of a light source. Our 2-choice experiments showed that light sources with lower ultraviolet radiance attracted lower numbers of flies in contrast to UV5, although their total light intensities and amounts of radiance in the visible region were higher than that of UV5 (see Table 2 and Figure 12).
General

Summarizing the results obtained in the flight chamber and in the experimental room, it appears that an ultraviolet lamp, irrespective of its spectral composition, is the best attractive light stimulus for houseflies from different origin and that the numbers of houseflies attracted by the lamp in the dark are higher than when the application area is illuminated. Besides, flies are caught faster in the dark. Hence, during daytime, the period during which houseflies are active, and especially in dark rooms, ultraviolet light should be used to attract houseflies towards a trap. Considering the proportion of flies they attracted and their catching rate, lamps UV5 and UV9 seem to be good candidates for this purpose.

Studies on the fruitfly *Drosophila melanogaster* have revealed that two different groups of flies can be distinguished as to their phototactic behaviour. One group shows a fast phototactic response, moving quickly towards a light source, 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 is connected with an escape response towards light which can be observed in many insects. According to Mazokhin-Porshnyakov (1969) ultraviolet light, of which the sky light is the main natural source, may signify ‘open space’ for free flight. Based on this hypothesis, Menzel (1979) suggested that the fast phototactic response of arthropods living in air is an escape response and that ultraviolet light is the most reliable signal for this response. This could explain why ultraviolet light attracts the highest number of houseflies.

Although lamps with an emission peak somewhere in the ultraviolet region attract the highest number of mature males and females, we found that even in a ‘dark’ flight chamber only a maximum of 60% of the flies was attracted to an ultraviolet lamp while flies younger than 3 days of age were even hardly or not attracted to light. This does not seem to be sufficient to reduce fly populations to acceptable levels. The experiments in the experimental room showed that a longer experimental time (2½ hours versus 5 minutes) slightly increases the percentage of flies attracted to the light sources. However, to eliminate a housefly population it will of course be necessary to kill all females present, since otherwise a population can recover quickly. One gravid female may lay a few hundred eggs during her life in batches of 75 to 150 and the life cycle may be as short as 2 weeks in optimum circumstances (Hewitt, 1910; West, 1951). The numbers of houseflies caught by the traps during the experiments described in this chapter are probably not sufficient for reduction of fly populations to acceptable levels. Hence, more studies are needed to find a way to improve the attractiveness of light traps to houseflies.

Traps usually rely on only one of the potential sensory modes of insects, whereas it is evident that several sensory systems are used to initiate and maintain behaviour. Light may attract flies from a distance, whereas, for
example, attractive odours may lure the flies into the trap from nearby or vice versa. Pickens and Thimijan (1986) claimed that adding an olfactory bait to a light trap may improve the efficiency of this trap. Experiments to examine this are described in Chapter 5.

The experiments described in this chapter have shown that both physiological and environmental parameters (age, sex, origin and activity of the flies, energy output of light, ambient illumination) affect the number of houseflies attracted to light. This indicates that these parameters have to be taken into account when efficient control measures are needed in specific environments, like restaurants or stables. In general, ultraviolet light appears to be a relatively good stimulus to attract mature houseflies towards a killing device in dark rooms during daytime (which is the period during which houseflies are active). However, to be able to reduce the fly population to acceptable levels other housefly control measures should be integrated (see Chapters 1 and 6).