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The biology of the sheep blowflies *Lucilia caesar* and *Lucilia sericata* (Diptera: Calliphoridae) in relation to their control by trapping

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Doctor of Philosophy

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and

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Abstract

This study was an investigation of aspects of the biology of sheep blowflies in relation to their control by trapping. In order to determine the species composition of blowfly larvae in ovine myiasis cases in Scotland, samples of dipteran larvae were collected from live sheep throughout Scotland, reared in the laboratory, and identified once adult flies emerged. *Lucilia sericata* was found in 77% of samples, and other species in 49%. The most common alternative species were *L. caesar*, which occurred in 31% of samples, and *Protophormia terraenovae*, which occurred in 18%. Three other calliphorid species, *Calliphora vomitoria*, *C. vicina*, and *L. illustris*, and the muscid *Muscina pabulorum* were also found. The proportion of samples containing alternative species was significantly lower in eastern Scotland than in western Scotland. Significantly higher proportions of samples containing alternative species were collected at altitudes of 200 metres and above; from sheep of hill breeds; from rough grazing conditions and moorland; in the absence of trees; and in the presence of bracken.

The importance of *Lucilia caesar* in myiasis cases in Scotland having been confirmed, the capture of this species was investigated using four different trap designs, all baited with beef liver and sodium sulphide solution. A horizontal target coated with a polybutene-based adhesive performed significantly better than a similar vertical target. Both of these adhesive designs demonstrated significantly higher catches of both male and female flies than a water trap and a commercially-produced enclosed trap, Fly City ($P<0.05$). Subsequent investigations showed that catches on adhesive targets were significantly greater at a height of 0.2m than at ground level ($P<0.05$), 0.6m, or 0.8m ($P<0.01$). Catches were also increased on larger targets ($P<0.05$), but there was no significant increase in catch per unit area with target size. Highly elongate targets caught significantly lower numbers of flies than other shapes ($P<0.05$), and angle of orientation also proved to be an important variable, with horizontal targets, and those oriented at 45°, capturing significantly higher numbers than vertical targets ($P<0.05$).

An investigation of the visual physiology of *Lucilia caesar* and *L. sericata* was carried out by the recording of electroretinograms. It was found that their spectral sensitivities both exhibited peaks in the ultraviolet, green and red portions of the spectrum, and were therefore similar to those of other flies. However, the results indicated that the xanthopsin visual pigment in *Lucilia* species may have its peak

absorbance at a higher wavelength than that in members of the closely related genus *Calliphora*. A subsequent field experiment involving a comparison of catches of *L. caesar* on targets of different colours found that yellow and white targets produced the highest catches, and that the responses of this species were similar in most respects to those obtained using *L. sericata* in previous studies. The results were consistent with a model in which trap performance was related positively to reflectivity in the 450-580nm (blue/green/yellow) band.

Electroantennograms were used to measure the physiological responses of *Lucilia caesar* and *L. sericata* females to various olfactory stimuli. Of eight organic compounds tested, dimethyl disulphide evoked the highest responses, and the mixture swormlure-4, a chemical attractant for the screwworm fly, *Cochliomyia hominivorax*, produced an even greater level of stimulus. Ammonium sulphhide solution elicited greater responses than beef liver extract, sodium sulphide solution, or combinations of liver extract and sulphides. However, field experiments found swormlure-4 and ammonium sulphide to be poor attractants for *L. caesar* in comparison to liver and sodium sulphide solution.

An investigation was made of the specificity and ecological impact of adhesive targets, by examining the numbers of all the invertebrates (over 4mm in length) captured on a group of targets over two periods of time. It was found that during a period of high abundance of *Lucilia* adults, they accounted for 50.8% of the specimens, with the total content of calliphorids being 65.2%. During a period of low abundance of *Lucilia*, they accounted for only 10.4% of the catches, but the total percentage of calliphorids remained high, at 53.4%. The results demonstrate a relatively high level of specificity for *Lucilia*. Hoverflies (Diptera: Syrphidae) of subfamily Syrphinae were the only beneficial insects captured in significant numbers.

The overall conclusion of the study was that adhesive targets are a potential supplementary control method for both *Lucilia caesar* and *L. sericata*.

Dedication

To Kate

with loving thanks for your encouragement and support

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Acknowledgements

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1. General Introduction

1.1. Myiasis

1.1.1. Classification of myiasis

Myiasis is the invasion of living tissue of animals by dipteran larvae (maggots) (Zumpt 1965). Worldwide, a considerable range of fly species are responsible. The dipteran families which contain the most important species are the Calliphoridae (blowflies), the Sarcophagidae (flesh flies), the Hippoboscidae (louse flies or keds), the Gasterophilidae (bot flies), the Hypodermatidae (warble flies), the Oestridae (headflies), and the Cuterebridae (skin bot flies or tropical warble flies). Members of several other families have also been recorded as agents of myiasis. Infestations caused by species for which a period of parasitism is essential for development are known as obligatory myiasis, while those caused by species for which parasitism is optional are called facultative myiasis (Schmidt and Roberts 1989). Most of the calliphorids and sarcophagids which cause myiasis are facultative agents which also utilise carrion as a larval food source. However, a few species, notably the New World screwworm fly, *Cochliomyia hominivorax* Coquerel (Diptera: Calliphoridae), are obligate parasites which require to pass the larval stage in a living animal.

From a pathological viewpoint, myiasis can be divided into four main categories. Nasopharyngeal myiasis involves invasion of head cavities, particularly the ear, nose, mouth and sinuses, and the headfly *Oestrus ovis* L. (Diptera: Oestridae), whose larvae reside in the sinuses of sheep and goats is a typical cause. Intestinal and urogenital myiasis result from the invasion of the digestive or urogenital systems. Some species, for example the horse bot fly, *Gasterophilus intestinalis* Deg. (Diptera: Gasterophilidae), are adapted to cause intestinal myiasis, while many others can cause accidental myiasis when inadvertently ingested. Sanguinivorous myiasis is caused by a very small number of highly specialised species, for example the Congo floor maggot, *Auchmeromyia senegalensis* (Diptera: Calliphoridae), whose larvae do not live permanently on the host, but visit to acquire a blood meal while it is sleeping (Schmidt and Roberts 1989; Kettle 1995).

The fourth category is cutaneous (or dermal) myiasis, which occurs in two forms. Furuncular cutaneous myiasis consists of a boil-like lesion containing a single larva, and infestations of the tropical warble fly *Dermatobia hominis* L. (Diptera: Cuterebridae) are typical of this type. Wound myiasis, also known as traumatic or creeping myiasis, involves open lesions which are often extensive, and contain a number of larvae. Blowflies of genus *Lucilia* (Diptera: Calliphoridae) are typical agents of wound myiasis, particularly in sheep (Schmidt and Roberts 1989; Kettle 1995). A member of this genus, and a typical large myiasis lesion are illustrated in Figures 1.1 and 1.2.

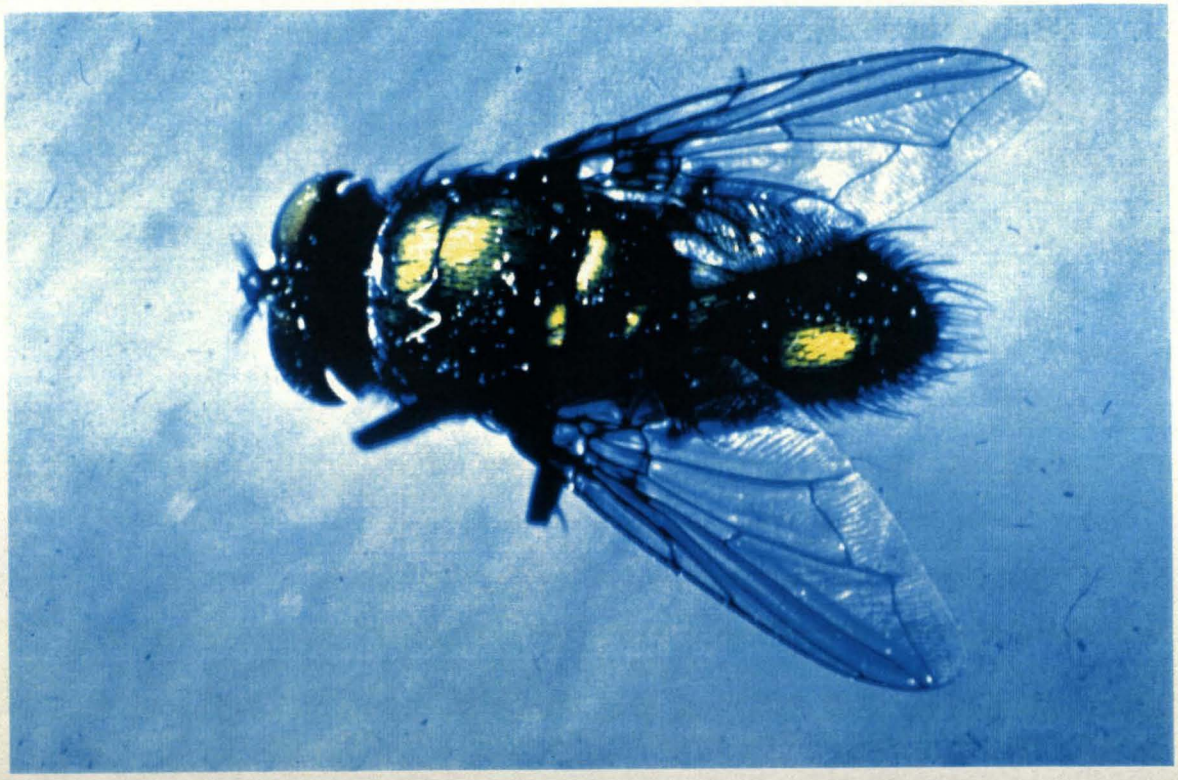

Figure 1.1: A male member of genus *Lucilia*. Photo courtesy of Professor Sir James Armour.

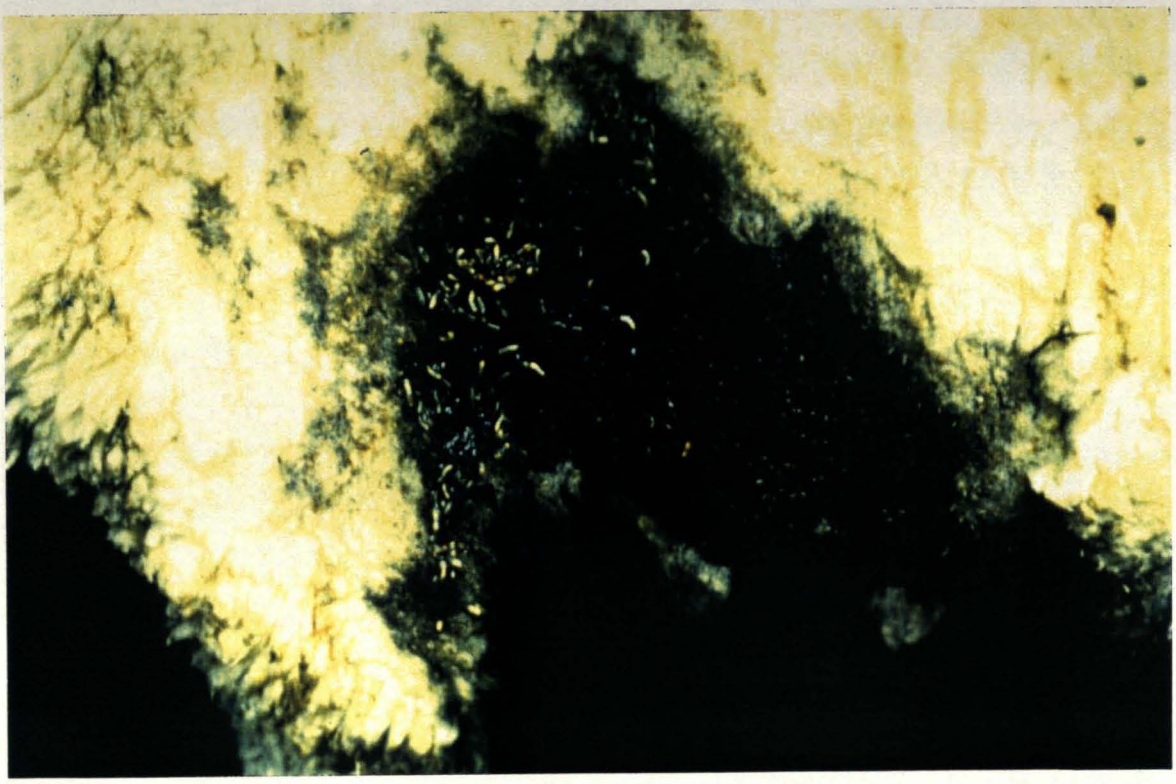

Figure 1.2: A typical large myiasis lesion in a sheep, caused by larvae of *Lucilia* species. Third instar larvae are visible in the lesion. Photo courtesy of Professor Sir James Armour.

The flies which are responsible for myiasis may also be classified, by the stage at which they become involved in an infestation of mammals. Some blowfly species are capable of initiating myiasis in unbroken skin, and may be classified as primary flies. Other species, the secondary flies, readily participate in myiasis once an infestation is established, or by using existing wounds, and some authors identify a third category, tertiary flies, which only add their eggs or larvae to myiasis lesions when the host is dying (Kettle 1995). A small number of calliphorid species, including *Lucilia cuprina* (Wiedemann), *L. sericata* (Meigen), and *L. caesar* (Linnaeus), are primary flies, but most other calliphorid and sarcophagid species are secondary (MacLeod 1943a; Zumpt 1965).

A wide variety of vertebrates, both wild and domestic, may suffer from blowfly myiasis, but one of the most common hosts, and in economic and animal welfare terms the most important, is the domestic sheep. Ovine cutaneous myiasis, or "sheep strike", can cause extensive epidermal damage, as untreated strike lesions will continue to enlarge as additional maggots enter the wound from eggs laid around the affected area. Loss of fluid and nutrients is detrimental to the health of the afflicted animal, and bacteria may also be able to gain entry through the lesion. However, the greatest danger is posed by the secretion of nitrogenous waste products by the blowfly larvae, whose optimum pH for development is 8-9 (Guerrini *et al.* 1988). The resulting alkalinity causes chronic ammonia toxicity in the sheep, and this becomes fatal when the ammonia concentration rises above 200μmol per litre. Death can therefore take place even when an infestation is at a relatively early stage (Guerrini 1988).

1.1.2. Worldwide extent of cutaneous myiasis

Ovine cutaneous myiasis occurs throughout the world, but the fly species involved vary from region to region. Different species of *Lucilia* predominate at different latitudes. In tropical and subtropical areas, *L. cuprina* generally poses the main threat to sheep, and in Australia, this species is responsible for the majority of strike cases, although *L. sericata* and five species of *Calliphora* have also been identified as primary flies (Mackerras and Fuller 1937). In temperate areas, *Lucilia sericata* tends to be the dominant blowfly species, and is responsible for most cases of sheep strike in the British Isles, particularly those in central and southern England (MacLeod 1943a; Wall *et al.* 1992a). This is also the case in the southern hemisphere. In New Zealand, *L. sericata* is one of the two most important myiasis agents, the other being *C. stygia*

(Fabricius) (Heath 1986). In northern temperate areas, the importance of *L. sericata* appears to decline, and in the northern British Isles, a significant number of sheep strike cases has been found to be caused by other blowfly species, particularly *L. caesar* (MacLeod 1943a), which has also, along with its close relative *L. illustris* (Meigen), been recorded from myiasis cases in Scandinavia (Brinkmann 1976; Nielsen 1984).

In addition to *Lucilia* and *Calliphora* species, certain other flies are important causes of cutaneous myiasis in certain parts of the world. Three species, all of which are obligatory parasites, are of particular note. In many tropical locations, screwworm flies are also important agents of myiasis, a wide variety of domestic and wild mammals. The Old World screwworm fly, *Chrysomya bezziana* Villeneuve (Diptera: Calliphoridae) is found in Africa, India, and south-east Asia, while *Cochliomyia hominivorax* extends from the southern United States to southern Brazil (Kettle 1995). In Hungary, despite the greater abundance of *L. sericata*, Wohlfahrt's wound myiasis fly, *Wohlfahrtia magnifica* (Schiner) (Diptera: Sarcophagidae) has been found to be responsible for the overwhelming majority of ovine myiasis lesions (Farkas *et al.* 1997).

1.1.3. Prevalence and distribution of ovine myiasis in Great Britain

A survey carried out in the 1930s, before the widespread introduction of organochlorine and organophosphorus insecticides, showed strike prevalences of between 3% and 40% in north Wales. It was found that farmers considered prevalences of between 3% and 8% to be mild, while severe attacks affected between 10% and 15% of sheep in upland areas and between 35% and 40% in the lowlands (Davies 1934). In Scotland, Ratcliffe (1935) found similar prevalences in Scotland with 18% of ewes and 47% of lambs affected.

Recently, a major survey of the prevalence, regional distribution and control of blowfly strike in England and Wales was carried out by French *et al.* (1992). It was found that strike occurred in 77.5% of flocks within this area in 1988, and in 80.0% of flocks in 1989. The proportion affected in the north of England was significantly lower at 58.6% in both years. Although the disease was so widespread, the proportion of sheep affected was relatively small, at 1.5% in 1988 and 1.6% in 1989. Prevalence ranged from 0.7% (in both years) in the north of England, increasing sequentially through central England, Wales and south-east England to 2.5% and 2.8% in south-west England. The increase in prevalence between 1988 and 1989 is of

interest because of the relaxation of the requirements of the Sheep Scab Order which reduced the number of compulsory dips by total immersion from two in 1988 to one in 1989.

1.1.4. Fleece factors and location of strike cases

The level of moisture in the fleece has been shown to be an important predisposing factor for blowfly strike. Davies and Hobson (1935) found that the microclimate at the base of the wool is normally too dry for the development of larvae of *L. sericata,* and that myiasis does not occur until a certain level of moisture is reached. At temperatures comparable to those found in sheep wool, a humidity of 60-80% is required for the hatching of *L. sericata* eggs (Davies 1948), and newly hatched first instar larvae require humidities in excess of 70% in order to avoid desiccation (Davies and Hobson 1935). It was concluded that fleece humidity is the most important factor predisposing sheep strike. A close association has been demonstrated between faecal soiling and the occurrence of ovine myiasis, in connection both with *Lucilia sericata* (Hobson 1935) and with *L. cuprina* (Mackerras and Mackerras 1944).

In Britain, *Lucilia sericata* was shown to cause strike more commonly in the breech region than any other part of the sheep (Hobson 1935). MacLeod (1943b) found that 66% of strike cases occurred on the hindquarters and flanks; 21% on the loins and back; 9% on the shoulders, and 4% on other areas. Of these cases, 51% were associated with soiled wool, a figure which rose to 67% on the hindquarters and flanks. The location of strike cases showed regional variation, with hindquarters strikes showing lower than average incidence in North, West and Central Scotland (51%), and higher than average incidence in the remainder of Scotland and northern England (79%). The incidence of back strike dropped to 14% in eastern and southern Scotland and northern England, and halved to 10% in South Wales, while shoulder strike rose significantly to 14% or higher in Wales and Ireland. It was noted that strikes on the neck, an unusual location, concentrated in western Scotland. These regional differences may have been related to the breeds of sheep farmed in different areas, as the data suggested that the incidence of strike was proportionately higher in Scottish Blackface sheep than in other breeds. With regard to the age of sheep affected, it was found that breech strikes were relatively more common in lambs than in ewes (MacLeod 1943b). Similar results were obtained in a more recent study (French *et al.* 1995), which found that 70.9% of strikes occurred on the breech, 19.7% on the body, and 11.4% on the feet.

In Australia, the most common location of ovine cutaneous myiasis is on the shoulders and back (body strike), which is particularly prevalent following periods of heavy rainfall during periods of warm weather (Belschner 1937; Watts *et al.* 1979). Small falls of rain have been found to be more conducive to strike than occasional heavy showers, and analysis of strike data suggested that while rainfall determined overall levels of strike, pasture conditions and cloud cover regulated the type of strike. Crutch strike appeared to replace body strike under dry conditions, and also when the density of *Lucilia cuprina* was low (Wardhaugh and Morton 1990). Fleece-rot, a condition caused by bacteria, appears to be a predisposing factor for sheep strike in Australia (Gherardi *et al.* 1985).

1.1.5. Seasonal and geographical influences on ovine myiasis

Collection of larval samples from strike cases between 1934 and 1941 identified the occurrence of strike as early as late April, and as late as late October (MacLeod 1943b). However, it was found to be unusual outside the months of June to September, and the highest number of cases occurred in late July and early August. Analysis of records from individual regions showed that a peak of strike cases occurred prior to shearing, often in late June. This was followed by a decline in incidence, and then by another peak, 5-6 weeks after the first. The number of strike cases involved in the second peak was generally larger than the first, but the intensity (number of cases per unit period) of the first was greater in certain areas, particularly in central and southern England. MacLeod (1943b) linked this pattern of incidence to the birth of lambs, and to shearing, giving four phases of incidence: a pre-shearing phase dominated by ewe strikes; a trough caused by shearing, with only occasional lamb strikes; a phase dominated by increasing lamb strikes with some recovery of the increase in ewes linked to wool growth; and finally a peak involving susceptibility of both ewes and lambs. The precise timing of the four phases varied depending on management factors related to the breed of sheep involved and to climatic conditions.

A recent study of strike incidence has shown a similar pattern (French *et al.* 1995). Strike cases were reported from early May (in south-east England) until late November (in south-west England). The lowest incidence was recorded from the north of England, where it peaked in ewes during August at 1.6 per 1000, and in lambs during September at 2.2 per 1000. The incidence of strike in lambs peaked earlier in the year in southern areas, with the highest level being recorded in the south-east of England during August (14.2 per 1000). There was also considerable

regional variation in the percentage of strikes which resulted in the death of the affected animal, which varied from 7.5% in northern England to 1.5% in south-east England. As a result of the study, it was suggested that diarrhoea (which can be associated with endoparasitic burdens) and temperature, which tends to be lower in northern areas, were important predisposing factors for strike in British lambs.

It has been shown that the risk of blowfly strike falls as altitude is increased. A total of 85.5% of farms at altitudes of less than 100 metres reported at least one case of strike in 1989, while the corresponding figure for farms situated above 400 metres was 52.9%. The proportion of farms reporting a high strike prevalence, defined as over 2%, was 44.4% at altitudes of less than 100 metres, and 12.5% above 400 metres (French *et al.* 1994a).

1.2. Biology of blowflies

1.2.1. Taxonomy

The Calliphoridae, blowflies, is a family of cyclorrhaphan Diptera containing more than 1000 species in about 150 genera worldwide. Over 250 species occur in the Palaearctic Region (Rognes 1991). According to the most recent taxonomical literature, about 49 species occur in the British Isles, in about 23 genera and eight subfamilies (Van Emden 1954; Rognes 1991). At least 80 species of calliphorid have been recorded as agents of myiasis, and eleven of these are found in the British Isles (Zumpt 1965; Rognes 1991).

Three British calliphorid subfamilies contain flies which cause myiasis. The Chrysominae contains *Protocalliphora* and *Protophormia*; the former specialising in myiasis of birds, and the latter containing a single British species, *P. terraenovae* (Robineau-Desvoidy), which is an agent of ovine myiasis. The Calliphorinae contains *Calliphora* and *Cynomya*, with six and one species, respectively, occurring in the British Isles. *C. vicina* Robineau-Desvoidy and *C. vomitoria* (L.) are involved in ovine myiasis in Britain, while *Cy. mortuorum* is a potential myiasis agent which has never been collected from sheep. The Luciliinae comprises the genus *Lucilia*, which has seven members in the British Isles. *L. sericata*, *L. caesar*, and *L. illustris* are causes of myiasis in British sheep, and other members of the genus have been recorded from infestations in other vertebrate species (MacLeod 1943a; MacLeod and Donnelly 1956b; Rognes 1991).

Lucilia species are generally between six and nine millimetres in length, and have a glossy green or coppery green thorax and abdomen and a bare lower calypter. *Calliphora* species are larger flies, measuring between 10 and 14mm, which have a black thorax, a blue to blue-black abdomen and a hairy upper surface to the lower calypter. *Cynomya* are bluish-green, and are also large, measuring up to 18mm. They share the hairy calypter of *Calliphora*, but have bright yellow-orange colouration over most of the facial area. *Protophormia* are dark blue to black flies, between eight and 12mm in length, with a ciliated stem vein and a bare lower calypter (Rognes 1991; Kettle 1995).

1.2.2. The calliphorid life-cycle

Blowflies are oviparous, and the larvae utilise carcases of various animals, especially vertebrates. The larvae comprise the most important component of the process of the decomposition of carrion. In addition, some species may infest the bodies of living animals, and others can feed on vegetable matter and faecal material. Larvae pass through three instars, with the time spent in each stage of development varying depending on the species involved, and on climatic factors, especially temperature. At 27°C and 50% Relative Humidity, *Calliphora vicina* has been observed to spend 24 hours in the egg stage, 24 hours as first instar larvae, and 20 hours as second instar larvae (Rognes 1991). At temperatures above 30°C (comparable to the lowest recorded at the skin of a living sheep), *Lucilia sericata* eggs hatched after 10-12 hours, and the larvae completed the feeding stages (the first and second instars and part of the third) in 2.5 days (Wall *et al.* 1992b).

Third instar larvae cease feeding and leave the food source to seek a suitable location for pupariation. They may travel up to 6.5 metres, in what is known as the wandering stage, before settling below the ground surface to pupariate. After the formation of a white prepupa the skin becomes tanned and then becomes dark brown. True pupation takes place within this puparium. Blowflies overwinter as wandering larvae, undergoing a diapause. In this case the normal progression to pupation is suspended, and the flies remain as third instar larvae until diapause is terminated. *Calliphora vicina* larvae spent just over seven days in the third instar, and about 11 days as a puparium when maintained at 27°C and 50% Relative Humidity (Rognes 1991). The length of the wandering stage of the third instar, after feeding has been completed, is like the earlier stages in being closely related to temperature. A study of wandering larvae of *Lucilia sericata* found that the time between the end of feeding and pupation was inversely proportional to the temperature over 9.5°C. The length of this period was found to be about 40 days at 10°C, and less than two days at 30°C. Similarly, pupation lasted about 20 days at 15°C, but less than six days at 30°C. In neither case was there found to be any additional effect of temperature above 30°C (Wall *et al.* 1992b).

After emergence the adult flies feed on carbohydrate, but they are anautogenous, and a protein meal, usually of meat, is required by female flies before vitellogenesis can take place. After mating the female blowflies may travel considerable distances in search of suitable oviposition sites (MacLeod and Donnelly 1963). The choice of site may be influenced by carcase size and type (Davies 1990), stage of decomposition (Lane 1975), position (Smith and Wall 1997), and the presence of

other ovipositing blowflies (Barton Browne *et al.* 1969). Eggs are usually laid at natural body openings and wounds, through which the larvae can gain access to the flesh. The time taken for the maturation of the first eggs is highly temperature dependent, ranging from more than 18 days for *Lucilia sericata* maintained at 15°C to less than five days for those at 30°C (Wall *et al.* 1992b). In the laboratory, female *L. sericata* may produce up to 13 egg batches, each containing an average of more than 200 eggs, and a maximum of 2373 eggs has been recorded during the lifetime of a single female (Mackerras 1933; Ratcliffe 1935; Wall 1993). The number of eggs produced per batch has been shown to depend both on the size of the adult female, and on the availability of protein for vitellogenesis, both in *L. sericata* (Wall 1993), and in *L. cuprina* (Barton Browne *et al.* 1979; Vogt *et al.* 1985b). Wall (1993) showed that individuals collected from the field were not significantly different in size from those reared in the laboratory, and matured very similar numbers of oöcytes. However, based on mortality rates computed from catches of wild females, the mean lifetime reproductive output of *L. sericata* was estimated at 44 eggs per female.

1.2.3. Larval ecology

Calliphorids are usually the most important component of the decomposition process in carrion, accounting for 58% of the total energy in carcases, and 83% of the consumption in a study by Putman (1978). Decomposition consists of a series of about eight stages, and members of the Calliphoridae are involved very early in the process, being in most habitats the very first insects to arrive on corpses. Mégnin (1894, as updated by Smith (1986)) places *Calliphora vicina* as the first species to arrive, followed by *Calliphora vomitoria*, and then by *Lucilia* species. These are followed by muscids, sarcophagids and other calliphorids such as *Cynomya*. Chapman and Sankey (1955) found that larvae of *Calliphora* species were present for the first three days, and those of *Lucilia sericata* from the third day onwards.

Flies inhabiting carrion typically reduce the size of emergent adults rather than undergoing mortality in the larval stage (Ullyett 1950; Hutton and Wasti 1980; So and Dudgeon 1989). However, the resulting smaller adults may have reduced fecundity (Ullyett 1950), longevity, and male mating success (Parker 1968; Hightower *et al.* 1972). The ability of fly species to greatly reduce the amount of food required for full larval development enables the production of a greater number of viable adults than could be produced if the larval food requirement was less flexible (Putman 1977). Although some calliphorids require to reach a relatively high proportion of their normal full size, for example *Chrysomya varipes* (Macquart),

which must attain 80.2% of the maximum mass (Levot *et al.* 1979), most exhibit much greater flexibility. *Lucilia cuprina* has been found to have a minimum pupal mass of 21.0% of the optimum (the mean under normal conditions), and *Calliphora vicina* of only 12.3% (Williams and Richardson 1983).

Prinkkilä and Hanski (1995) found that the size of emerging adults of *Lucilia illustris, L. caesar, L. sericata,* and *L. silvarum* (Meigen) decreased with increasing larval density, but that this effect was not linear in every case. In *L. illustris* and *L. caesar,* larval density affected adult size only at densities of 16 larvae per gramme and above. *L. caesar* generally did not emerge with a body size of less than 2mg (about 35% of optimum) at any density, whereas the other three species all produced live adults with masses of less than 1mg (about 15% of optimum in each case) at high densities. *L. sericata* maintained a level of emerging adults in excess of 50% at densities of up to 64 larvae per gramme, with a rapid decline thereafter, although a separate study of found 29% emergence from larvae reared at a density of 8.4 larvae per gramme (Hutton and Wasti 1980). At low densities, *L. caesar* was observed to have an emergence level of less than 20%, rising to over 30% at densities of 16 and 32 larvae per gramme, while *L. illustris,* having a similar pattern of emergence levels, showed higher emergence levels throughout, and a much higher peak, of nearly 80% emergence at 32 larvae per gramme.

Interspecific competition between *Lucilia illustris* and three other species of *Lucilia* produced complex results. Survival of *Lucilia caesar* was found to be generally worse than that of other species, although a high emergence rate was demonstrated when this species was present at a low density and as a low proportion of the initial population. *L. sericata* maintained emergence of over 70% except at 64 larvae per gramme, at which density emergence fell to between 30% and 60% (Prinkkilä and Hanski 1995) . Competition between *Lucilia sericata* and *Phormia regina* Meigen resulted in the elimination of *P. regina* at density levels of 2 larvae per gramme and above (Hutton and Wasti 1980).

Dipteran species which inhabit ephemeral or deteriorating environments in their larval stages usually have a reasonably constant reproductive investment over the entire range of possible body sizes (So and Dudgeon 1989), with most, including *Lucilia sericata* (Ullyett 1950) and *Calliphora vicina* (Williams and Richardson 1983), increasing their reproductive investment to some extent when smaller body sizes occur. *L. cuprina* increases reproductive investment greatly as mass is reduced, and this species also has a considerably larger investment in reproduction for their mass, even in conditions of plentiful larval food supply. Whereas most calliphorids produce between 5 and 10 eggs per milligramme of body mass, *L. cuprina* produces

22 in the largest flies, rising to 33 in the smallest (Williams and Richardson 1983). When investment in reproduction is increased, there must be a corresponding reduction in the investment in other faculties, for example flight, and *L. cuprina* has been found to have a weaker dispersive phase than some other blowfly species (Norris 1965).

It has been found that when calliphorid species encounter food shortages in the larval stage, they generally do not extend their development time in order to search for more food (Ullyett 1950; Hutton and Wasti 1980). This is probably because mortality in the larval and pupal stages can be very high due to factors such as predation, especially between the end of feeding and the emergence of the adults. Putman (1977) found up to 80% pre-adult mortality in *Calliphora vicina*. The penalty incurred by size reduction is therefore much less than that risked by remaining for longer in the larval stage (Collins 1980).

Blowflies of different species show preferences for different sizes and types of carcases. A study of carcase colonisers in upland areas of Wales and northern England found that *Calliphora vomitoria*, the most abundant species in these areas, was found exclusively in large carcases, while *C. loewi* Enderlein, *C. alpina* (Zetterstedt), and *C. subalpina* (Ringdahl) occurred exclusively in small carcases. *C. vicina* and *Cynomya mortuorum* L. were found to be present on both sizes of carcase (Davies 1990). Examination of blowfly emergence from sheep carcases found that the level of *L. sericata* emergence was low relative to that of *L. caesar*, except where a heavy infestation was already present at the time of death (Cragg 1955). It was therefore suggested that *L. sericata* larvae are poor competitors, and that populations of this species are maintained mainly through infestations of sheep rather than from carrion. Surveys of the composition of calliphorid larvae in small carcases also show relatively low levels of *L. sericata* (Blackith and Blackith 1990; Smith and Wall 1996). However the controlled studies by Prinkkilä and Hanski (1995) did not provide evidence that *L. sericata* is a poorer competitor than other *Lucilia* species, and one of the surveys of small carcases actually found substantially lower numbers of *L. caesar* than of *L. sericata* (Smith and Wall 1996).

1.2.4. Larval diapause

Diapause is an actively induced state which improves the ability of organisms to survive adverse conditions important component of many insect life-cycles. It can occur at almost any developmental stage, each species having a specific point at

which diapause can occur. The most common trigger for diapause initiation in temperate latitudes is photoperiod (day length), which has the great advantage of reliability, with very little variation from year to year. This enables insects to anticipate seasons of environmental stress, in a manner which is independent of short-term climatic fluctuations. Temperature also plays a role as an environmental cue, usually acting to modify the response to photoperiod by delaying or hastening the onset of diapause if temperatures are abnormally high or low. In tropical areas, where there is less variation in day length, the effect of temperature increases in importance, and in some species may be the most important factor in diapause initiation (Saunders 1982; Denlinger 1985).

Blowflies undergo a larval diapause, arresting their development near the end of the third larval instar, and that in *Lucilia sericata* was first described by Roubaud (1922). Hagmann and Barber (1948) observed that the species overwinters in the larval stage and does not pupariate until spring. Cousin (1932) and Mellanby (1938) showed that diapause can be induced by exposing post-feeding larvae to abnormal conditions such as high or low temperature, desiccation or overcrowding. Physiological studies indicated that diapause in calliphorids was linked to the action of a hormone produced by the larval *corpora allata* (Fraenkel 1935; Burtt 1937). Work by Cragg and Cole (1953) showed that there was, additionally, a maternal component of diapause induction. By the capture of wild females and rearing of their offspring, they found that the proportion of larvae entering diapause increased from about 10% in July to about 35% in early September, and then rapidly to more than 65% by late September. It was observed that the production of diapausing offspring ceased after 10-16 days in standard laboratory conditions, but it was not determined which environmental factor was responsible for the diapause stimulus.

Fraser and Smith (1963), studying *Lucilia caesar*, also found considerable variation in diapause incidence from parental sources, but very little from environmental effects on the eggs or feeding larvae. These researchers also confirmed that, like *L. sericata*, *L. caesar* larvae are susceptible to environmental influences after the completion of feeding. Their experiments showed that diapause incidence could be increased by sealing wandering larvae in test tubes, but were unable to terminate diapause by any of the methods supposedly effective for *L. sericata* larvae. Neither pricking larvae with a needle, chilling (Roubaud 1922), nor isolating larvae in empty tubes (Mellanby 1938) produced a significant increase in diapause incidence.

Ring (1965, 1967a, 1967b) carried out a more comprehensive study of *Lucilia caesar*, confirming that the diapause is maternally induced, and that the proportion of larvae entering diapause increased as it became later in the breeding season.

Sampling a wild population in central Scotland, he found that diapause had been induced in less than 10% of larvae before mid-June. In early July that figure rose to over 60%, and by early August to 100%. Ring (1965, 1967b) also carried out laboratory experiments which showed that *L. caesar* females do not respond to relative changes in photoperiod, but to the absolute levels of the light/dark cycle, with the critical level of photoperiod being approximately 15 hours at 27°C. Female flies were shown to take 5-10 days following a change in light regime before changes in diapause incidence were observed in their offspring.

The induction of diapause in blowflies is probably caused by a chemical compound secreted into the eggs prior to oviposition, possibly by the maternal nervous system, but the nature of this factor is unknown (Saunders *et al.* 1986). It has been proposed that the factor may accumulate in the egg, in response to long nights, both before and after oviposition, and then in the developing larva, causing those larvae which have accumulated a sufficient quantity to enter diapause prior to pupariation (Vaz Nunes and Saunders 1989).

The physiological inducers of moulting and metamorphosis of insects are a collection of closely related steroid compounds called ecdysteroids, the most plentiful and active of which is 20-hydroxyecdysone. This is produced by the modification of ecdysone, a steroid released in response to the secretion of prothoracicotrophic hormone (PTTH) from the brain neurosecretory cells (Wigglesworth 1985). Normal pupariation in blowflies is triggered by a pulse of ecdysone, leading to an increased titre of ecdysteroids in the haemolymph, and subsequently to the production of a series of proteinaceous compounds (pupariation factors) which are responsible for the physiological changes during pupariation (Zdarek 1985).

As blowfly larvae enter diapause, their brains cease to produce prothoracicotrophic hormone (PTTH), and their prothoracic glands also become refractory to this compound over a period of six days (Richard and Saunders 1987). Diapause only occurs in larvae maintained below a certain temperature (15°C in *Calliphora vicina*) so these events may be temperature-dependent (Vaz Nunes and Saunders 1989). Ecdysone continues to be produced throughout diapause, but only at a basal rate, which is unaffected by the application of PTTH or cyclic nucleotides (Richard and Saunders 1987), and the peak of ecdysteroids required for pupariation is therefore absent. A rise in temperature to 25°C leads to a rapid recovery of ring gland competency within 24 hours in entire blowflies. However no such recovery takes place in isolated brain-ring gland complexes, indicating that there is a need for *in vivo* reactivation of the gland. Ecdysone synthesis increases greatly once the

temperature has been raised, and pupariation follows within 36 hours (Richard and Saunders 1987).

1.2.5. Adult ecology

An ecological survey of carrion-feeding calliphorids, carried out at Crosby in Cumbria in northern England in the early 1950s, found that *Calliphora vicina* was the most abundant species, followed by *Lucilia illustris*, *L. caesar*, and *C. vomitoria* (MacLeod and Donnelly 1957b). *L. ampullacea* Villeneuve, *L. silvarum*, *L. sericata*, *Protophormia terraenovae*, and *Cynomya mortuorum* were present at very low levels. Similar results were obtained using several different trapping methods. The relative abundance of *C. vicina* was found to be highest (in excess of 70%) early in the season (May and early June), and late in the season (late September and early October), but it remained over 60% throughout the summer. *C. vomitoria* was found to be primarily a late-season fly, with the population peaking (8.5%) in late September and early October. The greatest abundances of *L. caesar* (14%) and *L. ampullacea* (2.75%) were recorded in late June and July, and that of *L. illustris* (17%) and *L. silvarum* (1.6%) in August and early September. Populations of all of these species declined very rapidly after mid-September (MacLeod and Donnelly 1957b). A later study found that the numbers of *L. illustris* fell very rapidly relative to those of *L. caesar* during September (MacLeod and Donnelly 1960). *Cynomya mortuorum* was found primarily between May and July (0.5%), and was completely absent after mid-September (MacLeod and Donnelly 1957b), and *Protophormia terraenovae* has also been shown to be an early-season fly (MacLeod and Donnelly 1956b).

The geographical distribution of carrion-utilising calliphorids was the subject of a study by MacLeod and Donnelly (1956b), which compiled trapping records from throughout Great Britain. It was found that *Lucilia caesar* was generally distributed and abundant, and that *L. illustris* was also widespread, although possibly less common in hill country, and in the north-west. *L. sericata* was generally distributed, but was not abundant, particularly in northern Britain. Both *Calliphora vicina* and *Calliphora vomitoria* were generally distributed and abundant everywhere. *Protophormia terraenovae* was found to be widely distributed, but not abundant, and was more common in northern Britain. *Cynomya mortuorum* was widely distributed in Scotland and northern England.

MacLeod and Donnelly (1956b, 1957b) found that *Calliphora vomitoria* and *Lucilia ampullacea*, and to a lesser extent *L. caesar*, showed a preference for woodland and

other shaded habitats. *C. vicina* occurred in larger numbers in the open, but particularly near hedgerows, while *L. illustris, Protophormia terraenovae,* and *Cynomya mortuorum* were more common at exposed sites (MacLeod and Donnelly 1956b, 1957b), and *L. sericata* has also been found predominantly in such locations (Holdaway 1933).

1.2.6. Evolution of myiasis in genus *Lucilia*

The substantial majority of calliphorids are free-living and saprophagous, but some will infrequently lay their eggs on wounded or dying animals, and this occasional behaviour is thought to have evolved over time into a more consistent habit of facultative myiasis (Zumpt 1965; Erzinçlioglu 1989). Ultimately, this process could have resulted in a small number of species becoming obligate parasites. Erzinçlioglu (1989) proposed that the use of living animals as a larval food source arose in various species of calliphorid after the arrival of humans and their associated domestic animals in the area where the flies were endemic. It is significant that the prevalence of sheep strike in Australia increased rapidly following the introduction of sheep breeds which had been selectively bred for the production of heavier fleeces (Norris 1990), while wild types of sheep rarely suffer from cutaneous myiasis.

A parsimony analysis using 14 morphological characteristics was carried out for 25 species of the genus *Lucilia* (Stevens and Wall 1996a). A strict consensus tree identified three groupings within the genus. One of these contained *L. caesar* and *L. illustris,* plus *L. ampullacea,* while another contained *L. sericata* and *L. cuprina,* along with five other species which are not agents of myiasis in mammals. On the basis of these results, it was suggested that the myiasis habit must have evolved separately on more than one occasion, in groups of flies adapted to different climatic regions. A genetic study was subsequently conducted involving analysis of material from ten species of *Lucilia* (Stevens and Wall 1997). This indicated that the interrelationships within the genus were similar to those proposed by the earlier parsimony analysis, and that the myiasis habit had evolved separately in *L. sericata* and *L. cuprina,* as well as in the *L. caesar* group (*L. caesar, L. illustris* and *L. ampullacea*). The specialised behaviour of *L. bufonivora* Moniez, which causes myiasis only in toads, required to be explained by a fourth evolutionary event.

Genetic studies may also help to explain whether apparent differences in the pathogenicity of blowfly species in different geographical locations are due to genetic factors, or simply to differences in farm management procedures and

climate. Although *Lucilia cuprina* has a substantial impact on the sheep industry in Australia (Foster *et al.* 1975), it has little or none in North America (Williams *et al.* 1985). Similarly, *L. sericata* causes significant damage to sheep stocks in Great Britain (French *et al.* 1992), and in New Zealand (Tenquist and Wright 1976), it does not do so in Australia, despite its presence there (Foster *et al.* 1975). An amplification procedure (Stevens and Wall 1995) used to analyse DNA from these two species found significant genetic variation between *L. cuprina* populations in different parts of the world, but very little variation within *L. sericata* (Stevens and Wall 1996b).

1.2.7. Studies of *Lucilia sericata* population ecology

A deterministic simulation model, developed from analyses of the effects of temperature on blowfly development, and based on the calculation of day-degrees (Wall *et al.* 1992b), was able to predict 67%, 52%, and 49% of variation in *Lucilia sericata* populations in three successive years (Wall *et al.* 1993a). It predicted that four generations of blowflies would emerge each season, with the fifth limited by the onset of diapause (Wall *et al.* 1993a). It also allowed the investigation of various potential control strategies, and predicted that strategic killing of blowflies early in the season could significantly reduce blowfly populations throughout the remainder of the season (Wall *et al.* 1993b). A trial was subsequently carried out involving the treatment of sheep with the larvicide cyromazine shortly before the predicted emergence of the first generation of *L. sericata* (Wall *et al.* 1995). It was found that the population was suppressed, but that the effectiveness of the treatment was reduced by immigration of flies from neighbouring areas, and by adverse weather conditions which increased the susceptibility of sheep to strike.

Subsequently, a stochastic model was derived, which took into account the inherent variation between the behaviour patterns of individual insects. This was able to predict the timing of blowfly emergence with greater accuracy, and suggested that blowfly abundance was in fact more sensitive to variations in base temperature than to changes in day-degrees (Fenton *et al.* 1997).

1.3. Methods of blowfly control

1.3.1. Insecticides and Repellents

The control of sheep strike has been assisted by legislation to control sheep scab, which made compulsory a twice-yearly dipping of sheep in an approved insecticide. However, this requirement was relaxed to one dip per annum in 1989, and was removed altogether in 1992, although penalties for the presence of scab still remain. Prior to the 1940s, the only effective insecticides available for use against sheep blowflies were highly toxic arsenicals (MacLeod 1938). Organochlorine insecticides such as dieldrin subsequently became widely used, but these were gradually withdrawn during the 1970s and 1980s because of their persistence in the natural environment. They were replaced with organophosphates, which, although more toxic than organochlorine compounds, are less persistent. Despite considerable concern over the effect of organophosphates on human users (for example, Stephens *et al.* 1995) and on the wider environment (for example, Littlejohn and Melvin 1991), they continue to be the most widely used insecticides for the treatment of sheep (French *et al.* 1994b). Other compounds used for blowfly control include synthetic pyrethroids and cyromazine, a larval growth inhibitor (Lonsdale *et al.* 1990).

A questionnaire survey carried out in England and Wales in 1990, referring to the blowfly seasons of 1988 and 1989, showed that dipping was the most common method of blowfly control (French *et al.* 1992). Throughout the survey area, 97.7% of farmers reported dipping of ewes in 1989, and 99.0% in 1990, with slightly lower proportions reporting dipping of lambs. However, dipping is also used for the control of other ectoparasites of sheep, and only 88.9% of respondents indicated that they had dipped specifically for the control of blowfly strike. Most farmers dipped their ewes twice in both years, but the proportion doing so reduced from 84.6% in 1988 to 66.9% in 1989, reflecting the reduction in the number of compulsory dips (French *et al.* 1992). By 1991, a further survey showed that the number of farmers conducting two dips had further reduced to 57.3% (French *et al.* 1994b). The insecticide most widely used for dipping was the organophosphate diazinon, which was used by 48.7% of farmers for the single compulsory dipping, and by 27.4% for an additional, summer, dipping. The corresponding figures for propetamphos, another organophosphate, were 32.4% and 23.1%. The only significant use of any other class of chemical was that of flumethrin, a pyrethroid licensed only for the

control of scab, which was used by 4.9% of farmers for the compulsory dipping, and by 0.2% for a summer dipping.

As an alternative to dipping by complete immersion, insecticides can be applied by spraying or pouring, and the proportion of farmers reported the use of this method of blowfly control on lambs or ewes increased from 22.5% in 1988 to 35.9% in 1989 and 41.2% in 1991 (French *et al.* 1994b). There were significant regional variations, with the proportion using spraying varying between 39.8% in south-east England and 11.3% in the north of England (French *et al.* 1992). The 1991 survey showed that organophosphate compounds were the most widely used as sprays, with 9.7% of farmers using diazinon, 5.8% propetamphos, and 4.1% chlorfenvinphos, despite the fact that some of these chemicals were licensed only for dipping. Cypermethrin, a pyrethroid used by 0.6% of farmers, was the most common non-organophosphate compound used as a spray (French *et al.* 1994b). In addition to sprayed insecticides, cyromazine 'pour-on' was used by 8.7% of farmers in 1988 and 1989, and this proportion varied from 14.4% in south-east England to 3.1% in the north of England (French *et al.* 1992). By 1991, the overall proportion using cyromazine had risen to 15.9% (French *et al.* 1994b).

Repellent substances are widely used in Australia to assist in the protection of sheep from *Lucilia cuprina.* A wide range of repellents has been tested using olfactometers (Hepburn 1943; Urech *et al.* 1994), and meat baits with repellents added to the surface (Virgona *et al.* 1976). Compounds used on farm include eucalyptus oil, 1,2-dichlorobenzene, and 1,4-dichlorobenzene, which are applied to wounds (Steiner and Harrington 1992). Two extracts of the neem tree, *Azadirachta indica,* have been shown to be repellent to *L. sericata* in the laboratory (Ntebela 1994).

1.3.2. Physical treatments of sheep

Tail amputation, known as docking, was reported as a method of blowfly control by 75.2% of respondents to the questionnaire survey, although there was significant regional variation in this practice, with its use varying from 86.8% in south-east England to 53.1% in Wales. The partial shearing of the perineum, known as dagging or crutching, was used by 61.7% of farmers, and this also showed regional variation, with its frequency varying from 74.6% in south-east England to 44.0% in Wales (French *et al.* 1992). In Australia, the 'Mules' operation is widely used. This is an extensive procedure which involves the removal of a considerable quantity of skin from the tail and breech area, with the purpose of preventing wool growth. It

reduces the level of faecal soiling and is considered important in the control of breech strike (Watts and Luff 1978). However, the wound resulting from the operation is highly attractive to *Lucilia cuprina* (Cook and Steiner 1990), and usually requires to be treated with larvicides, disinfectants and fly repellents (Steiner and Harrington 1992).

1.3.3. Immunological developments

Research has been carried out into two types of vaccine intended to reduce the incidence of strike. Firstly, a vaccine has been developed against *Pseudomonas aeruginosa*, the most common bacterial species found in Australian cases of fleece-rot, which is a predisposing condition for strike. Secondly, vaccines have been developed which act directly against *Lucilia cuprina* antigens, usually those from the gut of first instar larvae (Sandeman 1990). Several studies of the injection of extracts of *L. cuprina* larvae or their excised guts have demonstrated a significant reduction in the weight of larvae subsequently grown on the immunised sheep (Johnston *et al.* 1992). Immunoglobulin isolated from sheep vaccinated with larval material has been shown to significantly inhibit the growth of *L. cuprina* larvae in vitro (Johnston *et al.* 1992; Fry *et al.* 1994). In a vaccine trial, significantly fewer cases of strike were recorded on vaccinated sheep compared to controls (Bowles *et al.* 1996), but a commercial vaccine has yet to reach the market.

1.3.4. Farm management factors

Although *Lucilia sericata* has only been found to inhabit carrion at relatively low levels (Cragg 1955; Smith and Wall 1997), the carcase of a domestic animal such as a sheep has the potential to support a very large number of blowfly larvae, and relatively large numbers of *L. sericata* have been found to emerge from the carcase of a sheep which was suffering from severe myiasis at the time of death (Cragg 1955). The most common method of disposal was found to be to kennels, which was used by 58% of farmers, and this was followed by burial and transport to knackers, used by 34% and 33%, respectively. Only 6% disposed of carcases by burning them on the farm. There was significant regional variation in these figures, with burial being the most popular method of disposal in Wales (53%) and in the north of England (44.6%) (French *et al.* 1992). That carcase disposal is a significant consideration in the control of blowfly populations is indicated by further analysis of the data obtained from the survey, which showed that on-farm carcase disposal was associated with a

small increase in the risk of a high strike prevalence, which was defined as being more than 2% of the flock (French *et al.* 1994a).

Other farm management factors also affect the incidence of ovine myiasis. Increasing flock size also increases the risk of strike, but the risk of having a high prevalence of strike (over 2%), is lower for large flocks than for small ones. An increase in the stocking density of sheep was associated with increased risk of strike (French *et al.* 1994a).

1.3.5. Biological control

Several species of parasitoid wasps parasitise blowfly larvae, and have been considered as biological control agents for *Lucilia* species. However, although *Alysia manducator* (Panzer) has been found to parasitise a significant number of blowfly larvae, the fact that its reproductive rate is much lower than that of *Lucilia* means that it has little potential as an agent of biological control. It has been calculated that *L. sericata* could lose more than 99% of its population to *Alysia* in each generation and still maintain its numbers (Salt 1932). No other insect parasite of blowflies is as effective as *Alysia*, and therefore their use as part of a control programme for sheep blowflies appears unlikely. The introduction of *Nasonia vitripennis* (Walker) and *A. manducator* into New Zealand in the 1920s, in an attempt to reduce blowfly levels, has never been shown to have had any measurable impact (Dymock *et al.* 1991). A recent study of the pathogenicity of *Serratia* bacteria has shown that some strains of *S. marcescens* cause significant mortality in *Lucilia sericata* (O'Callaghan *et al.* 1996). Further research will be required to assess the usefulness of these bacteria as biological control agents of blowflies.

1.3.6. Trapping

A wide variety of traps has been developed for the capture of sheep blowflies and their relatives, the screwworm flies. These include static enclosed traps of various designs (Bishopp 1916; Newman and Clark 1926, MacLeod and Donnelly 1956a; Anderson *et al.* 1990), wind-oriented traps (Broce *et al.* 1977), electrified screens (Goodenough and Snow 1977), and adhesive targets (Wall *et al.* 1992c). These are often baited with liver and sodium sulphide solution (for example, Mackerras *et al.* 1936), although a wide variety of other baits have been tested. Recently the use of colour has been shown to affect catch levels (Wall *et al.* 1992c). Traps have been

shown to be capable of significantly reducing blowfly populations and levels of sheep strike (Mackerras *et al.* 1936; Anderson and Simpson 1991).

1.4. Aims and objectives

Concern about the potential dangers of organophosphate insecticides have led to an increase in interest in alternative methods of blowfly control. Trapping has proved successful for the control of other dipteran species such as tsetse flies, and several designs have been developed for the capture of blowflies.

The overall aim of the present study was to investigate the biology of sheep blowflies in relation to their control by trapping. There were four major components of the study. Firstly, an investigation was carried out to determine which blowfly species were involved in ovine cutaneous myiasis in Scotland. This was considered to be of particular importance because previous research has shown the species composition in these cases to differ in Scotland from that in the remainder of the British Isles. Secondly, various trap designs were tested in the field, with the aim of optimising a trap for the capture of sheep blowflies. Information about the blowfly species prevalent in myiasis cases in Scotland was taken into account in the planning of trapping experiments. The remaining components were studies of the responses of *Lucilia* species to visual and olfactory stimuli. In each case, these responses were investigated both by the use of electrophysiological methods, and in the field.

An additional component of the study was an investigation into the ecological impact of blowfly traps, by examining their catches of other types of insect.

2. Blowfly species in ovine myiasis in Scotland

2.1. Introduction

2.1.1. The distribution of blowflies involved in ovine myiasis in the British Isles

It appears that the infestation of sheep with blowfly larvae was a recognised problem in England as far back as the early 16th century, and Davies (1934) provides some literary references to this. However, the first systematic surveys of the blowfly species involved in British sheep myiasis were not carried out until the twentieth-century, in Scotland (MacDougall 1909; Ratcliffe 1935) and in North Wales (Davies 1934). Although the first study in Scotland involved samples from a variety of locations, these were mainly from southern and eastern areas (MacDougall 1909), and the second study was carried out entirely in Aberdeenshire (Ratcliffe 1935). All three studies found that *Lucilia sericata* Meigen was responsible for the overwhelming majority of cases, but *Calliphora vicina* was found in a small number of cases, usually accompanying *Lucilia sericata* in mixed infestations. This suggested that *C. vicina* was a secondary species, usually attacking sheep on which other larvae are already feeding.

A survey of sheep strike in South-West Scotland found that *Lucilia sericata* was involved in the vast majority of cases, but also revealed the involvement of a much wider range of fly species (Haddow and Thomson 1937). Six alternative species (those other than *L. sericata*) were found to be involved in sheep strike. Five of these were calliphorids: *L. caesar* , *Protophormia terraenovae*, *C. vomitoria*, *L. illustris*, and *C. vicina*, and the muscid fly *Muscina pabulorum* Fallén was also found in a small number of cases. Of these six alternative species *L. caesar* was the most widespread in sheep strike by a considerable margin, and the only one which was found other than in mixed infestations with *L. sericata* (Haddow and Thomson 1937).

A much larger investigation into the blowfly species involved in myiasis of British sheep was carried out by MacLeod (1943a), who reared larvae collected from strike cases from farms throughout the British Isles, and identified the emergent adult flies

cases from farms throughout the British Isles, and identified the emergent adult flies from 1307 samples. The number of samples used for identification from sources in Scotland was 518, although this included some cases from parts of Cumbria and Northumberland. This study confirmed that *Lucilia sericata* was the principal cause of sheep strike in every region, but identified important differences in the incidence and distribution of the other species involved. The proportion of cases in which *L. sericata* occurred decreased to the north and to the west. It was found that *L. sericata* was present in almost all cases sampled in central and southern England, South Wales, and Ireland, and alternative species were present in only 2% of these samples. In North Wales, the Pennines and Yorkshire, 15% of samples contained alternative species, and *L. sericata* was absent from 5%, and in Scotland the corresponding figures were even higher, at 26% and 8%. The highest incidence of alternatives was found to be in the Western Scottish Highlands, where 56% of cases involved alternative species and 27% included did not include *L. sericata* (MacLeod 1943a).

The most common alternative species was found to be *Lucilia caesar,* which was found in a total of 10% of cases (17% of those in Scotland), followed by *Protophormia terraenovae,* found in 3% of cases (7% of those in Scotland). *Calliphora vicina* was found in less than 2%, and *C. vomitoria* in less than 1%, although 5% of samples from Scotland involved one or both *Calliphora* species (MacLeod 1943a). MacLeod (1943a) totalled the results of his survey, and those of three others, showing that *Lucilia sericata* occurred in 96% of strike cases, *L. caesar* (including *L. illustris*) in 10%, *Protophormia terraenovae* in 3%, *Calliphora vicina* in 2%, and *Calliphora vomitoria* in less than 1%. *Muscina pabulorum* was also found in a very small number of cases.

Both *Lucilia caesar* and *Protophormia terraenovae* appeared to act in some cases as primary flies (initiators of strike) as they were found in a significant number of strike cases in the absence of *L. sericata. L. caesar* (including, in this instance, *L. illustris*) was found to be of importance in Scotland, northern England and North Wales, but was only found in 2% of cases from central and southern England. Only in the Western Highlands and in North Wales were significant numbers of cases found involving *L. caesar* in the absence of other species (16% and 4%, respectively). *Protophormia terraenovae* was absent from most of England, but was found in 6% of cases from the Solway and Lake District, and in 18% of those from the Western Highlands. In the Western Highlands 7% of cases contained exclusively *P. terraenovae. Calliphora* species were very scarce in strike samples from England, but occurred in small numbers throughout most of Scotland and North Wales, with the highest incidence

(7%) in the Central Lowlands, where 4% of the samples contained *Calliphora* larvae without the presence of other species (MacLeod 1943a).

Recently, a further survey of blowfly species involved in sheep myiasis in England and Wales broadly confirmed MacLeod's (1943a) findings. Wall *et al.* (1992a) found that 81% of 32 strike cases sampled consisted solely of *Lucilia sericata*, 6% solely of *L. caesar*, with the remaining 13% being a mixture of these two species. Although this survey was considerably smaller than that of MacLeod (1943a), it reinforces the conclusion of the earlier study that *L. sericata* is the principal agent of sheep myiasis in England and Wales.

Several other blowfly species which are found in Britain are potential agents of ovine myiasis, but have never been recorded as such. *Lucilia ampullacea* has been found in a hedgehog (*Erinaceus europaeus* L.) in Denmark (Nielsen *et al.* 1978), and *L. richardsi* in a nightjar (*Caprimulgus europaeus* L.) in Finland (Nuorteva 1959). *Cynomya mortuorum* has been recorded in an infestation of a hare (*Lupus timidus* L.) in Finland (Itämies and Koskela 1980).

2.1.2. Factors affecting the distribution of blowfly species in strike

The composition of strike cases has been shown to vary according to habitat. MacLeod (1943a) found that 82% of the samples examined containing *Lucilia caesar* were from "highland" areas, and *Protophormia terraenovae* was also found primarily in such areas. *Lucilia illustris* appeared to favour lowland habitats, but the number of samples in which this species was distinguished from other members of the "*L. caesar* group" was very small. No attempt was made to separate females of this group, and only 65 males were identified to species level, of which 59 proved to be *L. caesar*, and 6 *L. illustris* (MacLeod 1943a).

MacLeod (1943b) found that the great majority of strike cases caused by alternative species were in mountain breeds of sheep, and that crosses between mountain and lowland breeds also had a higher level of infestation by alternative species than pure lowland breeds. However, it seems probable that this finding is related to the fact that mountain breeds are the most common in areas where alternative species are common in strike samples, particularly in north-western Scotland and in North Wales. A strong association was found between the occurrence of alternative species and the type of grazing in which the strikes occurred. In areas where alternative species occurred frequently, 44% of cases on open mountain or moorland contained alternative species, compared to 22% of those on rough grazing, and 14% of those on

A significant association was also found between the occurrence of alternative species and vegetation type on the pasture, with 44% and 43% occurrence in bracken and heather, respectively, in areas where alternative species occurred frequently. The corresponding figures for rough grazing, gorse and wood, and good pasture were 26%, 23% and 12%. In other areas, 13% of strike cases in heather were caused by alternative species, compared with 5% in good pasture. Analysis showed that the association between alternative species and bracken and/or heather is present in enclosed grazing as well as on hill pastures, indicating that the presence of bracken and heather is of importance regardless of the type of grazing.

There were also seasonal variations in the species composition of myiasis cases. *P. terraenovae* and *L. caesar* had a higher relative incidence in the first half of the fly season than in the second half, and *Calliphora vomitoria* appeared to be restricted to the very beginning and end of the season (May, June and September) (MacLeod 1943a). Strikes involving *P. terraenovae* were almost exclusively found in adult sheep, an observation which was linked to its role as an early-season species (MacLeod 1943b).

2.1.3. Aims and objectives

No study of the species composition of strike cases in Scotland has been carried out since that of MacLeod (1943a). During the intervening period, the use of organochlorine, and subsequently organophosphate, insecticides became widespread. However, the end of compulsory dipping under the Sheep Scab Order in 1991 and growing concern over the harmful effects of organophosphate compounds on agricultural workers (Stephens *et al.* 1995), and on the wider environment (Littlejohn and Melvin 1991), has resulted in a decrease in the number of sheep dippings, and a corresponding increase in the incidence of sheep strike is believed to have followed. The object of the present survey was to determine whether any change had taken place in the distribution of dipteran species involved in sheep myiasis in Scotland.

2.2 Materials and Methods

2.2.1. Collection and identification of samples

Samples of blowfly larvae were collected from natural infestations in live sheep on farms from many areas of Scotland. Collection of samples was carried out by sheep farmers and shearers during the summers of 1993 to 1996, inclusive. Some contacts were obtained from staff and students at SAC Auchincruive. Others were made as a result of publicity in local newspapers and the farming press following a press release in early August 1996, intended to locate additional sources of strike samples.

Farmers and shearers were instructed to remove moderate numbers of larvae (with 50-100 larvae suggested as a guideline), and to place them on meat (beef liver suggested) on a layer of sand or sawdust in a container such as a margarine tub. Holes were to be made in the lid to allow air to permeate the container, and the collectors were then requested to keep the container in a cupboard or under a box, in order to prevent access to blowflies which might lay additional eggs into the culture. The samples were either collected from farms or brought to SAC Auchincruive by the collectors.

On arrival at the laboratory, samples were inspected. If the container was found to be unsuitable, or if the larvae were overcrowded or small, they were removed from the container and placed in a metal box with a gauze lid, containing a layer of sand 20-30mm deep. If larvae were small, a piece of beef liver was supplied to allow them to continue feeding. Once most larvae had left the meat, any remaining meat was removed. Larvae were then allowed to pupariate, and when adult flies emerged, these were left to die.

The dead flies were then identified using a binocular microscope. Bright green metallic colouration was used to determine the presence of *Lucilia* species. *L. sericata* was then identified by the presence of a white or yellow basicosta. *L. caesar* and *L. illustris* have a black basicosta, and were distinguished in males by the presence of a large and swollen epandrium (broader than the length of the fifth tergite at the midline) and bifid apices to the surstyli in the former species. Female *L. caesar* and *L. illustris* were distinguished by the absence of marginal setae on the middle section of the hind margin of the sixth tergite in the former species (Rognes 1992).

Protophormia terraenovae was identified by the presence of hairs on the stem-vein of the wing, and dark coloured calypters with black hairs on the upper surface of the upper calypter. The absence of hairs on the stem vein of the wing, combined with the presence of hairs on the upper surface of the lower calypter and the absence of bright yellow-orange colouration on the gena, was used to determine the presence of *Calliphora* species. *C. vomitoria* was then identified by a black coloured basicosta and the presence of orange hairs on the face, and *C. vicina* by a pale or brown basicosta and dark orange ground-colour on the face (Rognes 1992).

Details of the farms and sheep from which samples were taken were also obtained, either from personal knowledge of the sources, or by completion of a questionnaire by the farmer or a farm employee. The following information was collected: altitude of farm; approximate altitude of sheep when struck; type of grazing (permanent pasture, rough grazing or moorland); presence or absence of five vegetation types (deciduous woodland, coniferous woodland, gorse, bracken and heather); the breed of sheep affected by strike; and whether a lamb, ewe or tup was involved. A copy of the questionnaire is shown in Figure 2.1.

2.2.2. Statistical analysis of farm and sheep factors

The proportion of samples containing alternative species (those other than *Lucilia sericata*) was analysed using the information collected about farms, by the calculation of z-statistics. This was possible because proportional data (for example, the proportion of samples containing species other than *Lucilia sericata*) is binomially distributed, and a binomial distribution approximates a normal distribution when a sufficiently large sample size is used. The working rule that a sample size is sufficiently large when both $n\pi$ and $n\pi(1-\pi)$ both exceed 5 was utilised in this case. The null hypothesis used was that π (the proportion of samples containing alternative species) did not differ between two groups of samples (for example those from eastern Scotland and western Scotland). An estimate of π could therefore be used, which was the total number of pure samples divided by the total number of samples. A continuity correction was used to take account of the fact that the data was in the form of a discrete variable whose values were integers, which was being approximated by a continuous variable. This correction took the form of a deduction or addition of a half count from each proportion, *P* (Clarke and Cooke 1992).

SCOTTISH AGRICULTURAL COLLEGE AUCHINCRUIVE
SHEEP STRIKE SAMPLE COLLECTION
FARM QUESTIONNAIRE

1. What height is your farm above sea level? _____feet
   (if appropriate give a range of heights) _____metres

2. When your sheep were infested with maggots during the month of _____ 1996, at approximately what height were they grazing? _____feet
   _____metres

3. How would you describe the grazing at the site at which the sheep were infested?
   (tick one box)
   - Good pasture ☐
   - Rough grazing ☐
   - Moorland ☐
   - Other _____

4. Are any of the following vegetation types common at or near the site at which sheep were infested?
   (tick one or more boxes)
   - Deciduous woodland (e.g. sycamore; oak) ☐
   - Coniferous woodland (e.g. spruce, pine) ☐
   - Gorse ☐
   - Bracken ☐
   - Heather ☐

5. From which breed(s) of sheep were maggots collected? _____

6. Were the infested sheep
   - Lambs ☐
   - Ewes ☐
   - Tups ☐

THANK YOU FOR YOUR ASSISTANCE
PLEASE RETURN THIS QUESTIONNAIRE IN THE ENCLOSED STAMPED ADDRESSED ENVELOPE

Figure 2.1: Copy of questionnaire used during collection of myiasis larvae.

To find out whether two proportions, P_A and P_B, differed significantly, the difference between the two observed proportions was examined:

$$\mathrm{Var}[P_A - P_B] = \mathrm{Var}[P_A] + \mathrm{Var}[P_B] = \frac{\pi_A(1-\pi_A)}{n_A} + \frac{\pi_B(1-\pi_B)}{n_B}$$

The null hypothesis is that $\pi_A = \pi_B = \pi$, therefore:

$$\mathrm{Var}[P_A - P_B] = \frac{\pi_A(1-\pi_A)}{n_A} + \frac{\pi_B(1-\pi_B)}{n_B} = \pi(1-\pi)\left(\frac{1}{n_A} + \frac{1}{n_B}\right)$$

The normal approximation is that:

$$(P_A - P_B) \approx N(0, \mathrm{Var}[P_A - P_B])$$

so,

$$z = \frac{(p_A - p_B) - 0}{\sqrt{\mathrm{Var}[P_A - P_B]}}$$

The normal statistic, z, was then compared with values at various levels of significance on statistical tables for two-tailed distributions (for example, where $z > 2.576$, $P < 0.01$) (Clarke and Cooke 1992).

Statistical comparisons using this method were used to identify any effect of geography, altitude, or the presence or absence of certain vegetation types on the proportion of samples containing alternative species.

2.3 Results

2.3.1. Identification of samples

Thirty-nine samples of larvae were received alive and reared successfully to produce adult flies. The identification of these flies is shown in Table 2.1, and the full details of each sample and farm are tabulated in Appendix 1. *Lucilia sericata* was found in thirty samples (77%), of which twenty (51% of the total) contained no other species. *L. caesar* occurred in twelve samples (31%), of which three (8% of the total) contained no other species. *Protophormia terraenovae* occurred in seven samples (18%), of which three (8% of the total) contained no other species. In addition, *Calliphora vomitoria* was identified in two samples, and *L. illustris*, *C. vicina*, and the muscid *Muscina pabulorum* in one sample each.

	Lucilia sericata	*Lucilia caesar*	*Lucilia illustris*	*Protophormia terraenovae*	*Calliphora vicina*	*Calliphora vomitoria*	*Muscina pabulorum*
Pure	20	3	0	1	0	2	0
with other species	10	9	1	6	1	0	1
Total	30	12	1	7	1	2	1

Table 2.1: Occurrence of dipteran species in 39 strike samples from all parts of Scotland.

2.3.2. Importance of farm and sheep factors

For the purposes of statistical analysis the samples were divided into two groups according to the geographical location of their source. Western Scotland was defined as comprising the former Regions of Dumfries and Galloway, Strathclyde, Central and Highland, and eastern Scotland was defined as comprising the remainder of the Scottish mainland. The division between these two areas can be approximated by a line drawn between Ullapool in Highland Region, and Gretna in Dumfries and Galloway Region. Samples were not collected from Orkney, Shetland or the Western

Isles. Twenty-three of the samples (59%) were collected from eastern Scotland, and the remaining sixteen (41%) from western Scotland. The species composition in these two divisions is shown in Tables 2.2 and 2.3. The data are also represented graphically in Figure 2.2, which shows the occurrence of pure and mixed samples as proportions of the total in each area, and in Figure 2.3, which shows the distribution of the three most common species by area. The proportion of cases containing alternative species was significantly lower in eastern Scotland (26%) than in western Scotland (81%)(z=3.06; P<0.01). The proportion of samples containing *L. sericata* in eastern Scotland (95%) was also significantly greater than that in western Scotland (50%)(z=2.48; P<0.02).

	Lucilia sericata	*Lucilia caesar*	*Lucilia illustris*	*Protophormia terraenovae*	*Calliphora vicina*	*Calliphora vomitoria*	*Muscina pabulorum*
Pure	17	0	0	1	0	0	0
with other species	5	3	1	2	1	0	0
Total	22	3	1	3	1	0	0

Table 2.2: Occurrence of dipteran species in 23 strike samples from eastern Scotland.

	Lucilia sericata	*Lucilia caesar*	*Lucilia illustris*	*Protophormia terraenovae*	*Calliphora vicina*	*Calliphora vomitoria*	*Muscina pabulorum*
Pure	3	3	0	0	0	2	0
with other species	5	6	0	4	0	0	1
Total	8	9	0	4	0	2	1

Table 2.3: Occurrence of dipteran species in 16 strike samples from western Scotland.

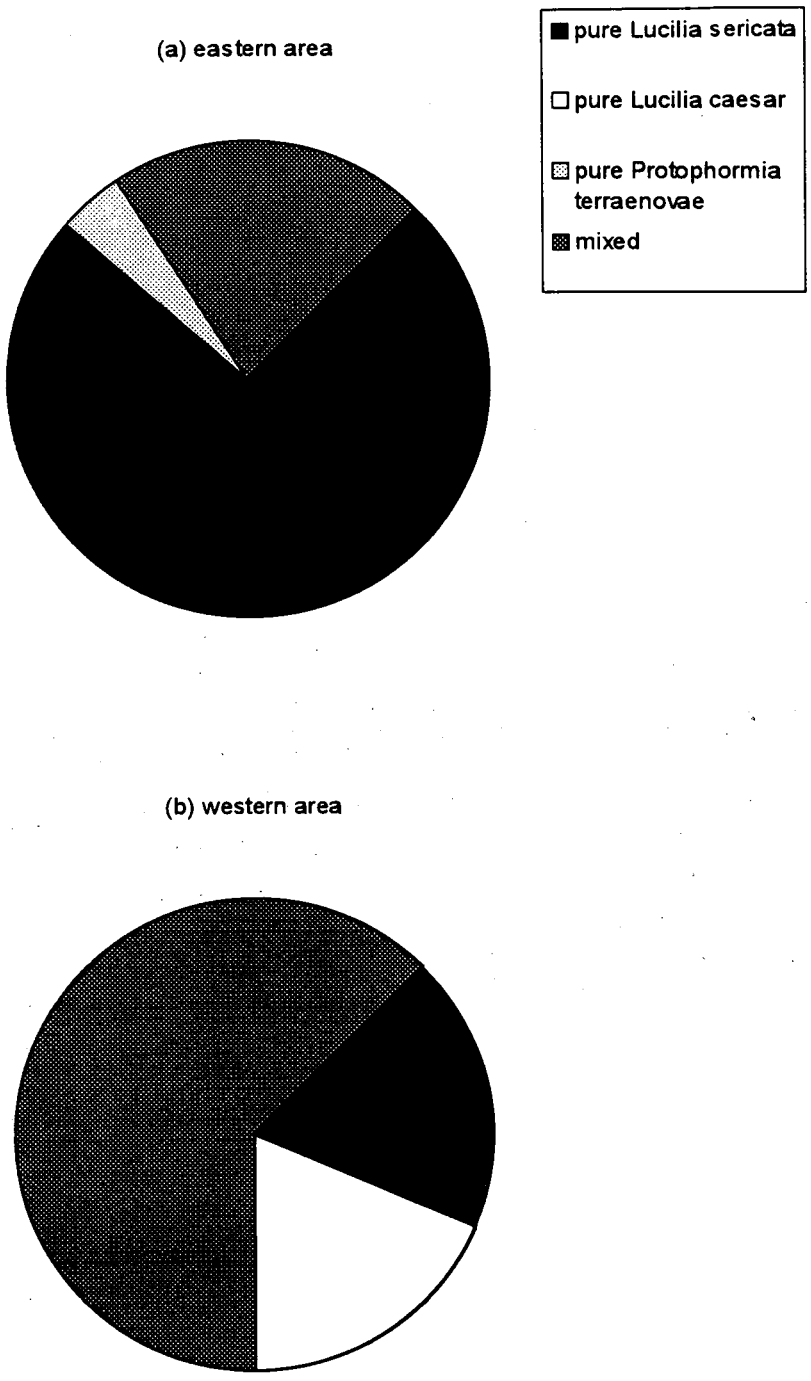

Figure 2.2: Distribution of pure and mixed samples as a proportion of the total collected from (a) the eastern area and (b) the western area (see text for geographical definition of areas).

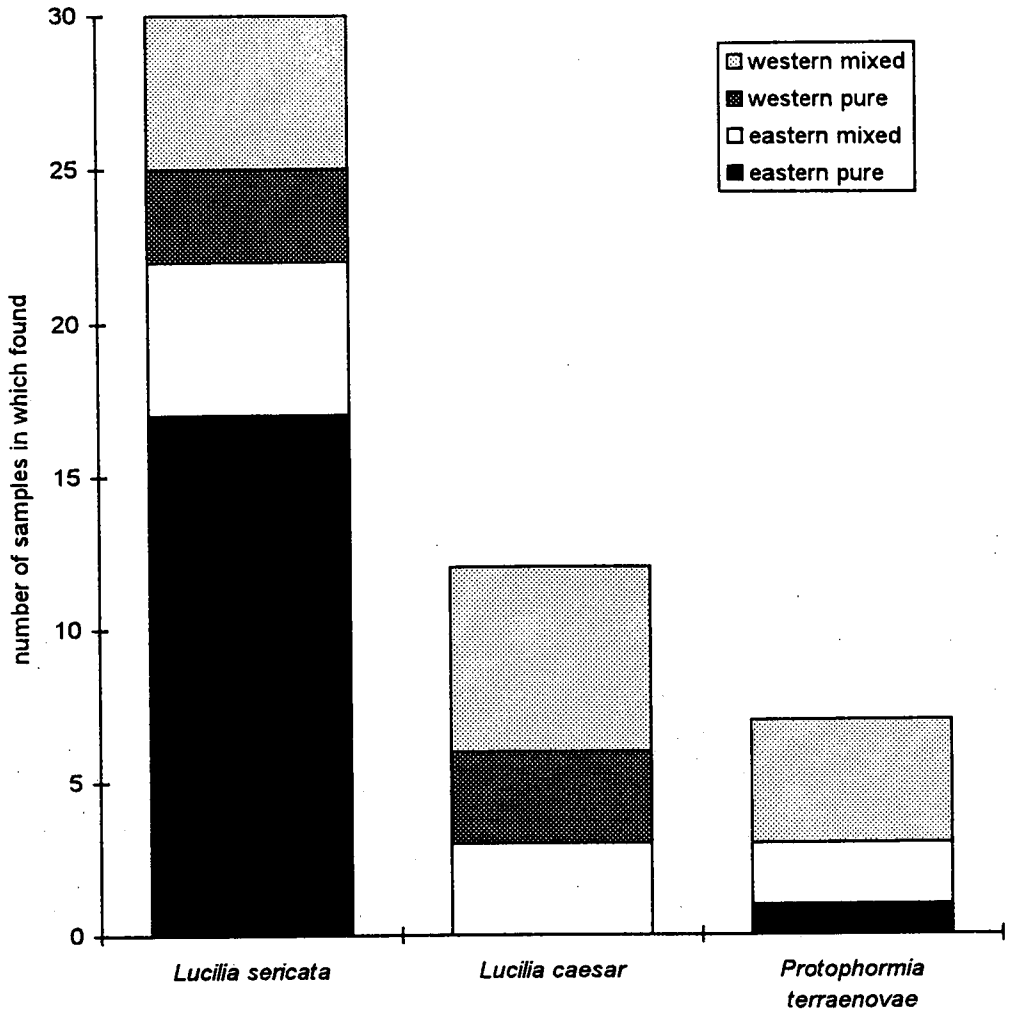

Figure 2.3: Number of pure and mixed samples in which the three most common ovine myiasis blowflies were found to occur.

The proportions of samples containing *Lucilia sericata*, grouped by other characteristics of the sheep and farms involved, are shown in Table 2.4. For the investigation of the effect of altitude, the samples were divided into two groups: those collected at 200m or higher above mean sea level, and those collected below this height. The proportion of samples containing alternative species was significantly lower in those samples collected at the lower altitudes (32%) than at the higher altitudes (91%) (z=2.95; P<0.01). Infested sheep were of a variety of breeds, and were divided into two groups: those of hill breeds and those of other types. The proportion of strike cases containing alternative species in hill breeds (81%) was significantly greater than that in other breeds (26%) (z=3.06; P<0.002). Similarly, the

proportion containing alternative species was significantly lower on permanent pasture (29%) than on rough grazing and moorland (80%) (z=2.76; P<0.01).

Deciduous and coniferous trees were grouped together as a single category for analysis. The presence of trees was associated with a significantly lower incidence of alternative species (z=2.15; P<0.05). In contrast, the presence of bracken was associated with a significantly greater incidence of alternative species (z=2.66; P<0.01). The presence of heather was not significantly linked to the incidence of alternatives (z=1.61; P>0.05). Gorse was not recorded at any of the sites at which sheep were struck. Insufficient data was collected to conduct any meaningful analysis of the distribution of infestations between lambs, ewes, and tups.

Factor		Total number of samples	Samples containing alternative species	
Location	Eastern Scotland	23	6	**
	Western Scotland	16	13	
Altitude	Less than 200m	28	9	**
	200m and over	11	10	
Sheep breed	Hill breeds	16	13	**
	Other breeds	23	6	
Grazing	Permanent Pasture	24	7	**
	Rough grazing/moorland	15	12	
Trees	Present	27	10	**
	Absent	12	9	
Bracken	Present	10	9	**
	Absent	29	10	
Heather	Present	9	7	
	Absent	30	12	

Table 2.4: Samples divided according to various factors relating to the farm and sheep from which they were collected, showing the number of alternative species (those other than *Lucilia sericata*) present in each case. Factors showing a significant difference (P<0.01) between the proportions of alternatives in their two groups are marked **.

2.4 Discussion

Although this study demonstrated that *Lucilia sericata* was the most common species involved in sheep strike in Scotland, the incidence of alternative species (49%) and the proportion of samples from which *L. sericata* was absent (23%) were substantially higher than corresponding figures from studies in England and Wales. MacLeod (1943a) found that *L. sericata* was present in almost all cases sampled in central and southern England and South Wales, and alternative species were present in only 2% of these samples. In North Wales, the Pennines and Yorkshire, 15% of samples contained alternative species, and *L. sericata* was absent from 5% (MacLeod 1943a). More recently, Wall *et al.* (1992a) confirmed the dominance of *L. sericata* in England and Wales, finding, in a study of 32 larval samples, that 19% contained alternative species (all *L. caesar*), and 6% contained *L. caesar* alone. The incidence of alternative species found in the present study, and proportion of samples from which *L. sericata* was absent, were also higher than the figures of 26% and 8% previously reported from Scotland, (which included, in this case, parts of Cumbria and Northumberland) by MacLeod (1943a).

The smaller size of this investigation, in comparison with the Scottish component of MacLeod's (1943a) study, precludes a detailed comparison of different areas of Scotland. However, the comparison of western and eastern divisions of the country demonstrates the substantially higher incidence of alternative species in the west. The incidence of alternative species in western Scotland (81%) and the proportion of samples in this division in which *L. sericata* was absent (50%) are higher even than the corresponding figures for the Western Highlands (56% and 27%), the area of highest incidence of alternatives in MacLeod's (1943a) study.

This study supports the finding of MacLeod (1943a) that *Lucilia caesar* and *Protophormia terraenovae* are the most important alternative species. The incidence of both these species (31% and 18%) was found to be higher than the figures for Scotland in the previous study (17% and 7%), despite the inclusion by MacLeod (1943a) of *L. illustris* with *L. caesar*. Additionally, each of the other calliphorid species previously recorded in sheep strike in the British Isles: *L. illustris, Calliphora vomitoria, C. vicina,* and the muscid species, *Muscina pabulorum,* was found in at least one sample in the present study.

MacLeod (1943b) identified several factors associated with those geographical areas in which alternative species of blowfly occurred frequently in strike cases. The levels

of alternative species were associated with hill or moor pasture types, and with the upland breeds of sheep found in such areas, but some upland areas, for example South Wales, showed much lower levels of alternative species. It was therefore suggested that vegetation types were important determining factors for the incidence of alternative species, and the strongest associations were shown to be with bracken and heather (MacLeod, 1943b).

It is probable that the factors used for the data analysis in the present study have a high level of correlation with one another. For example, sheep grazed at heights of over 200m are predominantly those of hill breeds. Due to the smaller size of this study, it was not possible to show that any one of the factors was independently associated with the incidence of alternative species. Nevertheless, the analysis broadly supports that of MacLeod (1943b), with significantly higher levels of alternative species collected from sites of higher altitude, from those with rough grazing or a moorland environment, and from hill sheep breeds. The presence of bracken was also linked significantly to higher proportions of alternative species collected, and although the association with heather was not significant, this is probably due to the smaller sample sizes involved in this study. The negative association between the proportion of alternatives and the presence of trees is probably due only to the lower abundance of trees at higher altitude.

A much larger study would be required to quantify the importance of each factor in determining the incidence of alternative species in strike cases. However, it seems probable that the high incidence of alternative species in cases from western Scotland can be at least partially explained by the coincidence in this part of the country of the identified predisposing factors. The samples from this area were predominantly collected from hill sheep on sites of rough grazing or moorland at which bracken was found, and a much greater proportion of them were obtained at altitudes in excess of 200m. Any further attempt to infer the relative importance of the factors would be purely speculative. Although the results are consistent with the conclusion of MacLeod (1943b) that the presence of bracken is of prime importance, it is probable that complex interactions exist between the factors, and that two or more of them are of real significance.

This study indicates that the distribution of blowfly species in sheep strike has not changed substantially over the past 50 years, although the incidence of alternative species found was higher than that previously recorded in Scotland. *L. sericata* is the most common species responsible for ovine myiasis in Scotland, but this species is present in strike cases at significantly lower levels than those found in England and Wales. The incidence of *L. sericata* is even lower in western Scotland, and *L. caesar* appears to be of comparable importance in this area, and at higher altitudes. *Protophormia terraenovae* could also be of local importance.

3. Development of traps

3.1. Introduction

3.1.1. The purposes of trapping

The trapping of insects has several purposes, all of which are at least potentially applicable to sheep blowflies. The ability to accurately sample and monitor insect populations is required for studies of their life-cycles and dynamics (for example, Wall *et al.* 1993a). Trapping is also important for the calculation of population data (for example, Vogt *et al.* 1983), which is often essential for the planning and execution of effective pest-control strategies. Furthermore, efficient traps have the potential to themselves play a role in the reduction of insect populations. Traps have proved highly effective for the control of tsetse flies, which are very susceptible to this type of control as they have low population densities (Glasgow 1963), but can also have a significant impact on blowflies, despite their very high densities (Mackerras *et al.* 1936).

Insect traps intended simply to sample or monitor a population may need no form of attractant. An example of a design having no intentional attractive component is the malaise trap, an arrangement of converging screens which mechanically intercept the flight of insects and channel them into a collecting container (for examples see Muirhead-Thomson 1991). Traps of this type have been extensively used against tabanids, but in most cases catch substantially lower numbers of insects than methods using an attractant (Tallamy *et al.* 1976). Other designs, which have been used both against mosquitoes and against blackflies (*Simulium* species) rely on a suction mechanism, and also make no use of attractants (Muirhead-Thomson 1991).

Traps with attractant properties usually make use of either visual and olfactory stimuli, or of a combination of the two. Light traps are primarily of use for nocturnal flies such as mosquitoes, although fluorescent electrocuting traps are also used within buildings against houseflies and blowflies. Coloured traps have proved effective for the capture of a wide variety of insects, including both phytophagous and haematophagous Diptera (see reviews in Muirhead-Thomson 1991), and those which are agents of myiasis (for example, Wall *et al.* 1992c). Traps containing odour

attractants have been used for many types of Diptera, and olfactory stimuli are widely used to attract blowflies and their relatives (Muirhead-Thomson 1991).

Traps which have been used for the capture of blowflies (and for the New World screwworm fly *Cochliomyia hominivorax*, a close relative) can be placed in three main categories according to their method of capturing the insects: enclosed traps (both static and wind-oriented), electrified traps, and adhesive traps. The first type may be subdivided into static enclosed traps, and those which are wind-oriented.

3.1.2. Static enclosed blowfly traps

Most of the early research work on sheep blowflies was carried out using metal traps baited with meat, which captured flies alive in an enclosed space. Typical of those used in Britain were the designs deployed by MacLeod and Donnelly (1956a). One of these consisted of a cylinder of fine wire netting (gauze), approximately 150mm in diameter, held in place at the top by a metal frame, and attached at the base to another frame containing a gauze cone, with a 6mm diameter hole at its apex. The cone rested on four lugs, 6mm above a pan containing the bait. This allowed entry of flies into the apparatus, and many were then trapped in the cylinder when they attempted to leave by passing upwards through the cone. The other trap design was similar, but consisted of a spheroid of fine tinned iron wire, 125mm in diameter, above a cone and small bait pan. Enclosed glass traps were used for the capture of blowflies in Australia (Mackerras *et al.* 1936; Freney 1937), but comparisons with designs based on netting showed the glass traps to be inferior (Cragg and Thurston 1950).

Similar in concept, the screen trap (Bishopp 1916), was designed for the capture of screwworm flies, *Cochliomyia* species, and various modifications of this design remained in widespread use for more than 60 years. It consisted of a vertical cylinder of plastic screen or netting with a vertical funnel attached to the base. Flies are attracted to the apparatus by bait in a container under the trap, move upwards towards the light, and are then captured in the cylinder (Goodenough and Snow 1977).

In Australia, a more complex design, the West Australian Blowfly Trap (WABT), has been widely used. This was originally designed by Newman and Clark (1926), with improvements made by Gilmour *et al.* (1946) and Vogt and Havenstein (1974). Cheaper versions using plastic components were described by Williams (1984) and Dymock and Forgie (1995). The former design, similar to previous versions of the

WABT, had a chamber (approximately 400mm high and 200mm in diameter) in which flies were collected alive. Four windows (150 x 110mm) were made in the sides of the chamber, and covered with fibreglass mesh to admit light while containing the flies. A cone, 8mm in diameter at the base with a 15mm diameter hole at the apex, admitted flies to the upper chamber from a plastic pipe, 140mm long, which hung below. This had 10 holes, each 16mm in diameter, through which the flies entered the apparatus. At the base, a bait pan, about 70mm high, was separated from the pipe by a screen to prevent flies reaching the bait. The entire trap was suspended from a steel stand, which raised the top of the trap about 450mm above the ground (Williams 1984).

Anderson *et al.* (1990) in Australia investigated the use of refuse bins as blowfly traps. Small bins proved ineffective, but three types of large bin were found to be effective: galvanised 55 litre bins, and plastic Otto® bins with a capacity of either 120 litres or 240 litres. The plastic bins had wheels, making them more mobile. Each was baited with an animal carcass, or part, and 0.75 - 1 litre of 20% sodium sulphide solution, and 1 litre of an insecticide, 4% triclorphon, was also added. They were painted yellow to increase their attraction to flies. No counts were made of the flies captured, because it was considered too difficult to separate them from the decomposing carcass and other contents of the bin. However, the researchers reported that the bait bins captured large numbers of *Lucilia cuprina* and other species, and that the incidence of strike in the area appeared to be reduced.

A variety of enclosed fly traps is now produced commercially, and the performance of four such traps was compared by Dadour and Cook (1992) in Australia. Of the designs tested, the Aussie Flybuster® captured the greatest number of calliphorids. In this design, flies entered from the underside through a funnel, passed upwards towards the light, and died, without reaching the bait, in a trap canister. It was baited with a rehydrated liver formulation, but the other designs used in the trial were used with different baits, as supplied by the manufacturer, and it is therefore unclear whether the design or the bait was responsible for the higher catch levels. Furthermore, no comparison was made with standard trap designs such as the WABT.

Enclosed trap designs developed for tsetse flies (*Glossina* species) have been tested against the New World screwworm fly *Cochliomyia hominivorax* (Torr and Hall 1992). It was found that neither the biconical trap, which consists of two cones, joined at their bases and mounted on a central pole, nor the F3 trap, an open-topped hollow cube, performed as well as a wind-oriented trap.

3.1.3. Wind Oriented Traps

A wind-oriented trap (WOT) for the capture of screwworm flies, *Cochliomyia hominivorax*, was developed by Broce *et al.* (1977). This consisted of a white plastic bucket (capacity 1 litre), with the 203mm diameter base removed and replaced with a metal mesh screen. A box to hold the bait bottles was attached to this screen, and a 100mm metal funnel with an opening of 8mm inserted into the wider end of the bucket and attached with a collar. Two metal vanes (100 x 230mm) were mounted on the collar, parallel to the long axis of the trap. Two small hooks were attached to opposite sides of the trap near to the centre of gravity, and the upper one used to suspend the trap. A weight of approximately 1kg was attached to the lower hook to provide stability against the wind. A variation on this design involved mounting the trap on a rod through its centre of gravity, allowing its use in open areas where it was not practical to hang it. A comparison of the performance of the WOT with a screen trap (both baited with a chemical mixture, swormlure-2) found that the WOT caught more *Cochliomyia hominivorax* on every collection date, and performed better than or equal to the screen trap at every trapping site. However, the WOT performed much more poorly against the secondary screwworm fly, *C. macellaria* (Fabricius) (Diptera: Calliphoridae), capturing less than half the number of female flies caught by the screen trap, and an even smaller proportion of males (Broce *et al.* 1977). A similar wind-oriented trap, mounted on a wind wave 1.5m above the ground, has also been developed for catching the Australian bushfly, *Musca vetustissima* Walker (Diptera: Muscidae) (Vogt *et al.* 1985a).

3.1.4. Electrified Traps

Goodenough and Snow (1977) modified an electrified grid trap previously used for the capture of lepidopterans (Mitchell *et al.* 1972) for use with the New World screwworm flies *Cochliomyia hominivorax* and *C. macellaria*. This trap was based around a cylindrical element 46cm high and 30cm in diameter, with a chemical bait (swormlure) suspended inside. It was made portable by use of a 12 volt car battery as a power source, with a transformer supplying about 2000 volts to the element. This apparatus was found to catch 92 times as many female *C. hominivorax* , 56 times as many male *C. hominivorax* , and 11 times as many *C. macellaria* as a screen trap of similar size with the same bait (Goodenough and Snow 1977).

Vale (1974) used wire grids with alternating charged and earthed wires of steel or copper to produce various types of electric traps for tsetse flies (Diptera:

Glossinidae). These designs included electric nets, designed to catch flies in flight. Sheets of fine nylon (90 x 90cm), were suspended vertically in aluminium frames, with an electric grid on either side at a distance of 6mm from the net. Green (1988, 1989) used $1m^2$ electric nets based on the same design, but incorporating cloth screens of various colours and combinations of colours, to investigate the use of colour as an attractant for tsetse flies. Similar electric nets have also been used for capture of the screwworm fly, *Cochliomyia hominivorax,* following its accidental introduction into Libya (Green *et al.* 1993) and for *Wohlfahrtia magnifica* and *Lucilia sericata* in Hungary (Hall *et al.* 1995).

3.1.5. Adhesive traps

Several studies have been carried out using adhesive traps to capture tabanids. Burgess *et al.* (1979), used plaster-board panels (310mm x 310mm) coated with a solution of polybutene in petrol to capture the common cleg, *Haematopota pluvialis* L. (Diptera: Tabanidae) in Wales, catching substantial numbers. Thomson (1986) carried out a comparison between various configurations of Manitoba trap and adhesive panels to catch the same species in the West of Scotland. The traps consisted of two square plywood panels (with sides of 1 metre) attached at right angles to one another on a post at a height of 1.5m. These were coated with a non-setting adhesive (Oppanol B3 and Oppanol B15 with white spirit), and painted grey. The study showed that the panels captured more than three times as many flies as the best Manitoba trap (Thomson 1986; Thomson and Saunders 1986).

An adhesive target was used by Wardhaugh *et al.* (1984) for the sheep blowfly *Lucilia cuprina,* which consisted of a horizontal square of particle board (sides 150mm). This was painted white, coated with Tanglefoot®, a polybutene-based non-setting adhesive, and was used horizontally near ground level. The target was baited with minced sheep liver and sodium sulphide solution (1.5% w/v), contained in a 20ml plastic vial in a central hole, 27mm in diameter. Wall *et al.* (1992c) designed an adhesive target to attract *L. sericata.* This was constructed from squares of aluminium sheet with sides of 410mm, and mounted vertically in the field on a piece of dowelling, forming a diamond with the base about 200mm above the ground. Both sides of the target were coated in Oecotak® A5 (Oecos Ltd., Kimpton, UK), another polybutene-based non-setting adhesive (Ryan and Molyneux 1981), and a 330ml soft drinks can was mounted on top of the flap with wire, half filled with lambs liver covered by sodium sulphide solution (approximately 10% w/v). This bait container was then covered with netting to exclude insects.

3.1.6. Effect of trap size

Wall *et al.* (1992c) compared square vertical targets with sides of three different sizes: 250mm, 410mm, and 610mm, for capture of *Lucilia sericata*. All these traps were covered with white cloth. It was found that increasing target size not only increased significantly the catch, but also increased the number of flies caught per unit area. The larger targets caught more flies than would have been expected from the simple increase in surface area, and were therefore more visually attractive. However, work in Hungary by Hall *et al.* (1995) did not corroborate these results. Using two sizes of vertical electric target of black colouration (1 x 0.5 m and 0.5 x 0.5 m), these workers found that the larger trap caught only 1.8 times the number of *L. sericata* caught by the smaller. There was therefore no increase in the catch per unit area in this case. Green *et al.* (1993) similarly found no effect of catch per unit area when catches of *Cochliomyia hominivorax* were compared using three sizes of black electric targets: 1 x 1m, 1 x 0.5m, and 0.5 x 0.5m.

3.1.7. Effect of trap height

A comparison of catches of *Lucilia sericata* and *L. caesar* at different heights was made by Cragg and Thurston (1950). It had been found that catches on sheep were almost totally composed of *L. sericata*, while those on the ground consisted predominantly of *L. caesar*, and this experiment was intended to indicate whether the preferences of the two species were entirely olfactory, or if they differed additionally in their height preferences. In the case of both species, catches in traps suspended approximately 60cm above the ground were much lower than those at ground level, but the researchers commented that flies could escape more easily from the suspended traps. However, *L. caesar* was found to predominate at both heights, despite the dominance of *L. sericata* on sheep in a neighbouring pen.

Dymock *et al.* (1991), using wind-oriented traps (WOTs) in New Zealand, found that those mounted at 0.65m caught more than seven times as many *L. sericata* and *L. cuprina* than those at 1.5m, and that the number of *Lucilia* as a proportion of the total blowfly catch was also greater at the lower height. In contrast, Vogt *et al.* (1995), using the same trap type in Australia, found that those mounted at 0.5 metres caught significantly fewer *L. cuprina* than those at 1.0, 1.5, or 2.0 metres, and that 1.5 metres was the optimum height.

3.1.8. Effect of other variables on trap catches

Analysis of catches from blowfly traps has shown distinct aggregation of flies throughout the blowfly season (MacLeod and Donnelly 1956a, 1957b, 1962; Wall *et al.* 1992c). However, this pattern of distribution does not appear to be the result of microhabitat selection, as data which demonstrated the presence of aggregation did not show significant differences between catches at different trap positions, showing that the location of the aggregations varied over time. It has been suggested that this is the result of the simultaneous emergence of cohorts of flies from the same case of strike or carrion infestation (Wall *et al.* 1992c). However, the position of traps can have an important effect on the overall catch levels. For example, Wall and Smith (1996) found that significantly higher catches of *Lucilia sericata* were obtained at sites exposed to full sunlight than at sites which were partially shaded by trees or walls.

Blowfly catches have also been found to vary according to the time of day, but it appears that different species have different activity patterns. Research in Australia found that during very hot weather catches of *Calliphora stygia* and *C. augur* (Fabricius) exhibited peaks in morning and evening. In contrast, those of *Lucilia cuprina* and *L. sericata*, which were not captured until later in the day, showed only a single peak (Norris 1966). Even within the genus *Lucilia*, however, there may be variation in behavioural responses to temperature. Nicholson (1934) recorded distinct differences between the reactions of *L. cuprina* and *L. sericata*. A study which related trap catches of *L. cuprina* to weather conditions found that 77.4% of variation in catches could be explained by temperature, wind speed, relative humidity, and solar radiation, and 74.9% by temperature alone (Vogt *et al.* 1983). Similarly, temperature was found to explain 77% of variation in trap catches of *L. sericata* (Wall *et al.* 1992b). Later research showed small but significant variations between the behaviour of male and female *L. cuprina*, including differences between their daily activity cycles. Male flies tended to be less active during the early morning (dawn to 9.00), and more active during the late afternoon (15.00 to dusk) (Vogt *et al.* 1985c).

3.1.9. The use of traps for blowfly population suppression

The first attempt to suppress blowfly populations using traps was by Mackerras *et al.* (1936). In a series of trials using "Meteor" glass traps and West Australian Blowfly Traps, at a density of about 0.1 traps per hectare, it was found that the number of strike cases caused by *Lucilia cuprina* could be reduced by over 50%. However, these experiments were carried out during the spring of a single year, and did not

measure the long-term impact on the blowfly population. Anderson *et al.* (1990) used large refuse bins to trap *L. cuprina* in an arid area of Australia. The bins were placed at a density of between 20 and 25 per hectare, strategically at sites preferred by blowflies. This trapping succeeded in reducing numbers of *L. cuprina* by 96%, and strike incidence by 85% over a period of 5 years (Anderson and Simpson 1991).

In New Zealand, Dymock and Forgie (1995) used modified West Australian blowfly traps to capture *Lucilia sericata, L. cuprina, Calliphora stygia,* and *Chrysomya rufifaces* (Macquart) over three seasons. In the second and third seasons of trapping, total catches were 71% of those in the first year. However, the populations of the four species did not follow the same pattern. That of *L. cuprina* decreased significantly to 5% of its initial level, but that of *L. sericata* increased significantly to 464% of its initial level. The corresponding figures for *C. stygia* and *Ch. rufifacies* were 168% and 53%, but these changes were not significant.

A simulation model of *Lucilia sericata* populations showed that trapping used throughout the blowfly season would have to double the normal daily rate of adult mortality in order to suppress the blowfly population. A strategic kill of second-generation adults was also predicted to have a significant season-long impact on the blowfly population (Wall *et al.* 1993a,b).

3.1.10. Aims and Objectives

The aim of this study was to optimise the design of a trap for the capture of sheep blowflies, particularly for *Lucilia caesar,* as this had been identified as an important agent of myiasis in western Scotland. Although research on adhesive targets for blowflies had previously been published (Wall *et al.* 1992c), this work was carried out in southern England, and only involved *L. sericata.* Furthermore, it did not include a comparison of adhesive traps with those of other designs, and considered the effect of only one trap variable: size. In the present study, the performance of a vertical adhesive target (Wall *et al.* 1992c) was compared with that of three other types of trap: a horizontal adhesive target, a water trap, and a commercially produced trap: Fly City® (Flycatchers Ltd., Banbury, UK). Following this, the effect of altering various parameters of adhesive traps was investigated. This involved comparisons of targets of differing size; height; shape; and angle of orientation.

3.2. Materials and Methods

3.2.1. Design of traps

The four trap types are illustrated in Figures 3.1 and 3.2. The standard horizontal target was constructed from hardboard using a jigsaw, as a square with 410mm sides. When used at ground level, two pieces of wood, square in cross-section (45mmx45mm), were attached to the underside of the board, close to two opposite edges, in order to raise the target above the level of the surrounding grass. Alternatively, the target could be mounted on fence posts using similar pieces of wood placed centrally beneath the target. In this case the distance between them was approximately equal to the width of a fence post (100mm), and they were secured to the post by hammering nails (65mm) through the ends, which protruded about 125mm from the edge of the board. The surface was covered with transparent adhesive plastic (Tenza, Saxmundham, Suffolk, UK), which was peeled off and replaced at the end of each experimental period, and coated in Oecotak® A5 (Oecos Ltd., Kimpton, UK). This compound, a polybutene-based non-setting adhesive (Ryan and Molyneux 1981), was spread thinly over the surface of the target in the field, using a piece of hardboard with a straight edge. The bait container was placed centrally on the board.

The vertical target used was constructed in a similar manner to the design of Wall *et al.* (1992c). This was constructed from squares of metal sheet with sides of 410mm. One corner of the target was bent at 90° to form a triangular flap, 100mm long, into which a piece of dowelling was inserted. The flap also provided a base on which the bait container was placed. The dowelling was used to mount the trap in the field, forming a vertical diamond raised above ground level. The trap used in the present study was modified slightly from the original design, by the use of removable plastic coverings in the same manner as on the horizontal trap. Both sides of the target were coated in the same manner as the horizontal target, with Oecotak® A5 (Wall *et al.* 1992c).

The open water trap was a circular plastic basin, measuring 315mm in internal diameter at the upper edge, 265mm in internal diameter at the base, and 150mm in height. The bait was suspended over the basin using pieces of string, which were attached to the rim of the bait container and to holes drilled in the rim of the basin. It was filled with approximately five litres of water, to which detergent was added

(giving a concentration of approximately 0.1% v/v) to reduce the surface tension and so inhibit the escape of flies. The water was replaced at the start of each period, and a band of Oecotak, 20mm wide, was smeared around the side, immediately above the waterline, in order to catch insects attempting to climb out.

Fly City® is a commercially produced trap designed for general use against nuisance flies in farmyards and gardens. It consists of a transparent polythene bag (265mm in depth) containing bait, suspended below a plastic disc (195mm in diameter). The disc contains a ring of narrow slits (7mm in height), with a diameter of 145mm, through which flies can enter. Odour from the bait is also released through the slits. After passing through the slits, flies can enter the bag through a circular opening, 10mm in diameter, and are then hindered from escaping, both by convex mouldings on the underside of the disc, which cause difficulty in reaching the opening, and by the fact that very little light passes through the disc, in contrast to the sides of the bag. The flies eventually drown in the liquid at the base of the bag.

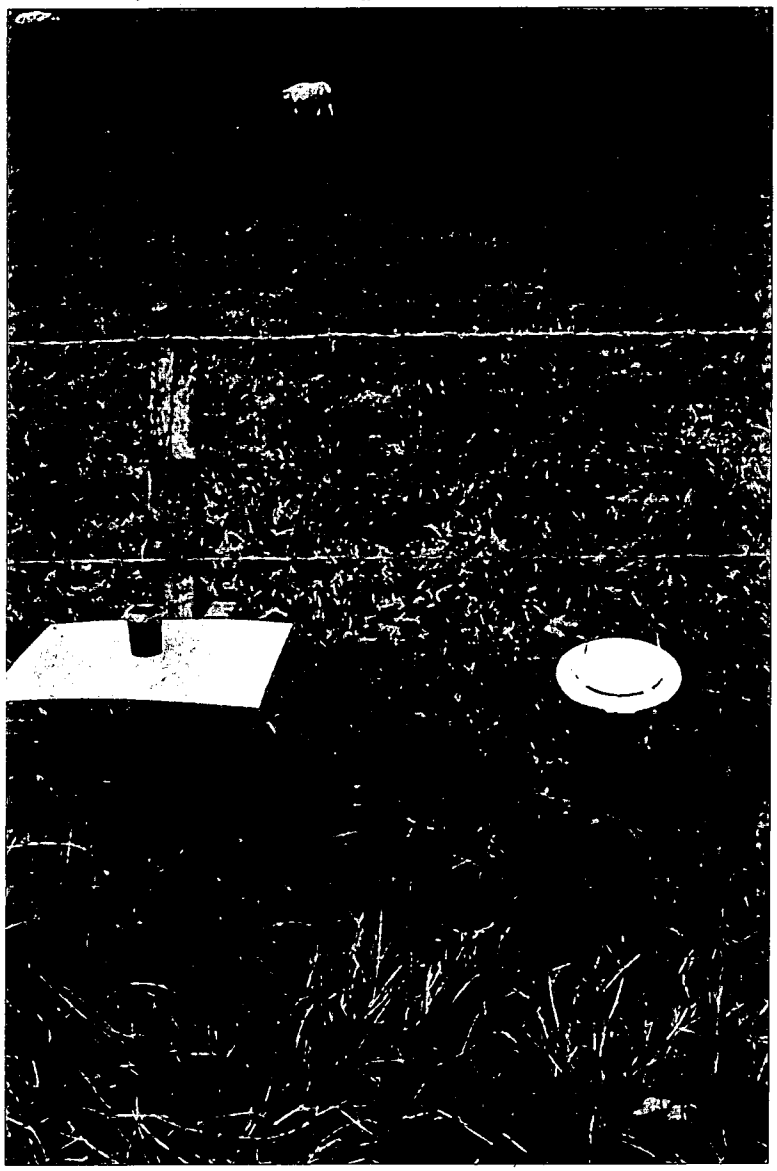

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Figure 3.1: Blowfly traps: Horizontal target and Fly City®.

Figure 3.2: Blowfly traps: Water trap and vertical target.

Each trap used in these experiments was baited with liver and sodium sulphide solution, which are standard blowfly attractants (Mackerras *et al.* 1936; Norris 1966; Wall *et al.* 1992c). Approximately 100g of liver was used for each trap, with a covering of sodium sulphide solution (approximately 10% w/v). Small plastic containers (measuring 60mm in upper diameter, 45mm in lower diameter, and 72mm in height) with a capacity of 120ml were used to hold the bait for both the adhesive targets and the water trap. Fly City® is designed for use with liquid baits, which can be poured into the bag through two circular openings in the centre of the disc. The upper of these is 25mm in diameter, and the lower is the 10mm opening previously referred to. It is intended that the upper opening be closed after baiting, using a sticker supplied with the trap. However, this method was unsuitable for use with liver, so a small vertical incision, about 40mm in height, was made in the bag using scissors. After the bait had been passed through, the incision was then closed with a clip.

All the traps were painted before use with two coats of white gloss paint. Fly City® is designed as an odour-based trap without a visually attractive component, but for uniformity the plastic disc at the top of this trap was also painted white, and a piece of white paper, measuring approximately 35x35mm, was used to cover the upper opening, in place of the coloured sticker provided.

Flies were removed from the adhesive targets using a wooden scraper, and placed in small plastic containers (capacity 120ml) containing White Spirit, a petroleum-derived solvent. This dissolved the adhesive, killed any flies which remained alive, and preserved the dead insects until they were required for identification. Catches from the water trap and Fly City® were also placed in White Spirit, in the latter case after freezing to kill the flies. When it did not prove possible to identify the specimens soon after collection, the containers were placed in a Cold Room at 4°C until identification took place.

3.2.2. Field site

The experimental work was conducted on a grassland site adjoining woodland on Auchincruive College Farm, near Ayr in southwestern Scotland (O.S. NS389234), between June and September in both 1995 and 1996. Figure 3.3 shows similar farmland close to the experimental site. One experiment was also conducted in 1994. Sheep were present at the site throughout, with the exception of a small number of short periods when the animals were removed for treatment with pour-on insecticides or for shearing.

3.2.3. Blowfly species composition on adhesive traps

Only *Lucilia* species were included in the analysis of the experiments involving comparisons of trap performance. However, in order to determine the relative sizes of the populations of the blowfly species, collections were made at the field site during July, August, and September of 1995 of all types of necrophagous calliphorid. The collections were taken from horizontal adhesive traps, painted white and baited with liver and sodium sulphide solution. Blowflies were identified to species following Rognes (1991), as described in sub-section 2.2.1. *Cynomya mortuorum* was identified by the presence of bright yellow-orange colouration on the

whole of the facial plate and parafacial, and the anterior two thirds of the gena (Rognes 1991).

Figure 3.3: Pasture close to the site of field experiments.

3.2.4. Experimental methodology

Five experiments were carried out in 1995, each of which was repeated in 1996. All were based on a Latin-square design, in which each trap was allocated randomly to a different position in each experimental period. In most cases, this resulted in ten period replicates being conducted for each experiment, five in each year. The number of periods used in each experiment was therefore equal to the number of traps. The structure of this design allows the identification of variation due to position and changes in weather conditions, and the random distribution of the traps assists in the minimisation of interactions between them. Latin squares were derived from standard squares such as the one shown below, in which each letter appears once in each column, and once in each row:

A	B	C	D
B	C	D	A
C	D	A	B
D	A	B	C

The square was then randomised by rearranging both the columns and the rows using random numbers. The Latin squares used in each experiment are shown in Appendix 2.

Traps were placed along the edges of fields, at intervals of approximately 20 metres. In each case, the distances between traps were maximised within the environmental limitations of the site, in order to minimise interactions between them. However, the intervals were often constrained by the need to place traps in comparable positions, to reduce variation between them. For example, it was necessary to avoid excessively shady positions, and those which were highly exposed to wind. Each experimental period lasted approximately 24 hours, although some were extended when the weather proved unsuitable for fly activity. This preserved the balanced design of the experiment, by allocating to each period an approximately equal length of time in which blowflies were active.

The first experiment was a comparison between the four different trap designs: the horizontal adhesive target, vertical adhesive target, the water trap, and Fly City®. The water trap remained at ground level, and the other traps were mounted on fences, with their centres at a height of approximately 400mm. A total of eight period replicates of this experiment were conducted, four in each year.

All of the experiments investigating the effect of size, height, and shape were conducted using horizontal adhesive targets at ground level, with pieces of wood attached to the underside to raise them above the grass. Ground level targets were used to facilitate ease of movement from one position to another. In each case the bait container was placed in the centre of the target. The variables considered were size, height, shape, and angle of orientation. In the first three cases, a total of ten period replicates were conducted, and in the fourth case, fifteen.

Five different trap sizes were compared, all of which were square in shape, with sides of 210mm, 310mm, 410mm, 510mm, and 610mm. The areas of these targets were $0.044m^2$, $0.096m^2$, $0.168m^2$, $0.260m^2$, and $0.373m^2$ respectively. The sides of the largest of these targets were the same length as the large version of the vertical trap

used by Wall *et al.* (1992c), although the surface area differed due to the use of both sides of the vertical trap, and because the corner of the vertical traps is bent over, and is therefore not used for the capture of flies. Five different heights were also compared: ground level and heights of 200mm, 400mm, 600mm and 800mm above ground level. To investigate the effect of shape, the standard square horizontal target (with sides of 410mm) was compared with four other rectangular targets of differing elongation, all having the same surface area of 0.168 square metres. The series of targets was designed so that the longest side of each successive elongation was 137mm (one third of the length of the sides of the original square) longer than its predecessor. The additional shapes used were therefore 307x547mm; 246x683mm; 205x820mm; and 176x957mm.

To determine the effect of angle of orientation, five different angles were compared: 0°, 22.5°, 45°, 67.5°, and 90°, with reference to the horizontal. The angled targets were attached to the fence at the upper edge with string, and at the lower edge were raised up with pieces of wood cut at the correct angle. They were mounted so that the midpoint of each was at the same height (300mm) above ground level. The bait containers were attached to the fence with string to ensure that they remained in place at the centre of the target, with the exception of the horizontal target, on which the bait container was placed centrally as in the previous experiments. This experiment was carried out in 1994, as well as in 1995 and 1996, giving a total of fifteen period replicates.

3.2.5. Analysis of trap data

Counts from all five experiments were analysed by ANOVA using the computer statistical package GENSTAT 5 (Release 3.2 for Windows). Normalisation by log(n+1) transformation was carried out prior to analysis, as insect catch data is often highly skewed (Williams 1951). Comparisons between trap means have been made in various ways by different researchers. It is common practice to calculate a least significant difference between means (for example, Green 1993; Mhindurwa 1994) or confidence limits (for example, Wall *et al.* 1992c), but this is considered by statistical authorities to be a procedure of dubious validity. If such tests are used to compare two means using P=0.05 (95% confidence), there is a 5% probability of a false positive result. However, if three means are compared, three comparisons must be made, each with the same 5% probability of a false positive result. It can be shown that in this case the overall probability of a false positive result is about 13%, and when six means are compared, the corresponding figure is 40%. Clearly such

figures are unacceptably high, as they far exceed the intended level of *P*. Although these levels of error are reduced by the practice of applying such tests only when the ANOVA produces a significant value of F, the use of the least significant difference test remains unsatisfactory for making multiple comparisons (Steel and Torrie 1960).

An alternative to the least significant difference test is Duncan's new multiple-range test (Steel and Torrie 1960), which takes into account the number of means in an experiment. Instead of using a single least significant difference to compare every pair of means, this test uses least significant ranges, with a different range being used for means of differing proximity to each other. The least significant range, *R*, is calculated by the following procedure:

$$R = S\sqrt{E/r}$$

where S= Significant Studentised Range (from tables)
E= Residual mean square (from ANOVA)
and *r*= number of replicates of each treatment

The significant studentised range depends on the proximity of the two means being compared; the means having been arranged in ascending order. The range is smaller for two adjacent means than for two which are separated by one or more intermediate means. The result of this process is that the probability of the difference between two means falsely appearing significant is greatly reduced (Steel and Torrie 1960). This test has been used previously for the analysis of fly trap data (for example Randolph *et al.* 1991), and was chosen for use in comparing the trap means in all the experiments in the present study.

3.3. Results

3.3.1. Identification of blowflies

The surface of a horizontal adhesive trap is shown in Figure 3.4, illustrating the mode of capture of insects on the non-setting adhesive.

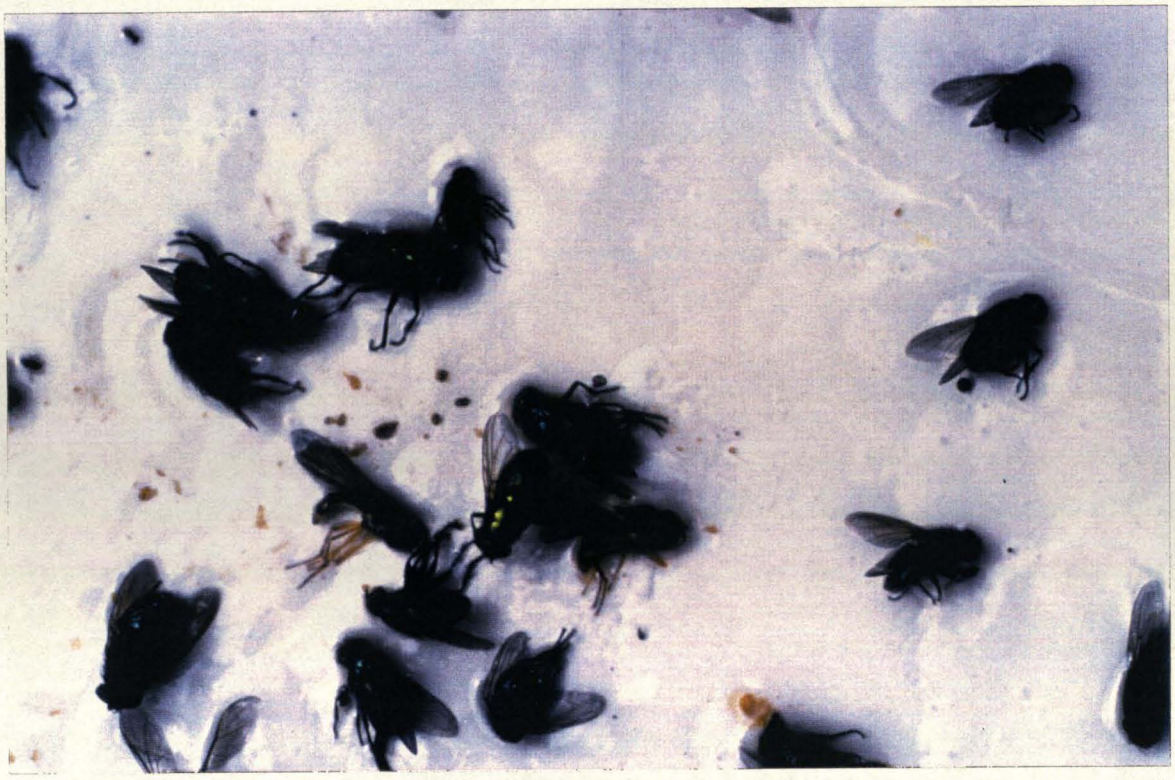


Figure 3.4: Surface of a horizontal adhesive trap showing captured calliphorids, muscids, and syrphids.

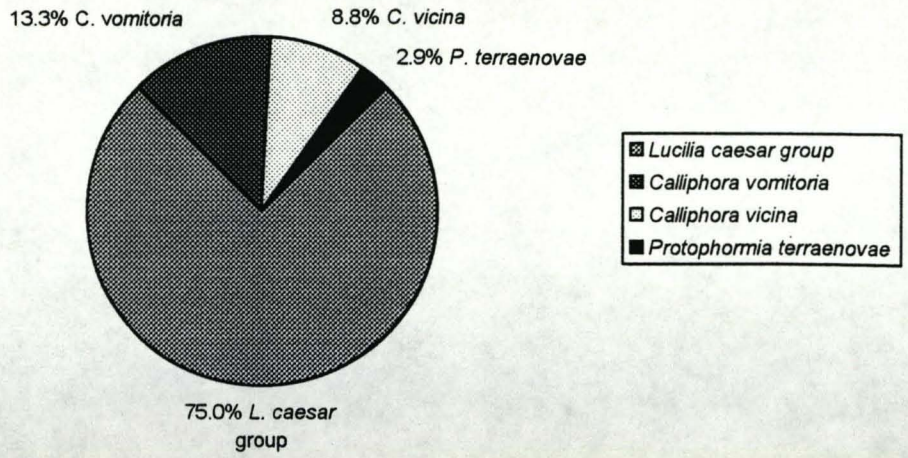
Males of the closely related species *L. caesar* and *L. illustris* (members of the '*L. caesar* group') can be readily distinguished by examination of the genitalia, and the identifications of those collected during July and August 1995 are detailed in Table 3.1. However, females of these two species are very similar, and identification to species level was carried out only on random samples of female flies of this group. From those trapped in 1995, 240 specimens of good quality were selected at random, half collected during July, and half collected during August. The precise identification of these flies is also shown in Table 3.1. The third member of the *L. caesar* group, *L. ampullacea*, was not found among any of the samples precisely identified.

Sex	Month	*Lucilia caesar*	*Lucilia illustris*	*L. illustris* as percentage of total
Male	July	192	30	13.5%
Male	August	235	23	8.9%
Female	July	110	10	8.3%
Female	August	112	8	6.7%

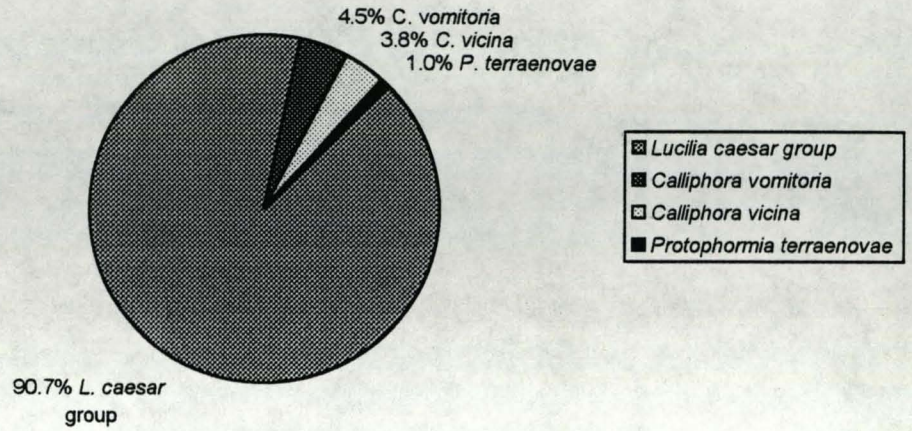
Table 3.1: Identifications of *Lucilia caesar* and *L. illustris* collected during July and August 1995. The data include all males trapped during this period, and a random selection of 120 females from each month.

The composition of the trap catches on horizontal adhesive traps during 1994 and 1995 are detailed in Appendix 2, and shown as pie graphs in Figures 3.5 (females) and 3.6 (males). *Lucilia caesar, L. illustris, Calliphora vicina, C. vomitoria,* and *Protophormia terraenovae* accounted for almost all the necrophagous calliphorids captured. However, very small numbers of *Lucilia sericata* (one female in July and four females in August) and *Cynomya mortuorum* (one female and one male in July) were also collected, and are included as "other" in the figures. The catches are divided into those collected during the months of July (n(females)=3200; n(males)=576), August (n(females)=3898; n(males)=424), and September (n(females)=159; n(males)=17).

(a) July



(b) August



(c) September

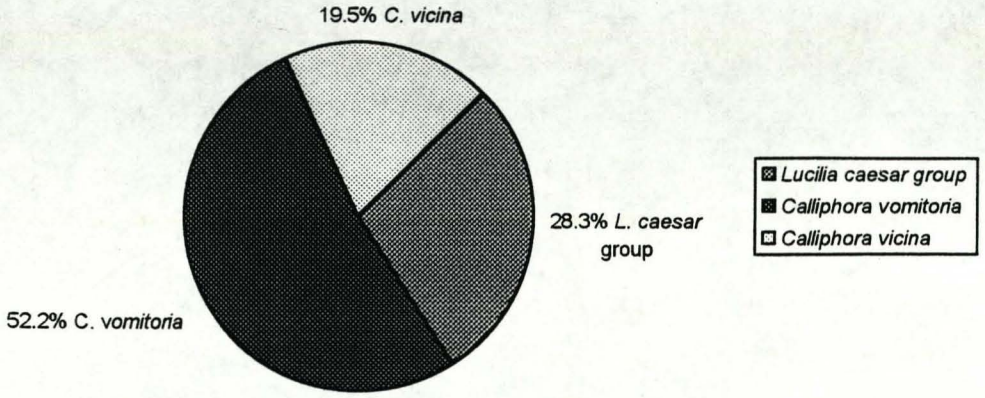
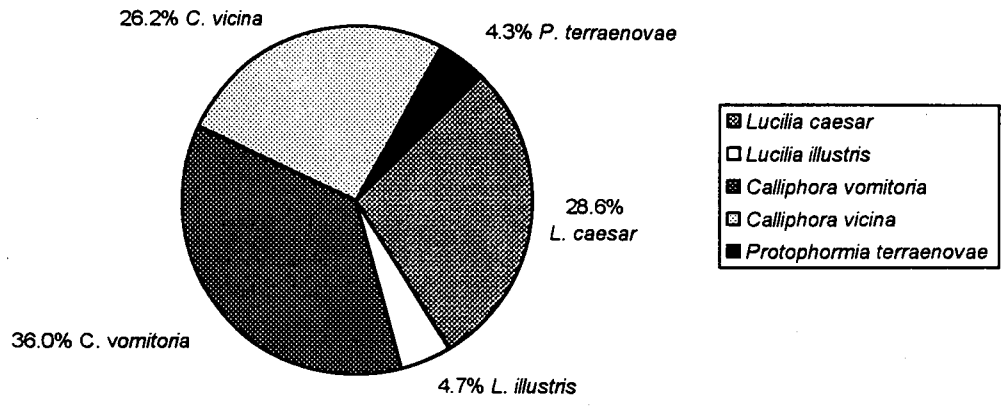
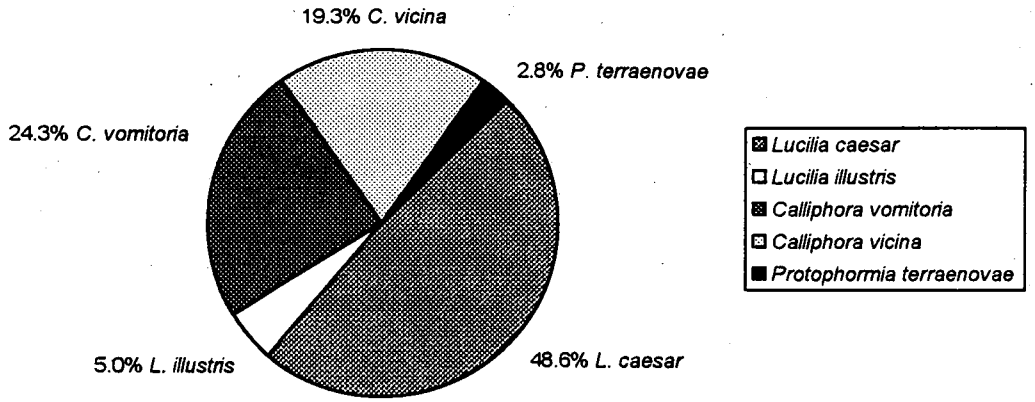


Figure 3.5: Female necrophagous calliphorids captured on adhesive traps during 1995, expressed as a percentage of the total catch.

(a) July



(b) August



(c) September

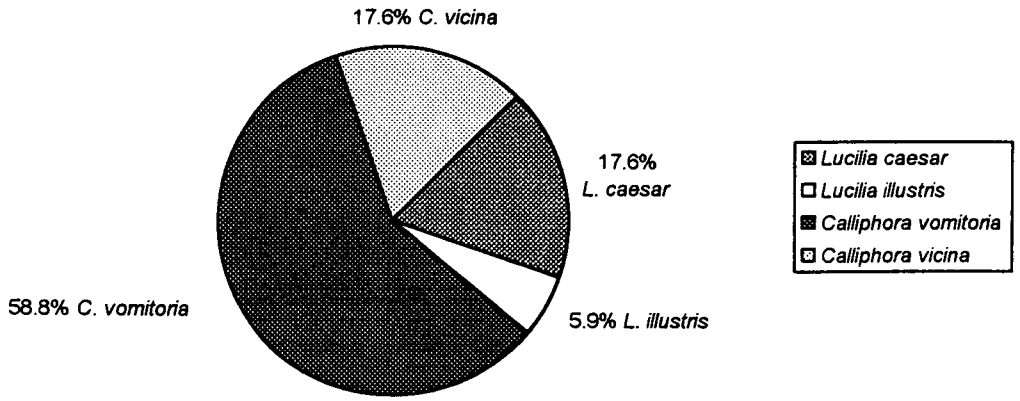


Figure 3.6: Male necrophagous calliphorids captured on adhesive traps during 1995, expressed as a percentage of the total catch.

3.3.2. Comparison of trap types

As described above, females of *L. caesar* and *L. illustris* were generally not separated, and analysis of experimental results for female flies therefore includes both these species. Counts of male *L. caesar* were analysed separately. Catches of *L. sericata* and of male *L. illustris* were too low to allow analysis.

Analysis of data from the first experiment (Table 3.2) demonstrated significant differences in trap performance for both *Lucilia caesar* group females ($F=18.8$, residual df=15, $P<0.001$) and *L. caesar* males ($F=8.97$, residual df=15, $P=0.001$). The horizontal target performed significantly better than the vertical target for both sexes of fly ($P<0.05$), while both of these adhesive targets caught higher numbers than the water trap and Fly City. For female flies, Fly City performed significantly better than the water trap ($P>0.05$), but for male flies there was no significant difference. The catch data for this experiment are contained in Appendix 2.

Trap	Females			Males		
	detransformed	transformed		detransformed	transformed	
Water trap	0.6	0.200	a	0.2	0.075	ab
Fly City®	4.9	0.774	b	0.1	0.038	a
Vertical adhesive	17.7	1.273	b	0.8	0.248	b
Horizontal adhesive	60.8	1.791	c	1.9	0.464	c

Table 3.2: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) on four different trap designs (eight replicates). Standard Errors of Difference (for transformed data) = 0.226 (females) and 0.092 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

3.3.3. Effect of trap variables

The catch data for all four experiments involving the manipulation of variables on adhesive traps are contained in Appendix 2. Counts and analysis for female

blowflies are for flies of the *Lucilia caesar* group (and therefore include *L. illustris*), while those for male flies include *L. caesar* only.

The comparison of adhesive targets of different sizes demonstrated a significant effect of size both on the catch of *Lucilia caesar* group females ($F=8.1$, residual df=28, $P<0.001$), and on that of *L. caesar* males ($F=6.49$, residual df=28, $P<0.001$). The mean catch increased with every increase in target size (Table 3.3), and the largest catch was observed on the largest target, which showed a significantly larger catch than the three smallest targets ($P<0.05$). In contrast, as shown in Table 3.4, the equivalent mean catch per unit area did not differ significantly between targets of different size, either for females ($F=0.43$, residual df=28, $P=0.784$) or males ($F=0.71$, residual df=28, $P=0.595$), although in both cases the smallest catches per square metre were obtained on the smallest target.

Target size (m)	Females			Males		
	detransformed	transformed		detransformed	transformed	
0.21x0.21	7.0	0.901	a	1.0	0.306	a
0.31x0.31	17.4	1.264	ab	2.5	0.545	ab
0.41x0.41	24.6	1.409	b	4.2	0.719	b
0.51x0.51	27.1	1.449	bc	4.4	0.731	b
0.61x0.61	57.6	1.768	c	10.9	1.076	c

Table 3.3: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets of five different sizes (10 replicates). Standard Errors of Difference (for transformed data) = 0.157 (females) and 0.157 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

Target size (m)	Females		Males	
	detransformed	transformed	detransformed	transformed
0.21x0.21	110.9	2.049 a	9.2	1.012 a
0.31x0.31	174.4	2.244 a	19.9	1.321 a
0.41x0.41	143.5	2.160 a	17.1	1.258 a
0.51x0.51	103.7	2.020 a	16.5	1.243 a
0.61x0.61	154.6	2.192 a	28.9	1.476 a

Table 3.4: Mean catches per square metre of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets of five different sizes (10 replicates). Standard Errors of Difference (for transformed data) = 0.205 (females) and 0.282 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

The height of targets had a significant effect on the catch of both females ($F=6.28$, residual df=28, $P<0.001$) and males ($F=4.44$, residual df=28, $P=0.007$). The highest numbers of flies of both sexes were captured on the trap at 0.2m (Table 3.5) with the catches decreasing as target height increased, and significantly lower numbers were found on the targets at ground level ($P<0.05$), and on those at 0.6m and 0.8m ($P<0.01$). The comparison of increasingly elongate rectangular targets (Table 3.6) also showed a significant target effect on catches of females ($F=2.80$, residual df=28, $P=0.045$). The most elongate target performed significantly less well than several of the other shapes ($P<0.05$). Although the value of F for males did not demonstrate significance ($F=1.94$, residual df=28, $P=0.132$), the Duncan's test indicated a significant difference between the two most elongate shapes. Angle of orientation had a significant effect on the catch of females ($F=3.29$, residual df=44, $P=0.019$) and of that of males ($F=2.39$, residual df=40, $P=0.027$). As shown in Table 3.7, the highest mean catch was obtained, for both sexes, at 45°, and the lowest at 90° (vertical), which was significantly lower than that at 45° and that at 0° (horizontal) ($p<0.05$).

Target height (m)	Females			Males		
	detransformed	transformed		detransformed	transformed	
0.0	24.0	1.399	a	2.6	0.557	a
0.2	71.5	1.860	b	8.9	0.997	b
0.4	42.2	1.635	b	4.9	0.774	ab
0.6	16.7	1.249	a	2.6	0.562	a
0.8	9.6	1.037	a	2.1	0.492	a

Table 3.5: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets at five different heights (10 replicates). Standard Errors of Difference (for transformed data) = 0.182 (females) and 0.138 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

Length of longest side (m)	Females			Males		
	detransformed	transformed		detransformed	transformed	
0.410	46.8	1.679	ab	4.0	0.697	ab
0.547	54.3	1.743	ab	4.5	0.741	ab
0.683	80.2	1.910	b	5.5	0.813	ab
0.820	81.3	1.916	b	6.4	0.867	b
0.957	32.3	1.522	a	2.4	0.533	a

Table 3.6: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets of the same area but differing elongation (10 replicates). Standard Errors of Difference (for transformed data) = 0.140 (females) and 0.130 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

Target angle to the horizontal	Females			Males		
	detransformed	transformed		detransformed	transformed	
0°	16.8	1.251	b	3.2	0.619	b
22.5°	13.4	1.157	ab	2.2	0.506	ab
45°	22.3	1.367	b	3.7	0.669	b
67.5°	15.9	1.229	b	2.6	0.559	ab
90°	6.7	0.887	a	1.1	0.328	a

Table 3.7: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) at five different angles of orientation (15 replicates). Standard Errors of Difference (for transformed data) 0.140 (females) and 0.120 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

It should be noted that it was not possible to compare the absolute catch figures from any one of the five experiments with those from any other, because none of the experiments was carried out over exactly the same time period, and several different locations were used within the trapping area. The resulting differences in the levels of fly abundance are reflected in the experimental data. For example, the first traps in both the third and fourth experiments (see Tables 3.3 and 3.4) were identical standard horizontal traps with 410mm sides, placed at ground level, but the mean catches differ substantially.

3.4. Discussion

3.4.1. Comparison of trap types

The horizontal adhesive target is the most effective of those tested for the capture of *Lucilia caesar* group females. The differences in the performance of traps is related both to the level of attraction, and the ability to capture flies once they arrive at the trap. The two adhesive targets and the open water trap all had exposed baits in identical containers, and so presumably had very similar levels of odour attraction, although the results of the later experiment on trap height suggest that the water trap may have suffered from being at ground level. Fly City® probably has a lower level of odour attraction, as the bait is not directly exposed to the air, and volatiles have to pass through relatively small gaps in the plastic disc. It also presents a much poorer visual stimulus than the other designs used in this study.

The difference in performance between the two adhesive targets may be explained either by a preference for the blowflies to land on horizontal surfaces, or by greater contact between fly and adhesive on horizontal surfaces. The water trap proved to be very poor at catching blowflies. This was may have been due either to small numbers of flies landing on the water, to their success in escaping once they touched the water, or to both of these factors. The band of adhesive above the waterline proved effective in capturing those flies which reached it, but many apparently were able to fly away from the water before becoming immersed in it, despite the presence of detergent. It is possible that the detergent concentration was not high enough to sufficiently reduce the surface tension of the water. Fly City® efficiently contained flies once they entered the bag, but the necessity for the flies to pass through narrow slits was probably a factor in reducing the catches by this trap.

3.4.2. Effect of trap variables

It is to be expected that an increase in target size will lead to increased catches of flies, and this has already been shown to be the case with regard to *Lucilia sericata* (Wall *et al.* 1992c, Hall *et al.* 1995). However, of greater interest is whether a larger target will capture more flies per unit area, demonstrating greater powers of visual attraction. Previous research has been divided on this. Wall *et al.* (1992c), using vertical adhesive targets, found that a larger surface area did result in higher

numbers of *L. sericata* per unit area, but Green *et al.* (1993), studying the New World screwworm fly *Cochliomyia hominivorax*, and Hall *et al.* (1995), using electric grid traps to catch *L. sericata*, found that it did not. The results of the present study, using horizontal adhesive targets, tend to support the latter conclusion. There was a large increase in catch per unit area between the smallest and second-smallest targets, but the difference was not statistically significant, and the remaining targets had smaller catches per square metre.

Little research has previously been undertaken on the optimum height for the capture of *Lucilia* species. Cragg and Thurston (1950) found that numbers of both *Lucilia caesar* and *L. sericata* were much lower at a height of about 600mm than at ground level, although these researchers called into question their own results by reporting that flies could escape more easily from the suspended traps. Dymock *et al.* (1991), using wind-oriented traps in New Zealand, found that those mounted at 0.65m caught more than seven times as many *L. sericata* and *L. cuprina* than those at 1.5m, and that the number of *Lucilia* as a proportion of the total blowfly catch was also greater at the lower height. In contrast, Vogt *et al.* (1995), in a study of the capture of *L. cuprina* using the same type of trap in Australia, found that those at 0.5 metres caught significantly fewer flies than those at 1.0, 1.5, or 2.0 metres, and that 1.5 metres was the optimum height. The results of the present study show that 200mm was the optimum height for catches of *L. caesar*, with significantly lower figures for traps at 600mm and 800mm. It may be that the optimum height of a trap varies depending on weather conditions, which could therefore also affect the performance of one trap design compared with another. For example, a particular pattern of wind conditions could favour the distribution of bait odour from a particular trap design.

No research has been published relating to the responses of calliphorids to traps of differing shape, but experiments involving the use of three-dimensional traps to capture members of other dipteran orders have demonstrated the importance of trap shape. Responses have shown considerable variation between related species and also between different conditions of trap use. Tsetse flies of the *Glossina palpalis* group are most attracted to vertically oriented traps such as the biconical trap, whereas those of the *G. morsitans* group prefer compact or horizontally oriented shapes (see review by Jordan 1995). Trap shape is also important for the capture of phytophagous flies, but their responses have been shown to vary in their response to trap shape depending on the visual context. For example, female onion flies, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae), demonstrated a higher level of attraction to spherical traps than to cylindrical ones when tested either against a background

of onions, or in a situation of high trap density (4 per metre) on bare soil, but showed no significant preference when the trap density on bare soil was reduced to 0.1 traps per metre (Judd and Borden 1991). The results of the present study suggest that highly elongate targets catch lower numbers of *Lucilia caesar* group flies than square targets, but that moderate elongation may be of some benefit in increasing catch sizes.

Although work with phytophagous insects has demonstrated that catches on adhesive traps at different angles of orientation may vary greatly (for example, Collier and Finch 1990), no previous research has been published on this subject with regard to blowflies. The largest catches in the present study were achieved using a target angled at 45°. This may be explained by the fact that this angle provides a greater visual stimulus than a horizontal surface to flies at a range of heights, while in comparison to a vertical surface the flies are more likely to land on the adhesive target, and therefore become attached to it. However, the catches on horizontal targets were not significantly lower than those on any of the angled ones.

3.4.3. Conclusion

When selecting a trap design, some consideration must be given to the ease of construction and use, as well as the performance against the target species. A variety of commercially-produced fly traps are now available, most of which capture flies inside an enclosed space, and can be deployed very easily and quickly. The only previous study of blowfly catches using such traps (Dadour and Cook 1992), showed considerable variation in effectiveness. However, different baits were used with each trap, and it was therefore impossible to determine whether differences in catches were due to the trap design, or to the bait. Furthermore, no trap previously used in scientific studies was included for comparison. The commercially-produced trap used in the present study, Fly City®, did not perform well when compared to the adhesive targets, and appears to have little potential for blowfly control, although its ease of use in contrast to adhesive designs should be noted.

All of the hardboard-based designs used in the present study can be constructed more quickly and cheaply than the metal traps used by Wall *et al.* (1992c). Although they are less durable in the long-term, many of those used in the present study survived three field seasons. The disposable plastic coverings add considerable expense, but they reduce the time taken to service the targets, by removing the need for cleaning with solvents. If adhesive targets are ever to be used on farms as a

method of blowfly control, such conveniences will be necessary to avoid the servicing operation becoming too labour-intensive. Much more time could be saved if coverings were used which were pre-coated with adhesive. It might be possible to develop an ultimately disposable target with multiple layers of non-setting adhesive separated by coverings which could be removed at regular intervals, perhaps weekly. Alternatively, a heavy base could be used, to which adhesive surfaces, constructed of plastics or cardboard, could be attached as required.

The largest catches of *Lucilia caesar* group flies were obtained on targets mounted at 200mm above ground level and on those angled at 45°. However, angled targets proved less straightforward to deploy and service than horizontal ones. They are also less robust, and did not capture significantly higher numbers of flies than horizontal targets. Although the largest targets were shown to catch more flies, there was no improvement in the catch per unit area, and very large targets are unwieldy to operate. For a monitoring or control programme utilising traps of this type, there does not appear to be any significant benefit from the use of targets with sides larger than 410mm.

The experiments were carried out in an area of low abundance of *L. sericata*, and it was not therefore possible to assess the performance of the traps against this species. There is some evidence that different species of *Lucilia* may differ in their responses to odour (Cragg 1956; Cragg and Cole 1956), and it is possible that they may also differ in their responses to other trap variables. It cannot therefore be assumed that a trap design optimised for *L. caesar* will be the most effective against other blowfly species. However, unpublished work conducted at the University of Bristol has found that catches of *L. sericata* are also greater on horizontal targets than on vertical ones, and that the optimum height in this case is also approximately 200mm (Dr. R. Wall, personal communication). Further research into the similarities and differences of the responses of the two species could prove worthwhile.

4. Visual Physiology

4.1. Introduction

4.1.1. The physiological basis of dipteran vision

Dipteran eyes are complex structures, each containing several thousand units known as ommatidia, which in turn each contain eight photoreceptors or retinula cells. Within each retinula cell, visual pigments are contained in a photoreceptive membrane which is composed of microvilli, arranged into a long organelle known as a rhabdomere. The tips of the rhabdomeres lie in the focal plane of the lens in a precise trapezoidal pattern, which allows a consistent numbering system to be used for the eight retinula cells within each ommatidium (R1-8). Retinula cell R8 is positioned below R7, and its rhabdomere is contiguous with that of R7. Light is therefore filtered by R7 before reaching R8 (Hardie 1986).

The arrangement of rhabdomeres in Diptera is unlike that of most other arthropods, which have fused rhabdomeres. The visual axes of the rhabdomeres in each ommatidium diverge by exactly the same amount, with the result that the axis of each rhabdomere coincides with those of six other rhabdomeres in neighbouring ommatidia. The axons of each of these sets of seven rhabdomeres converge, allowing the summation of their signals. This process, known as the neural superposition principle, substantially enhances the intensity of the retinal image, because light from each spatial point is collected through six different facets (Hardie 1986).

Unlike visual systems in other animals, the R1-6 cells of dipteran eyes use the chromophore 3-hydroxy retinal. The visual pigment is called xanthopsin, and like other invertebrate visual pigments it is not bleached on illumination. Instead, xanthopsin is converted into a thermostable metaxanthopsin, and the process is reversible by the absorption of further light energy. The absorbance maximum of xanthopsin in Diptera has been found to be at about 490nm, while that of metaxanthopsin is at about 570nm. Only light absorption by xanthopsin results in a response of the cell, and this response is approximately proportional to the concentration of the pigment in the cell. The screening pigments in the eye is transparent to long wavelengths, and metaxanthopsin is therefore automatically

converted back to xanthopsin by ambient light diffusing through the cell. There is therefore always a high concentration of xanthopsin available in the cells (Hardie 1986). A second chromophore is also present in these cells (Horridge and Mimura 1975). This compound, 3-hydroxy retinol, is photostable, and absorbs in the UV range, with an absorbance maximum at about 350nm, and transfers the absorbed energy to the xanthopsin molecule (Hardie 1986).

Two main classes of R7 cells exist in blowfly eyes: those which fluoresce green (R7y) and those which do not fluoresce (R7p). R8 cells are classified with the same postscripts as the R7 cells above them (Kirschfeld *et al.* 1977, 1978). R7y and R7p cells are distributed randomly over the retinas of flies of both sexes; the former type being found in 70% of all ommatidia (Hardie *et al.* 1981). R7p and R8p photoreceptors have simple spectra, with a UV absorbance maximum (335nm) and a blue absorbance maximum (460nm), respectively. In contrast, the absorbance spectra of R7y and R8y photoreceptors (peaks at 355nm and 530nm, respectively) suggest complex pigment interactions (Hardie *et al.* 1979). Marginal photoreceptors, R7marg and R8marg, are a third category, which occurs only in specialised eye regions such as the dorsal margin of the eye. These rhabdomeres are greatly enlarged in diameter, but shorter in length, and are specialised for polarised light detection (Hardie 1986).

4.1.2. Physiological responses of blowflies to colour stimuli

Spectral sensitivity is calculated using measurements of the voltage change in response to light stimuli of various wavelengths. This can either be measured in intact eyes or in individual optical cells. In the former case, the resulting signal is known as an electroretinogram (ERG). These are measured by placing an active electrode on or beneath the cornea. Because the signals from a large number of highly aligned photoreceptors may be recorded simultaneously by a single electrode, quite large current voltages can be generated. The maximum response measured by insect ERGs can be in excess of 10mV, in contrast to measurements of only a few 100μV in vertebrate ERGs (Devoe 1985). Measurements in cells from *Lucilia* eyes were found to be composed of two components: a transient spike-like potential, and a lower one maintained throughout illumination (Naka 1961).

Spectral sensitivity curves calculated for individual R1-6 cells from the eye of the blowfly *Calliphora stygia* show a peak at about 350nm followed by a trough at about 400nm, where the response obtained was about 20% of the maximum. A second peak, about 80% of the height of the first, is present at about 500nm, and sensitivity

then declines rapidly, showing less than 15% of the maximum response at 560nm (Horridge and Mimura 1975).

When an intact eye of *Calliphora vicina* (or of other red-eyed Diptera) was used in place of individual cells, a third peak appeared on the spectral sensitivity curves, in the red at about 620nm. However, it has been shown that this is not due to the presence of a red receptor, but is caused by the presence of screening pigments known as ommochrome. These pigments are transparent in the red, and so admit more light to the receptor cells at red wavelengths, resulting in an increased response. When the *chalky* mutant of *C. vicina*, which has white eyes containing no ommochrome, was used in place of the wild-type, the additional red peak was not present, and the sensitivity curve closely resembled that obtained from individual R1-6 cells (Goldsmith 1965; Paul *et al.* 1986).

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4.1.3. Behavioural responses of blowflies to colours in the laboratory

A laboratory study using cellophane-covered light traps identified yellow light, as the most attractive for *Lucilia cuprina*, followed by blue and pink (Lee 1937b). However, little further research on colour discrimination in blowflies was carried out until that of Fukushi (1985), which demonstrated that walking *Lucilia cuprina* with clipped wings could be trained to visit light spots of either blue (460nm wavelength) or green (520nm wavelength) in response to a sugar stimulus, and that the discrimination between the colours is based on wavelength rather than intensity. Additional research showed that untrained flies had a preference for yellow pieces of coloured paper over blue and red, with green being the least preferred colour (Fukushi 1989). However, a subsequent study found the preference to be for red followed by yellow and blue, and then by green (Fukushi 1994). Flies trained to any particular colour were found to show a preference for this colour thereafter. Yellow and blue were most easily learned and best discriminated, followed by white. Green was discriminated from blue, but only weakly from yellow and orange, while red performed no better than black. The colours appeared to be discriminated mainly by hue, although brightness was also of some importance (Fukushi 1989).

A further study using the same methodology confirmed the importance of hue by the use of grey shades of similar brightness to each colour. In the case of blue, green, and yellow, the blowflies were able to distinguish the colour from the corresponding grey. Only red was confused with a grey shade. Furthermore, flies trained to a grey shade could not distinguish it from another grey shade, despite the difference in

brightness being greater than that between the blue and yellow colours. It was therefore concluded that brightness perception plays a subsidiary role to hue in blowfly visual systems (Fukushi 1990).

Using an automatic training test apparatus, Troje (1993) suggested that *Lucilia* has three spectral categories: UV (up to 400nm); blue (400-515nm); and yellow (over 515nm). The flies could not discriminate between wavelengths within a category, but could precisely discriminate between wavelengths in different categories. Fukushi (1994) identified an additional category, finding responses to blue in the range 429-491nm; to green in the range 502-511nm; and to yellow in the range 522-582nm. The maximal generalisation for blue was found at 429nm and that for yellow at 543nm. When flies were trained to a mixture of light from different categories, they did not respond to blue, green, or yellow, suggesting that the mixtures were perceived as a neutral or achromatic light, possibly due to cancellation of the response to one colour by that to another (Fukushi 1994). Analysis of these results suggests that R7y/R8y and R7p/R8p are the main photoreceptors involved in colour vision, although R1-6 may also have some role (Troje 1993; Fukushi 1994).

Adhesive targets bearing black bands alternating with coloured ones were used in a laboratory experiment to examine the responses of *Lucilia sericata* (Wall and Smith 1996). One side of the targets was placed in a brightly illuminated position while the other side was relatively shaded. The illuminated surfaces showed significantly higher catches on yellow and pale blue bands, followed by black, green, dark blue and red. On the shaded surfaces, however, there was no significant difference between the catches on different colours. There was no difference in the distribution of sexes between the different colours. Although the reason for the differences in catch between the two sides of the targets could not be ascertained from this study, the authors suggested that it could be due to the intensity of the reflected light, changes in the spectral reflectivity of the materials due to differences in the incident illumination, or simply that the size of the catches (which was much lower than on the illuminated sides) was too small to enable any colour discrimination to be detected (Wall and Smith 1996).

4.1.4. The use of colour as an attractant in insect traps in the field

Adhesive traps have been widely used to catch small winged insects, predominantly plant pests, and colour is often used to attract specific species (Muirhead-Thomson 1991). Yellow adhesive cards were found to attract the largest numbers of the greenhouse whitefly, *Tialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae), and these can form the basis of a successful control strategy (Webb *et al.* 1985). Yellow has also been found to be the most attractive colour for the carrot fly, *Psila rosae* (Fabricius) (Diptera: Psilidae) (Collier and Finch 1990), and the cabbage root fly, *Delia radicum* L. (Diptera: Anthomyiidae) (Kostál 1991; Finch 1992).

Bracken *et al.* (1962) found that five species of *Hybomitra* (Tabanidae) responded to red and black, with green and yellow being totally unattractive. Similar results were obtained in a study of eight species of *Chrysops* and eight of *Hybomitra* , which were most attracted to red and blue, followed by black and white, with yellow and green being the least attractive (Browne and Bennett 1980). Burgess *et al.* (1979) found red and grey to be the most attractive colours for *Haematopota pluvialis,* followed by blue, black, white and green, with yellow being the least attractive colour, although this study took no account of site or interference effects. Thomson (1986), using the same paired panels as in his earlier study, investigated the colour responses of *Haematopota pluvialis,* by painting the traps in various colours. Red, blue, white and grey were shown to be the most attractive colours, with black being less attractive, and yellow and green very unattractive.

The use of colour to enhance catches of the tsetse fly *Glossina pallidipes* was investigated by Green and Flint (1986). These workers compared trap coverings of 53 different colours, and found that colour was an important determinant of catch size. Materials which selectively reflected light in the blue-green and red bands tended to be attractive, and those which reflected in the green-yellow-orange and ultraviolet bands unattractive. Bright royal blue was shown to be the most attractive trap material. However, investigation of the trap responses of *Glossina palpalis palpalis* revealed that flies reaching an attractive coloured target did not necessarily land on the trap surface, whereas traps of some other colours (reflecting, for example, in the ultraviolet) induced landing responses despite being relatively unattractive (Green 1988). It was attempted to increase catches by adding panels of electrified netting on each side of the coloured target, in order to trap flies even when the did not land on the target, but a better solution was found to be the use of two-coloured screens. The best catches of female flies were obtained using a cloth target which was half pthalogen blue and half ultraviolet-reflecting white. This

arrangement, in which the blue component draws flies to a position near the target, and the white component induces landing responses, caught 2.4 times as many female flies as an all-blue screen, and 3.6 times as many flies as an all-white screen. Several other colour combinations, for example black-and-white, and a particular combination of blue-and-light-blue gave similar catches of female flies, while blue-and-black was found to be the best combination for males. A diagonally-divided screen with the lower triangular portion being white and the upper one blue provided the best results (Green 1989).

The use of colour to attract the New World screwworm fly, *Cochliomyia hominivorax* (Diptera: Calliphoridae) was investigated by Peterson (1982), with Wind Oriented Traps (WOTs) baited with swormlure-2. It was found that yellow and white traps consistently caught more flies than black ones. However Torr and Hall (1992), using electric targets and swormlure-4, found blue to be the most attractive colour, followed by black and then yellow, although the colour effect in this experiment was not significant, and neither was the presence or absence of a target. When pairs of targets of different colours were used, black was significantly more attractive than blue and yellow, with white proving the least attractive colour. These workers suggest that the difference between their results and those of Peterson (1982) can be explained by *C. hominivorax* being attracted to black WOTs, but not entering them. This would be due to a distinction between those colours which attract the flies and those which elicit landing responses, similar to that found in *Glossina* species (Torr and Hall 1992). A later experiment showed that black was also significantly more attractive than red (Green *et al.* 1993).

4.1.5. Responses of *Lucilia* species to coloured traps in the field

Following the findings of Lee (1937), yellow colouration has been used in several traps for the capture of *Lucilia cuprina* in Australia (Vogt and Havenstein 1974; Anderson *et al.* 1990), but no systematic study of the use of colour in blowfly traps was conducted until that of Wall *et al.* (1992c). Their experiment, carried out at the University of Bristol farm in southwestern England, compared the catches of *L. sericata* on adhesive targets baited with liver and sodium sulphide and covered in cloth of five different colours plus uncovered targets of plain aluminium. It was demonstrated that white traps performed best, followed by yellow, aluminium, black, red and blue. The mean daily catch on white targets was nearly twice that on blue targets. There was no effect of ambient temperature on the relationship between colour and catch size, and both sexes of blowfly showed the same relationship

between these two variables, although catches of females were consistently higher than males (Wall *et al.* 1992c).

The relationship between catch numbers and target colour, measured as spectral reflectivity, was analysed by multiple regression using the method developed by Green and Flint (1986). The resulting model related the catch of female flies negatively to reflectivity in the ultraviolet and blue (300-450nm) component of the spectrum, and positively to reflectivity in the blue-green-yellow (450-580nm). It explained 79% of the variance among catch means. The model showed why red, black and blue targets, which had low reflectivities in the attractive region, were relatively unattractive. It did not fully explain the superiority of white over yellow, but allowed the prediction that a bright and highly saturated yellow hue, with no blue component and a plateau around 550-560nm would perform better than white. The results strongly suggested that *Lucilia sericata,* like *L. cuprina,* discriminates primarily by hue rather than brightness (Wall *et al.* 1992c).

Hall *et al.* (1995) used two methods to study the colour responses of *Lucilia sericata* (and also the Sarcophagid species *Wohlfahrtia magnifica,* another cause of myiasis in domestic animals) in Hungary. A simple comparison of four different colours of target showed black to be the most attractive, followed by blue, white, and yellow, with the mean daily catch on black targets being nearly ten times higher than that on yellow targets. Very similar results were obtained with *W. magnifica.* In the second experiment, electric targets were paired, side by side, creating 1 x 1 m screens with a choice of two colours. The black:blue pairing produced the highest catch of *L. sericata,* followed by black:yellow, black:white, blue:yellow, white:yellow and blue:white. The black:blue pairing caught nearly four times the number of blowflies caught by any of the three poorest pairings (Hall *et al.* 1995).

A further study by Wall and Smith (1996) found that there was no significant difference between four colours tested on adhesive targets. When liver and sodium sulphide solution were used as bait, red targets caught slightly higher numbers of *Lucilia sericata* than black, white, and yellow targets. When swormlure-4 was used, the highest catches were obtained on white targets, followed by yellow, black, and red targets. It was also found that there was a significant interaction between the exposure of targets to sunlight and the effect of the target colour. The effect of colour on the number of *L. sericata* caught was evident at exposed sites, but not at those which were partially sheltered by trees and walls (Wall and Smith 1996).

4.1.6. Aims and Objectives

Although a considerable quantity of research has been carried out to investigate the behavioural responses of *Lucilia* species to coloured stimuli, both in the laboratory and in the field, no physiological study has been published showing the magnitude of response of any *Lucilia* species over a range of wavelengths. The objective of this study was to measure and compare the electroretinograms (ERGs) of the sheep blowflies *Lucilia sericata* and *Lucilia caesar*, the most important agents of sheep strike in the British Isles. Additionally, as previous studies of behaviour in natural conditions have been confined to *Lucilia sericata*, and because of the significance of *L. caesar* as an agent of strike in Scotland, an experiment was conducted to examine the responses of this species to coloured targets in the field.

4.2. Materials and Methods

4.2.1. Source and culture of experimental animals

Laboratory colonies of blowflies were cultured in an insectary at the Scottish Agricultural College, Auchincruive, which was maintained in constant light at a temperature of approximately 21°C. Adult flies were accommodated in metal cages (300mm in length, 200mm in width, and 210mm in height), which were covered with tubular gauze (Tubegauz T2). One end of the gauze was tied securely, while the other was tied loosely to allow access. The latter end was cut so as to extend approximately 250mm beyond the cage, forming a sleeve which hindered the escape of flies when a hand was inserted through it. Unlimited sucrose and water were supplied on petri dishes (95mm in diameter), which in the case of water contained cotton wool to prevent flies from drowning. A protein source, in the form of beef liver (approximately 20g per cage), was provided from the fourth day after eclosion, and this was replaced on alternate days, or daily when eggs were being collected. Cages were maintained until the majority of flies were dead, typically 30-40 days after eclosion.

Once maturation of the ovaries had taken place, typically about 11 days after eclosion, eggs were laid on the beef liver, and these were used for the establishment of new cages of blowflies. When a petri dish containing the liver and eggs was removed from a cage, a lid was placed on it, in order to provide the high level of humidity required for the eggs to hatch. If the meat appeared desiccated, a few drops of water were added, to increase the humidity. After 24 hours, by which time most of the eggs would have hatched, a circular metal box (105mm in height and 175mm in diameter), with gauze embedded in the lid to allow air to permeate, was prepared by the addition of sand to a depth of about 30mm. A large piece of beef liver (typically 300-400g) was placed on top of the sand. First instar blowfly larvae were then removed from the petri dish using a knife or fork, and these were placed onto the liver in the box, which was then either covered or placed in a cupboard, in order to prevent any escaped blowflies from laying additional eggs into the culture.

If the meat was entirely consumed before the blowfly larvae reached full size, an additional piece of beef liver was added to the box. Otherwise no further action was taken until the majority of larvae had reached the wandering stage (late third instar), which often took place 10-12 days after hatching, and migrated from the meat into

the sand. Any remaining meat was then removed from the culture, frozen to kill any larvae still attached to it, and discarded. If necessary, some water was sprinkled into the culture at this stage to prevent desiccation of the wandering larvae, which were then allowed to remain in the sand until the majority had undergone pupariation (6-8 days later). The entire culture was then sieved to remove the sand, and the puparia and larvae placed in petri dishes or small plastic containers. These were then inserted into newly prepared cages with a supply of water and sugar for the use of the flies after eclosion.

A colony of *Lucilia sericata* was established using larvae collected from cases of sheep strike in southern Scotland during the summer of 1994. Several different sources were used in order to ensure genetic diversity. *L. caesar* proved difficult to maintain in captivity, and this species was not successfully reared beyond the fourth generation. A new colony was therefore established each summer, by the collection of larvae from beef liver exposed on Auchincruive College Farm. Larvae collected in this way usually contained other blowfly species in addition to *L. caesar*, and it was therefore necessary to carry out a sorting process. *Calliphora* species could usually be removed after pupariation, as their puparia are noticeably larger, and often darker, than those of *Lucilia* species. *Lucilia* species were distinguished as adults, using the procedure described in sub-section 2.2.1, after anaesthetisation by cooling in a freezer. Because *L. caesar* could not be accurately distinguished from *L. illustris* without damaging the insects, the identity of each newly established colony was therefore confirmed by examination of the first generation flies after death, to ensure that only one species was present.

The blowflies used in the physiological studies were all taken from the laboratory colonies, the *Lucilia caesar* being descended from larvae collected during the summer of 1995. Flies were used for experimentation at an age of approximately 10-12 days.

4.2.2. Equipment used to stimulate and measure ERGs

The apparatus used in this experimental work is represented diagramatically in Figure 4.1.

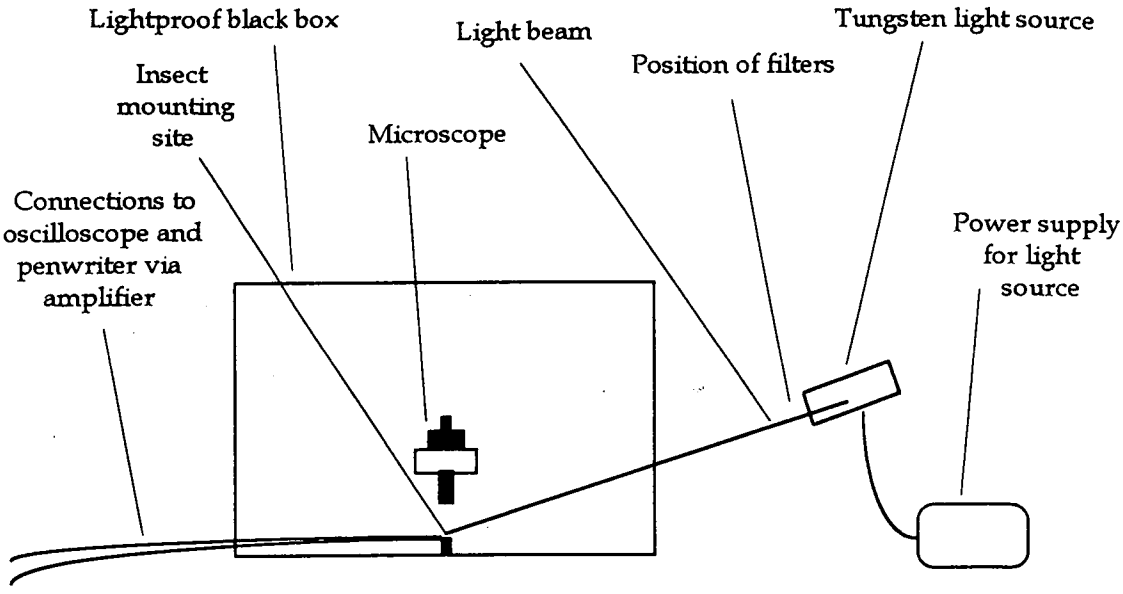


Figure 4.1: Diagram showing apparatus for stimulation of ERGs.

The experiments were carried out in a small room in the Ashworth Laboratories at the University of Edinburgh. The room was illuminated by a fluorescent strip light, but this was switched off while recordings were being made, and external light was excluded by a heavy black curtain across the doorway. During experimentation the only illumination came from instrument lights and from a small amount of stray light from the light source, and the experimental insects were shielded from this by a black wooden box, measuring approximately 0.65m in depth, 0.60m in height, and 0.85m in length.

The light source used in these experiments was a 100W, 12V tungsten-halogen light (Muller LXH100) powered by a dedicated power supply unit (Muller XH100). Neutral density filters (Balzers) were used to alter the light intensity. For the first fly, fourteen of these filters were used, having the following transmissions: 0.09%; 0.23%; 0.54%; 1.0%; 2.2%; 5.0%; 6.4%; 10.2%; 19.8%; 30.2%; 40.3%; 50.1%; 63%; and 84.6%. Four of these: 0.23%; 10.2%; 50.1%; and 84.6% were then discarded as unnecessary and only the remaining ten used for the second and subsequent flies. The wavelength was adjusted using bandpass filters. Fourteen of these were circular narrow-bandwidth filters (Ealing; diameter 2.5cm), which possessed the following wavelengths: 300nm; 332nm; 360nm; 380nm; 409nm; 440nm; 470nm; 500nm; 530nm; 559nm; 590nm; 620nm; 650nm; and 679nm. Additionally, two square narrow-bandwidth filters (Balzers; sides 4cm) were used: 489nm and 759nm. Due to negligible responses when the latter filter was used, it was replaced from the ninth fly onwards with a wide-bandwidth square filter (Balzers; sides 4cm) of centre wavelength 705nm. The light was focused onto the insect by a biconvex lens, placed

at a distance of approximately 10cm from the insect. During the recording of ERGs, the light beam could be interrupted by a shutter close to the bulb, or by a rotating wheel attached to an electric motor. Slots had been cut in the wheel to deliver a light pulse lasting 0.2 seconds every 4 seconds.

Electroantennograms were recorded using two electrodes. The first of these was a glass electrode which was formed by pulling a capillary tube of internal diameter 1.16mm (GC200F-10, Clark Electromedical Instruments) to produce a fine point, using a microelectrode puller unit (H104, Palmer, London). The resulting electrode, designed for insertion into the eye of the insect from which measurements were being taken, was filled with Ringer solution to ensure that it was approximately in equilibrium with the laminar cells. It was held in place by a clamp which could be manipulated in three planes by adjusting small wheels. The electrical connection was made by a piece of silver wire, approximately 30mm in length, which was inserted into the wide end of the electrode. At least once each day, prior to the start of recording, the silver wire was attached to a 9V battery (PP9) and inserted into a beaker containing Ringer solution, along with a second electrode attached to the other pole of the battery. The electrode was left connected to the battery for at least 20 minutes, by which time it had gained a brown-coloured coating containing chloride ions, which was intended to improve conductivity. The indifferent electrode was a piece of fine gold wire, attached to an insulated cable using solder. The signal from the electrodes was amplified using a purpose-built amplifier, and the output from this was supplied to an oscilloscope (Tektronix 2220) and to a penwriter (Bryans 28000).

The site where the insects were mounted was on a small metal cylinder, approximately 20mm in diameter, and 40mm in height. This was secured to the base plate by magnetism, which prevented movement during the recording of ERGs, but allowed the cylinder to be removed for flies to be mounted upon it. A binocular microscope was positioned over the mounting site, in order that the insects could be oriented correctly, and so that the electrodes could be accurately inserted. To the microscope was attached a light which was used to illuminate the insect while it was being prepared for recording. The mounting site and microscope were contained within the wooden box. The front of the box was open, but to it was attached a thick black curtain which completely excluded light, but could be raised to allow setting up of the fly and equipment within. The only other opening was a circular hole, approximately 20mm in diameter, which allowed the light beam to pass into the box.

4.2.3. Calibration of equipment

The penwriter was calibrated using a PP9 battery whose output was measured using the oscilloscope and was found to be 5.3mV. The battery was then attached to the system in place of an insect, and switched on and off repeatedly while the penwriter was running at a speed of 1 millimetre per second. This procedure was followed with the penwriter set to the 250mV scale and repeated at the 1V scale. The penwriter deflections were then measured to the nearest half millimetre using a ruler, and the mean of four pulses calculated for each scale. These measurements were then used to calculate a conversion factor (in millivolts per millimetre) for the 250mV scale, and a second factor by which readings on the 1V scale could be multiplied to allow them to be analysed by the same process as that used for the 250mV scale.

The intensity of light passing through each combination of filters was measured using a Tektronix J16 digital photometer and a J6502 probe. The probe was placed on the wax block in place of an insect, and lighting conditions were identical to those present during the recording of ERGs. The photometer readings, in milliwatts per square metre, were recorded for each combination of bandpass and neutral density filters. However, data sheets accompanying the photometer showed that its response reduced at wavelengths below 450nm, and the size of the reduction in response was not quantified below 380nm. It was therefore necessary to calibrate the photometer against another piece of equipment of known performance.

The further calibration was subsequently carried out using a photodiode unit borrowed from the University of Birmingham, which contained a large-area photodiode (303-674; RS Components, Corby, UK). Each of the bandpass filters, with the exception of the 705nm filter, was used during the calibration with a wide range of neutral density filters, and the light intensity measured using both the Tektronix photometer and the photodiode in conjunction with a voltmeter. The readings from the voltmeter were recorded for each combination of filters, and were later converted into voltages using multiplication factors supplied by the University of Birmingham. The factors were 985.51 for the 'x1000' range on the photodiode unit; and 99.97 for the 'x100' range. A data sheet (232-3894), supplied by the manufacturer of the photodiode, contained a graph showing the spectral responsivity of the component to various wavelengths of light, and this was used to calculate adjustment factors for each bandpass filter (relative to an arbitrarily chosen point: 590nm), by which the photodiode voltages were multiplied.

Using a spreadsheet created in Claris Works 2.0, running on an Apple Macintosh LC475, logarithms (base 10) were taken, both of the adjusted output from the photodiode, and of the readings from the Tektronix photometer. The difference between each pair of data was calculated, and a mean difference obtained for each wavelength of light used. Pairs of data were excluded in cases of very low light intensity where one of the instruments had not registered a response, and the first viable pair at each wavelength was also omitted, as these were often noticeably different from the rest. The mean differences were then adjusted relative to that calculated for 590nm. Finally, the resulting calibration factors (adjusted mean differences), were subtracted from the readings recorded from the Tektronix photometer at the time of the ERG experiments. This allowed a true comparison to be made between the ERG responses recorded at different wavelengths of light.

4.2.4. Experimental procedure

Prior to recording ERGs, a piece of wax measuring approximately 20mm in diameter and 8mm in height was attached to the top of the metal cylinder, and an indentation made in it, approximately 4mm in both depth and width. Each fly was placed in a small plastic container, and anaesthetised by inserting, for approximately 20 seconds, a small piece of cotton wool dipped in ether. This immobilised the insect, allowing it to be mounted in the indentation in the dental wax. A further small piece of wax was then placed over the abdomen in order to restrain the insect after its recovery from the anaesthetic.

The fly's head was gently manipulated using a pair of pointed forceps, until one of its eyes was facing in a direction in which the light beam would be incident upon it. The wax was then pressed against the sides of the thorax, and over the side of the head distant from the light, providing further restraint. Following this, the cylinder on which the fly was mounted was replaced on the base plate. The light beam was switched on, in the absence of any filters, and the fly observed through the microscope, with the assistance of the adjacent light, while it was positioned by moving the cylinder. The desired position was with the light spot placed centrally on the insect's eye. Once this had been achieved, a small hole was made in the first thoracic segment using an entomological pin, and the end of the indifferent electrode was inserted into the haemolymph to a depth of approximately 2mm. The electrode was pressed lightly into the wax at least two points to prevent movement during recording.

Finally, the glass electrode was inserted into the eye by adjustment of the wheels controlling its position. It was often possible to puncture the eye using the tip of the electrode, but if this did not succeed at the first attempt, an entomological pin was used to make a small hole. The electrode tip was then inserted to a depth of approximately 1mm in the central part of the eye. If unintentional damage, such as tearing, was caused to the eye, then the other eye, or failing that a new fly, was used instead.

When the fly and electrodes were in position, the amplifier was switched on. If a green Light-Emitting Diode (LED) was not illuminated, all electrical connections were checked. Once the green LED was visible, the lights illuminating the insect were switched off, the curtain closed, and the amplifier and oscilloscope adjusted until a biological trace was visible on the oscilloscope screen. The rotating wheel was then switched on, and the insect's eye illuminated periodically by the light beam, without the use of any filters. If the insect's responses to this maximum white light illumination at this stage did not exceed 5mV, the preparation was discarded, and a new one prepared.

Once a satisfactory response had been achieved, the hole in the side of the box was covered with a piece of black cardboard secured with tape, and the insect was left in total darkness for a period of at least 45 minutes to allow for dark-adaptation. After this time, assuming a relatively flat base-line was registering on the oscilloscope, the penwriter was switched on, running at a speed of 1mm per second and set to the 250mV scale. The insect was then exposed to pulses of light from the light source. A bandpass filter was selected at random, and used with all ten neutral density filters. The neutral density filters were always used in the same order, starting with that transmitting the lowest proportion of light. After all ten had been used, the bandpass filter was used alone, giving 100% transmission of the light passing through it. In each case, four pulses of light were given, although occasionally additional pulses were given due to miscounting. Four seconds elapsed between each flash, and a 12 second interval was given between successive intensities. Once the first bandpass filter had been used at each intensity, the same procedure was followed with the others. An interval of at least five minutes was allowed between exposure to different wavelengths, and the hole in the side of the box was again covered during these periods. The order in which the bandpass filters were used was randomised for each different insect.

Activity by the fly, usually in the form of movement of antennae or attempted movement of limbs, sometimes caused large electrical responses to register. When this occurred over a very brief period, any light response which had been distorted

by it was simply repeated. If activity persisted over a longer period, recording was stopped until a reasonably flat base-line had resumed. In a few cases, the activity continued without significant interruption for more than 20 minutes, and when this occurred the preparation was abandoned.

A small number of recordings were interrupted by rapid electrical oscillations of increasing amplitude, and the cause was identified as lack of Ringer solution in the electrode. When this occurred, the electrode was removed, refilled with Ringer solution, and replaced in the fly's eye. The insect was then allowed to dark-adapt once again, for a period of at least 45 minutes, and following this the preparation was recalibrated by recording the magnitude of responses to white light in the absence of a filter. Measurements were then resumed where they had been left off.

4.2.5. Analysis of ERG data

The electroretinograms were measured peak-to-peak, using a ruler, to the nearest half millimetre. The measurements were entered into a spreadsheet created in Claris Works 2.0. The measurements were converted from millimetres into millivolts using the conversion factors previously calculated, and means obtained. A study of the electroantennogram responses of tsetse flies, which used a similar experimental protocol, found that the first ERG of a set of four was substantially larger than those which followed it, and it was excluded from the calculation of mean responses (Green and Cosens 1983). An investigation was therefore made to ascertain whether this was the case in the present study, and so to determine how many ERGs should be used in the calculation of each mean. One set of results from each sex and each species of blowfly was chosen at random, and the mean variation in the responses calculated for each filter combination which had produced penwriter deflections in excess of 10mm.

The light intensity readings from the photometer, adjusted as described in sub-section 4.2.3, were converted from measurements of power (Wm^{-2}) into measurements of quanta per unit area per second (photons m^{-2} s^{-2}) by firstly calculating the energy of a single photon of a given wavelength:

$$E_p = \frac{hc}{\lambda}$$

where h = Planck's constant = 6.62×10^{-34} Js
c = speed of light = 3×10^{8} ms^{-1}
and λ = wavelength (m)

Then, the number of photons $= \frac{P}{E_p}$ where P = light intensity (Wm^{-2})

Logarithms were taken of the converted measurements of light intensity, and graphs produced by the spreadsheet with the response, in millivolts, (y-axis) plotted against the logarithm of the light intensity, in photons per square metre per second, (x-axis). When seen in their entirety, these intensity-response curves tend to be sigmoidal in shape. In order to permit comparisons to be made between them, the linear portion of each was determined by inspection, and the spreadsheet was used to calculate a best-fitting line of the form:

$$y = a + bx$$

where: $b = \frac{\sum(x-\bar{x})(y-\bar{y})}{\sum(x-\bar{x})^2}$ and $a = \bar{y} - b\bar{x}$

Spectral sensitivity is often expressed as the inverse of the intensity required at each wavelength to give a criterion response (Jahn 1946), and this convention was followed in the analysis of the ERG data. The criterion response was taken to be 35% of the response to white light in the absence of any filter, and the best-fitting line for each bandpass filter was used to calculate the light intensity (in quanta per square metre per second) corresponding to the criterion response. A spectral sensitivity curve was then plotted for each insect. In order to allow for scale differences between different insects, each point was expressed as a percentage of the response at a particular point, 380nm, within each curve. Means and standard errors were calculated for female and male flies of both species.

4.2.6. Field experimentation

The field experiment (4.F) consisted of a comparison of adhesive targets painted with six different colours: white, yellow (Ford Signal Yellow; Hycote, Oldham, UK), blue (Vauxhall Regatta Blue), green (Ford Modena Green), red (Ford Sunburst Red) and black (Ford Black). The spectral reflectivities of these colours, as measured by the manufacturer, are shown in Figure 4.2, with the exception of black, which had a reflectivity of 4.4% or less throughout the spectrum. The targets were horizontal, as described in sub-section 3.2.1, and they were used at ground level to allow them to be serviced more rapidly. The experiment was carried out in August 1996 at the site detailed in sub-section 3.2.2, using a single Latin square as described in sub-section

3.2.4. The trap arrangement is shown in Appendix 3. The results were analysed by ANOVA and target means compared using Duncan's new multiple-range test (sub-section 3.2.5).

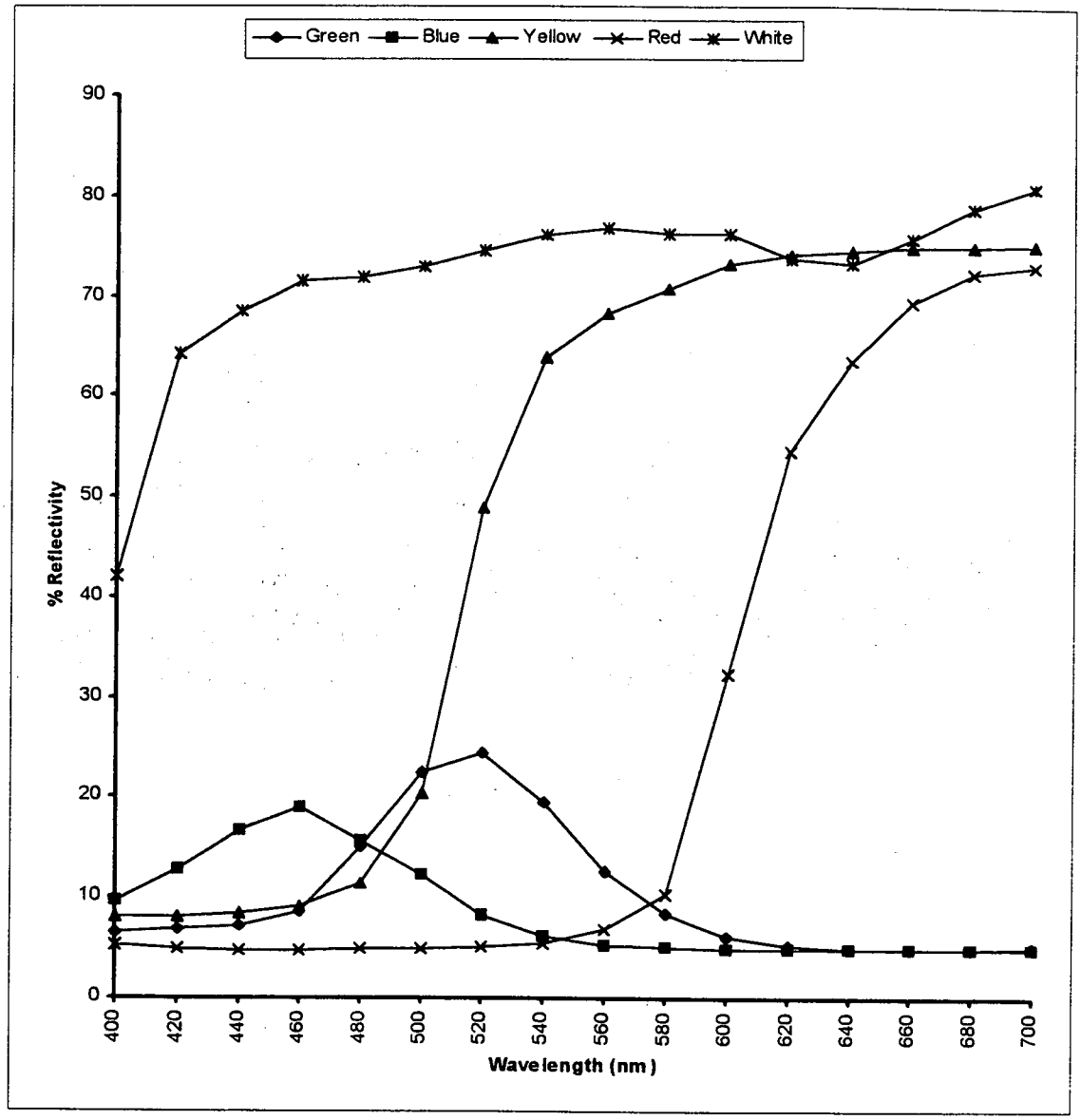


Figure 4.2: Reflectivity of paints used for coloured targets (from manufacturer's data).

4.3 Results

4.3.1. Calibration measurements

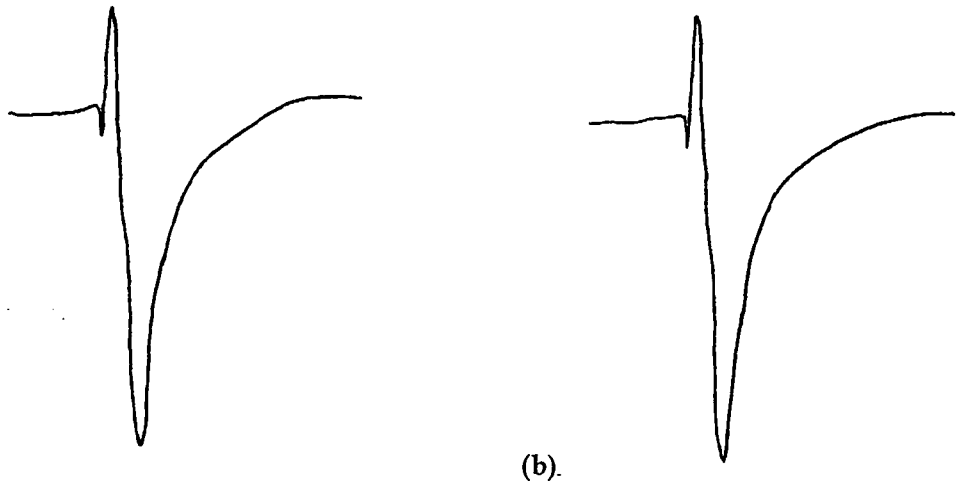
With the penwriter set to the 250mV scale, the standard battery pulse produced a mean deflection of 67mm. A conversion factor of 0.0791 millivolts per millimetre was therefore calculated for recordings on the 250mV scale. Set to the 1V scale, the deflection was 17.5mm, and recordings on the 1V scale were therefore multiplied by 3.829 before analysis.

The light intensities measured for each combination of filters are tabulated in Appendix 3.

4.3.2. Electroretinograms (ERGs)

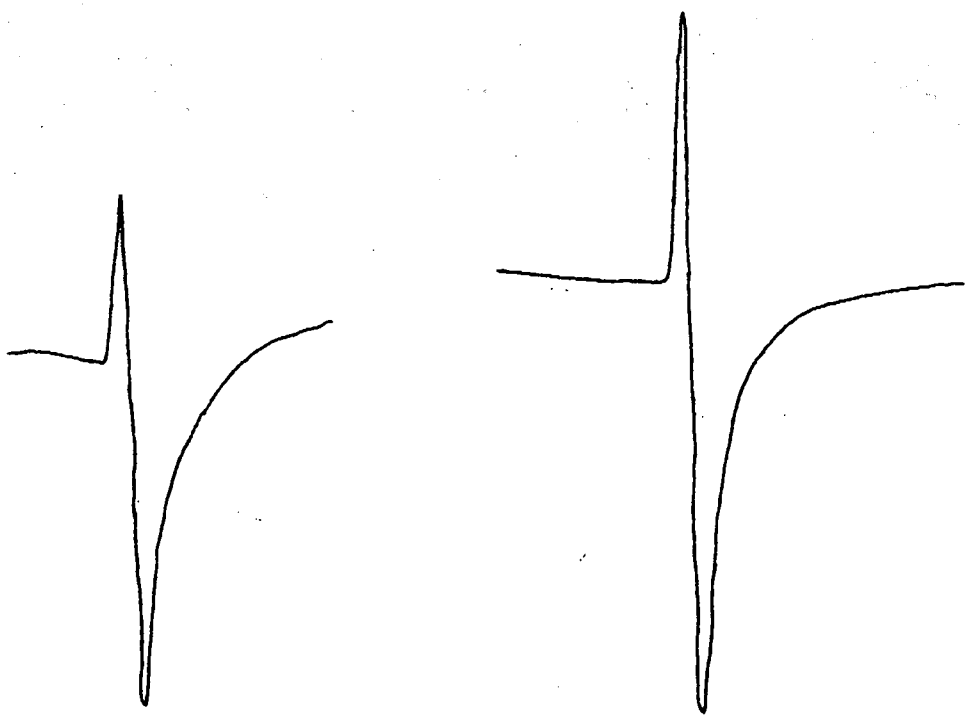
The first response was found to be, on average, 1.0% greater than the mean of the remaining three in Fly 5 (*Lucilia caesar* female); 1.8% greater in Fly 13 (*L. sericata* female); 3.3% greater in Fly 19 (*L. caesar* male); and 2.4% greater in Fly 21 (*L. sericata* male). These differences were considered to be small, and all four responses were therefore used in the calculation of averages.

Examples of ERGs are shown in Figures 4.3 to 4.5, each of which was recorded from Fly 28, a female *Lucilia sericata*. The figures show recordings using four different bandpass filters: 360nm, 409nm, 500nm, and 590nm. Additionally, the response in the absence of any filter is shown (Figure 4.5).



(a). (b).

Figure 4.3: Electroretinogram (ERG) recording from a female *Lucilia sericata* (Fly 28) during a stimulus of light using (a) the 360nm bandpass filter, and (b) the 409nm bandpass filter (to scale with Figures 4.4 and 4.5).



(a) (b)

Figure 4.4: Electroretinogram(ERG) recording from a female *Lucilia sericata* (Fly 28) during a stimulus of light using (a) the 500nm bandpass filter, and (b) the 590nm bandpass filter (to scale with Figures 4.3 and 4.5).

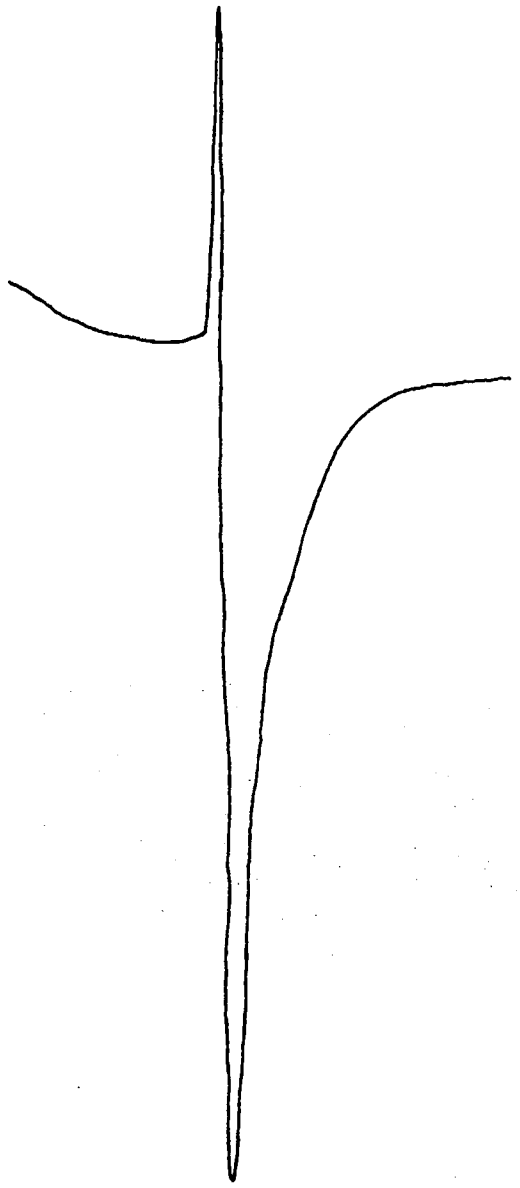


Figure 4.5: Electroretinogram(ERG) recording from a female *Lucilia sericata* (Fly 28) during a stimulus of light in the absence of any filter (to scale with Figures 4.3 and 4.4).

Seven complete sets of ERG data were recorded for each sex of each species, and an eighth set of data for male *Lucilia sericata* was also recorded. The measurements of the ERGs are tabulated in Appendix 3, and a typical set of V/LogI graphs (for Fly 9, a female *L. caesar*) are shown graphically in Figures 4.6, 4.7, and 4.8. Tables 4.1 to 4.4 show the spectral sensitivity data calculated for each fly.

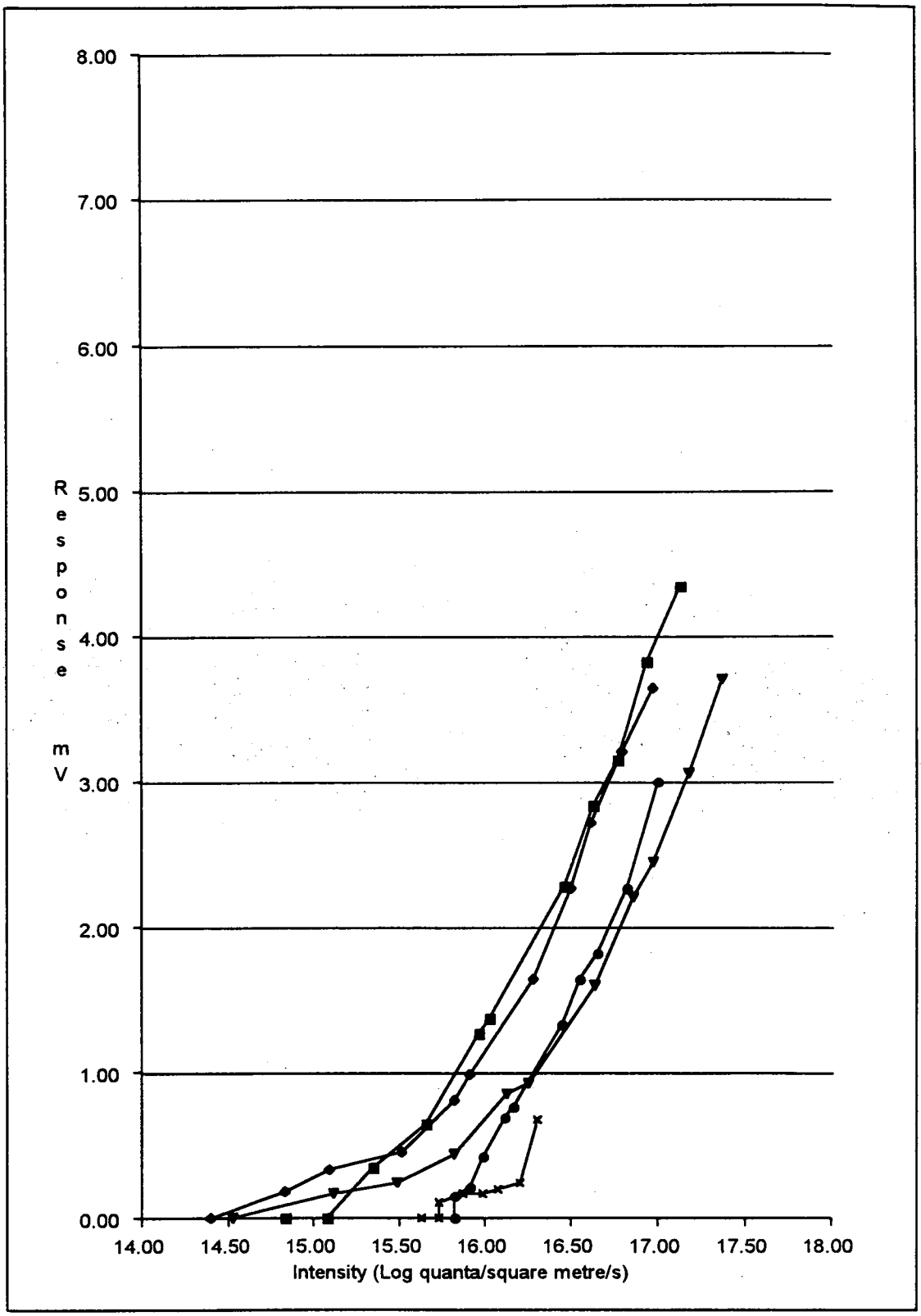


Figure 4.6: Graph of electroretinogram(ERG) responses of Fly 9, a female *Lucilia caesar*, plotted against light intensity (four ERGs averaged for each point) (300nm - 409nm). Cross = 300nm; Circle = 332nm; Square = 359nm; Diamond = 380nm; Triangle = 409nm.

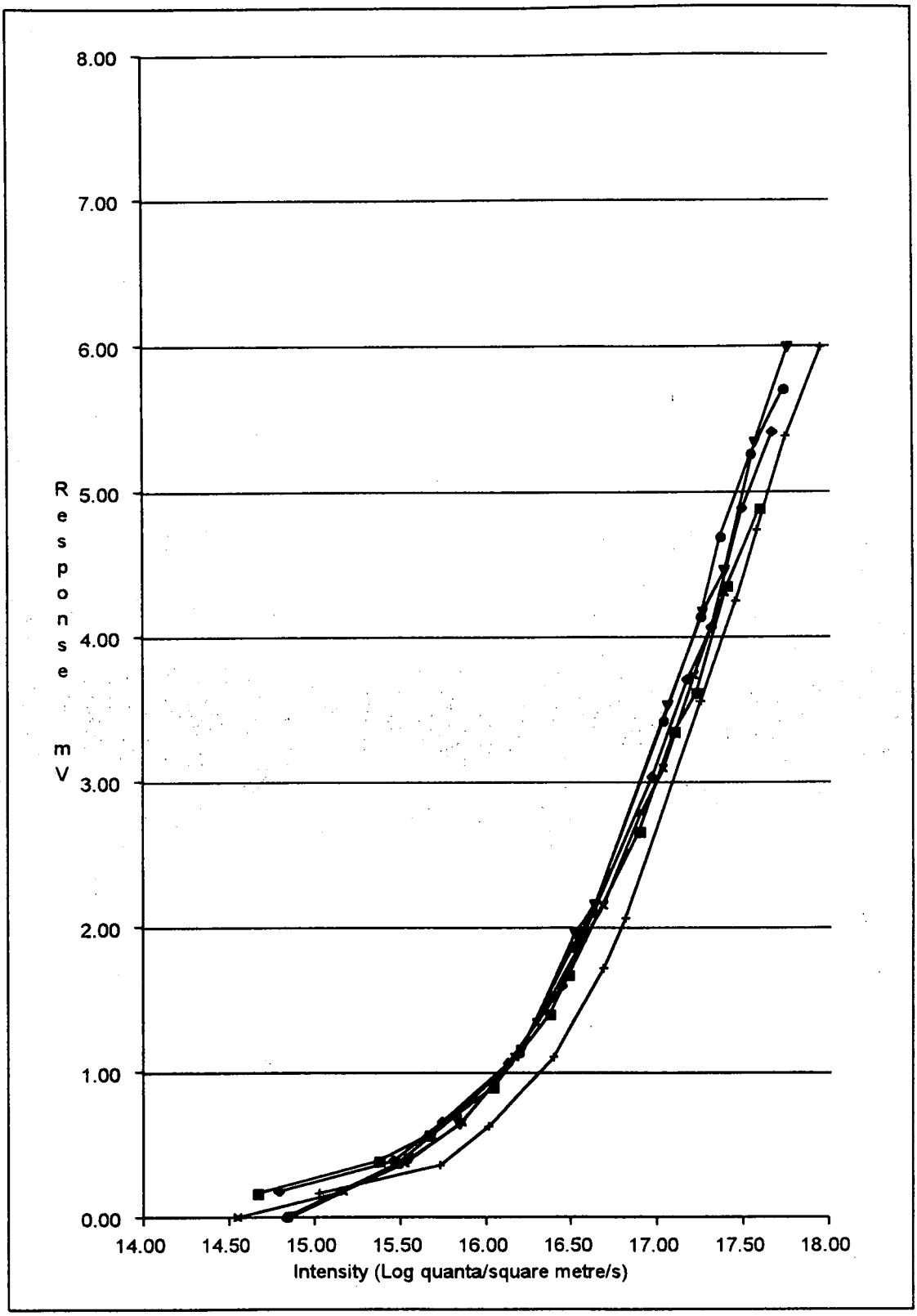


Figure 4.7: Graph of electroretinogram(ERG) responses of Fly 9, a female *Lucilia caesar*, plotted against light intensity (four ERGs averaged for each point) (440nm - 560nm). Cross = 440nm; Circle = 470nm; Square = 489nm; Diamond = 500nm; Triangle = 530nm; Plus = 560nm.

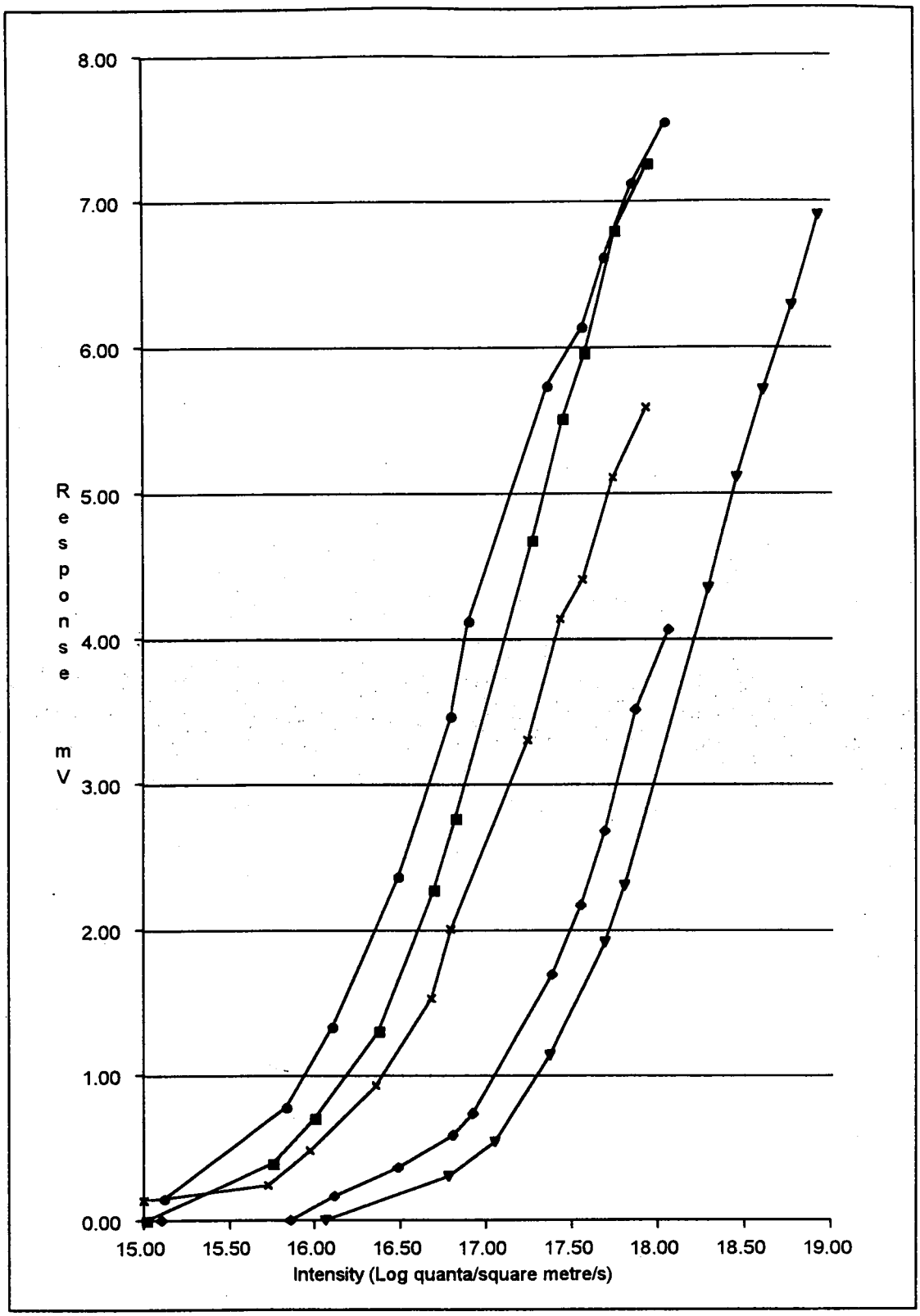


Figure 4.8: Graph of electroretinogram(ERG) responses of Fly 9, a female *Lucilia caesar*, plotted against light intensity (four ERGs averaged for each point) (590nm - 705nm). Cross = 590nm; Circle = 620nm; Square = 650nm; Diamond = 679nm; Triangle = 705nm.

wavelength (nm)	Fly 1	Fly 2	Fly 5	Fly 9	Fly 11	Fly 15	Fly 22
300	0.996	1.052	0.983	0.998	0.983	1.004	1.000
332	1.002	1.011	0.978	0.987	0.986	0.992	0.980
359	0.998	0.997	0.977	1.004	1.010	0.966	0.983
380	1.000	1.000	1.000	1.000	1.000	1.000	1.000
409	0.990	0.986	0.968	0.976	0.980	0.969	0.959
440	0.980	0.976	0.965	0.987	0.978	0.974	0.977
470	0.974	0.955	0.955	0.993	0.979	0.978	0.948
489	0.979	0.965	0.953	0.986	0.972	0.971	0.953
500	0.977	0.969	0.974	0.989	0.986	0.970	0.950
530	0.982	0.981	0.985	0.991	0.986	0.978	0.976
559	0.962	0.982	0.966	0.982	0.987	0.973	0.974
590	0.939	1.002	0.955	0.979	0.960	0.959	0.960
620	0.980	1.052	0.990	1.015	1.005	0.985	1.022
650	0.999	1.036	0.976	0.997	0.987	1.000	0.984
679	0.956	0.988	0.931	0.946	0.939	0.958	0.950
705	*	*	*	0.938	0.920	0.928	0.918

Table 4.1: Spectral sensitivity of seven female *Lucilia caesar*. All data were calculated from means of four ERGs, and are expressed as proportions of the sensitivity at 379.7nm. * see section 4.2.2 for explanation of missing values.

wavelength (nm)	Fly 4	Fly 10	Fly 14	Fly 18	Fly 19	Fly 20	Fly 26
300	0.982	1.026	1.044	1.020	1.006	1.003	1.011
332	0.960	0.996	1.012	0.992	1.016	1.014	0.993
359	0.987	1.006	1.020	0.996	1.019	1.004	1.004
380	1.000	1.000	1.000	1.000	1.000	1.000	1.000
409	0.954	0.975	1.030	0.978	0.973	0.972	0.971
440	0.968	0.988	0.990	0.965	0.989	0.981	0.975
470	0.960	0.980	1.011	0.968	0.985	0.975	0.955
489	0.990	0.980	1.014	0.989	0.984	0.983	0.982
500	0.977	0.987	0.994	0.983	0.993	0.996	0.979
530	0.973	0.978	1.038	0.983	1.004	1.005	0.984
559	0.967	0.974	1.034	0.998	1.001	0.998	0.979
590	0.937	0.954	1.022	0.982	0.993	0.980	0.979
620	0.941	0.990	1.050	1.013	0.996	0.994	1.022
650	0.951	0.970	1.017	0.993	0.980	0.978	0.992
679	0.900	0.911	0.982	0.947	0.919	0.925	0.937
705	*	0.897	0.956	0.923	0.914	0.911	0.933

Table 4.2: Spectral sensitivity of seven male *Lucilia caesar*. All data were calculated from means of four ERGs, and are expressed as proportions of the sensitivity at 379.7nm. * see section 4.2.2 for explanation of missing value.

wavelength (nm)	Fly 3	Fly 13	Fly 16	Fly 17	Fly 23	Fly 25	Fly 28
300	0.978	0.963	1.016	1.020	1.000	0.996	0.991
332	0.992	0.970	0.995	0.992	0.990	0.997	1.015
359	1.007	0.945	1.008	0.996	1.016	0.987	0.987
380	1.000	1.000	1.000	1.000	1.000	1.000	1.000
409	0.977	0.958	0.979	0.978	0.963	0.973	0.962
440	0.951	0.966	0.998	0.965	0.989	0.979	0.984
470	0.965	0.943	0.987	0.968	0.985	0.979	0.995
489	0.973	0.943	0.986	0.989	0.994	0.988	0.985
500	0.973	0.943	0.999	0.983	0.992	0.984	0.986
530	0.946	0.960	1.002	0.983	1.009	1.004	1.004
559	0.954	0.969	0.981	0.998	1.008	1.014	1.007
590	0.974	0.964	0.970	0.982	0.982	0.995	0.995
620	0.987	0.952	0.998	1.013	0.973	1.005	1.015
650	0.933	0.969	0.972	0.993	0.955	0.974	0.989
679	0.907	0.915	0.927	0.947	0.891	0.923	0.945
705	*	0.888	0.910	0.925	0.896	0.909	0.928

Table 4.3: Spectral sensitivity of seven female *Lucilia sericata*. All data were calculated from means of four ERGs, and are expressed as proportions of the sensitivity at 379.7nm. * see section 4.2.2 for explanation of missing value.

wavelength (nm)	Fly 6	Fly 7	Fly 8	Fly 12	Fly 21	Fly 24	Fly 27	Fly 29
300	1.017	1.009	1.029	1.022	1.032	1.000	1.032	1.029
332	0.998	0.961	0.986	1.012	1.017	1.008	1.009	0.993
359	1.010	1.001	1.005	1.022	1.026	1.008	0.975	1.018
380	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
409	0.945	0.935	1.003	0.998	0.990	0.993	0.964	0.981
440	0.992	0.965	1.007	0.980	0.990	0.990	0.970	1.001
470	0.967	1.000	1.004	0.983	0.990	0.996	0.984	0.988
489	0.973	0.983	1.016	0.999	0.989	1.008	0.983	1.005
500	0.883	0.993	1.017	0.991	0.995	1.001	0.983	1.001
530	0.960	0.989	1.020	1.011	0.996	1.011	0.965	1.013
559	0.887	0.954	1.021	1.010	1.005	1.015	0.978	1.021
590	0.925	0.968	1.019	0.996	0.988	1.000	0.962	1.010
620	0.944	1.007	1.024	1.001	1.003	1.009	0.988	1.059
650	0.977	0.962	0.997	0.975	0.984	0.975	0.965	1.029
679	0.921	0.874	0.925	0.909	0.940	0.936	0.907	0.986
705	*	*	*	0.912	0.909	0.920	0.915	0.966

Table 4.4: Spectral sensitivity of seven male *Lucilia sericata*. All data were calculated from means of four ERGs, and are expressed as proportions of the sensitivity at 379.7nm. * see sub-section 4.2.2 for explanation of missing values.

For the calculation of mean spectral sensitivity, six individuals were selected from each group of flies. The mean for *Lucilia caesar* females excludes Fly 2, as this individual produced ERGs of abnormal shape. In the remaining cases, the six flies with the smallest variation in their response to white light during the experiment were selected. This process excluded Fly 14 from the calculation for *L. caesar* males, Fly 28 from the calculation for *L. sericata* females, and Flies 6 and 7 from the calculation for *L. sericata* males. The mean spectral sensitivities and standard errors for each group are shown in Table 4.5, and graphically in Figures 4.9 to 4.12.

All four graphs have three major maxima, but their positions vary to a certain extent between sexes and species. The first peak is in the ultraviolet (UV), and for female flies of both species, the highest responses were measured using the 379.7nm filter. In contrast, males of both species demonstrated a greater response with the 300.0nm filter. A second peak is present in the green, with both sexes of *Lucilia caesar* showing the highest response with the 529.6nm filter, and both sexes of *L. sericata* showing the highest response with the 559.2nm filter. Finally, there is a maximum in the red, with all four groups of flies recording a peak with the 620.5nm filter. The relative heights of the three peaks is identical in every case, with the UV peak being the highest, and the green peak being the lowest, although the spectral sensitivity of the *L. caesar* females was almost as high at the red peak as at the UV peak.

wavelength (nm)	*Lucilia caesar* Female		*Lucilia caesar* Male		*Lucilia sericata* Female		*Lucilia sericata* Male	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
300	0.994	0.0037	1.008	0.0062	0.996	0.0090	1.024	0.0051
332	0.988	0.0036	0.995	0.0083	0.990	0.0040	1.004	0.0049
359	0.989	0.0067	1.003	0.0043	0.993	0.0105	1.009	0.0076
380	1.000	0.0000	1.000	0.0000	1.000	0.0000	1.000	0.0000
409	0.974	0.0044	0.971	0.0035	0.971	0.0035	0.988	0.0056
440	0.977	0.0029	0.978	0.0041	0.975	0.0070	0.990	0.0056
470	0.971	0.0067	0.971	0.0047	0.971	0.0067	0.991	0.0033
489	0.969	0.0054	0.985	0.0015	0.979	0.0077	1.000	0.0050
500	0.974	0.0056	0.986	0.0031	0.979	0.0081	0.998	0.0047
530	0.983	0.0023	0.988	0.0054	0.984	0.0105	1.002	0.0081
559	0.974	0.0038	0.986	0.0058	0.987	0.0095	1.008	0.0066
590	0.959	0.0053	0.971	0.0085	0.978	0.0045	0.996	0.0081
620	1.000	0.0069	0.993	0.0115	0.989	0.0092	1.014	0.0102
650	0.990	0.0040	0.977	0.0064	0.966	0.0082	0.987	0.0094
679	0.947	0.0042	0.923	0.0070	0.918	0.0077	0.934	0.0118
705	0.926	0.0045	0.916	0.0061	0.906	0.0063	0.924	0.0106

Table 4.5: Spectral sensitivity of *Lucilia caesar* and *L. sericata* of both sexes. All data were calculated from means of four ERGs, and are expressed as proportions of the sensitivity at 379.7nm.

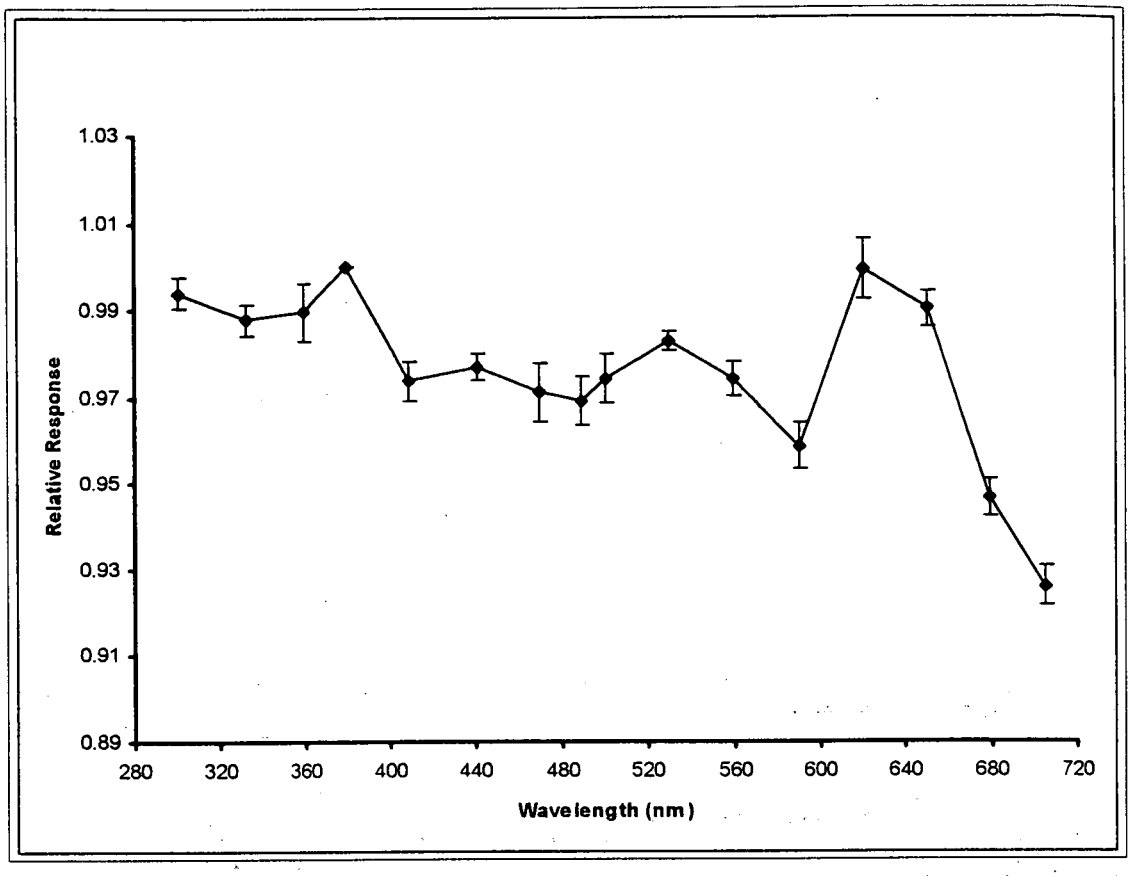


Figure 4.9: Spectral sensitivity of female *Lucilia caesar*. Means of six flies with standard errors, expressed as proportions of sensitivity at 380nm.

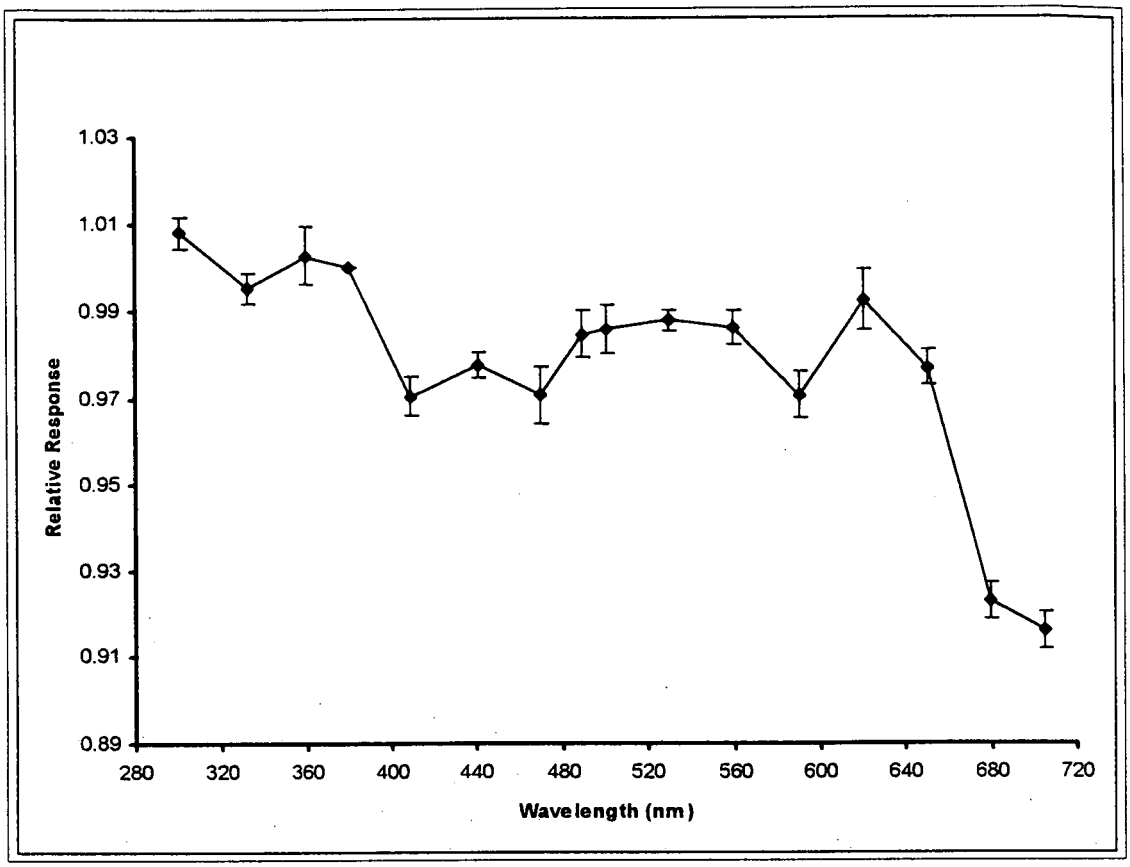


Figure 4.10: Spectral sensitivity of male *Lucilia caesar*. Means of six flies with standard errors, expressed as proportions of sensitivity at 380nm.

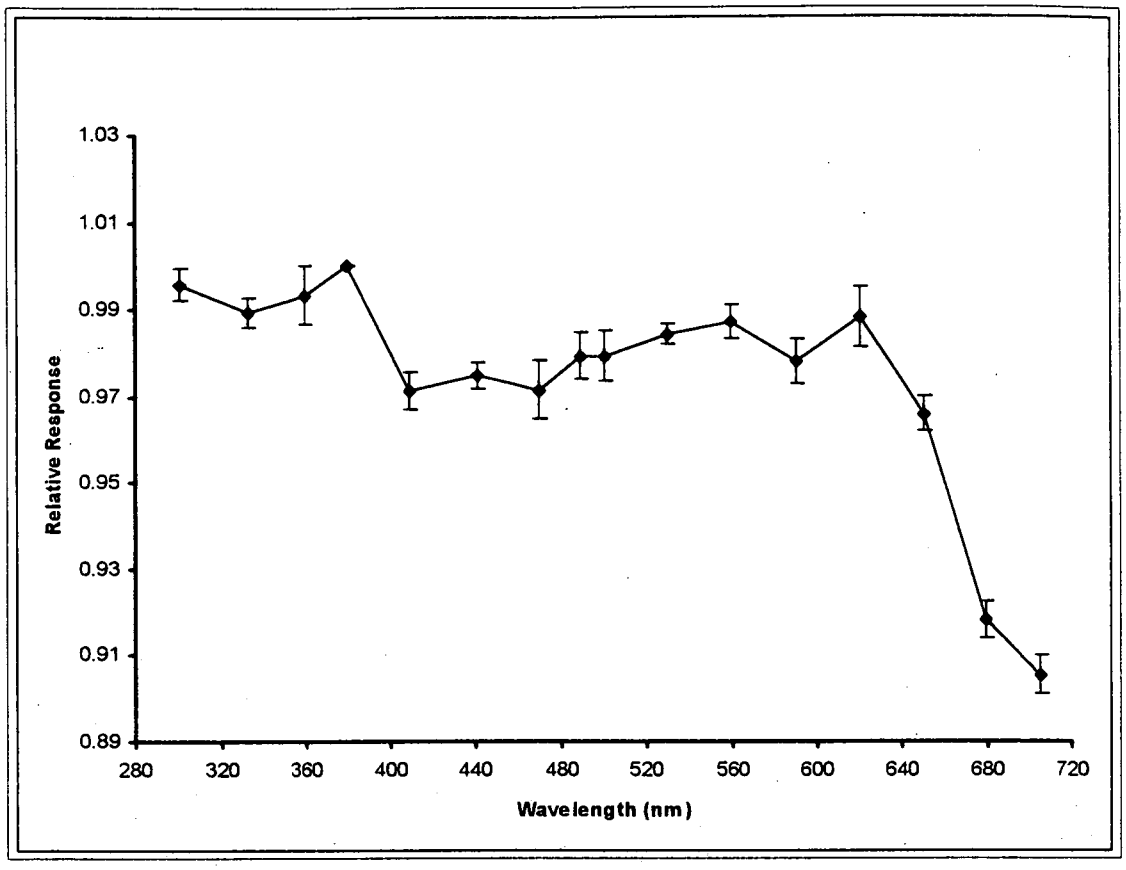


Figure 4.11: Spectral sensitivity of female *Lucilia sericata*. Means of six flies with standard errors, expressed as proportions of sensitivity at 380nm.

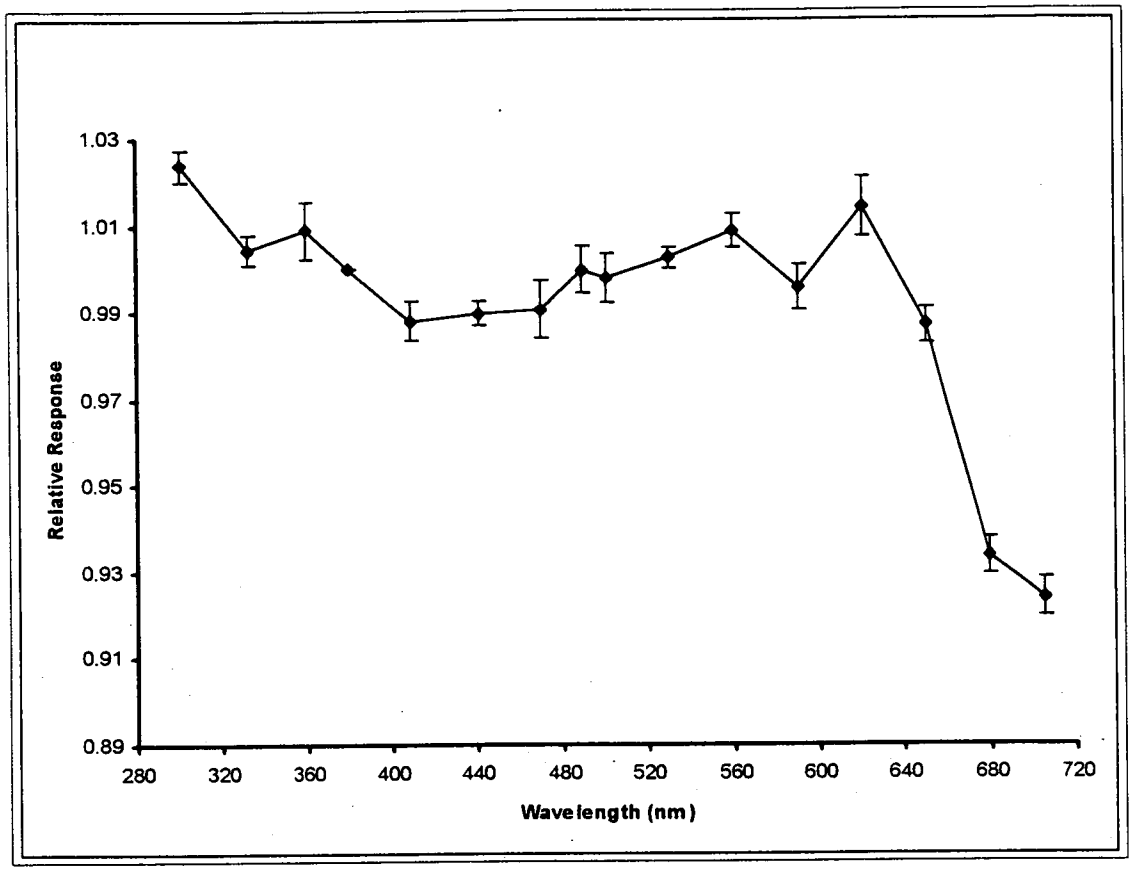


Figure 4.12: Spectral sensitivity of male *Lucilia sericata*. Means of six flies with standard errors, expressed as proportions of sensitivity at 380nm.

4.3.3. Field experiment

The field experiment (4.F) demonstrated a significant effect of target colour on the capture of both female *Lucilia caesar* group ($F=6.52$, residual df=20, $P<0.001$) and male *L. caesar* ($F=6.38$, residual df=20, $P=0.004$). Target means are shown in Table 4.6. The yellow target captured the highest numbers of both sexes, but its catches were not significantly higher than those on the white and blue targets. The red, green, and black targets caught lower numbers.

Target colour	Females		Males	
	detransformed	transformed	detransformed	transformed
White	32.5	1.525 bc	4.9	0.773 bc
Yellow	38.8	1.600 c	7.1	0.910 c
Blue	22.3	1.368 bc	4.2	0.717 bc
Green	7.8	0.943 ab	1.4	0.389 a
Red	12.5	1.130 b	2.5	0.547 ab
Black	4.7	0.756 a	1.1	0.330 a

Table 4.6: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets of six different colours. Standard Errors of Difference (for transformed data) 0.185 (females) and 0.143 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

4.4. Discussion

The electroretinograms recorded are similar to those obtained in electrophysiological studies of other Diptera (for example, Green and Cosens 1983). Goldsmith and Bernard (1974) identified three components of the dipteran ERG. In the first of these there is a sudden positive voltage change from the baseline, quickly reversed. In the second, there is a larger, negative voltage change, after which the voltage begins to stabilise, at a negative value relative to the baseline. In the third, there is a sudden negative voltage change, following which the voltage returns to the baseline. It is believed that first and third of these components represent the activity of second order cells in the lamina, while the second is produced by the stimulation of receptor cells. The first is visible in the ERGs recorded in the present study. However, the second and third cannot be distinguished, possibly because the light stimulus in the present study was given for a shorter period of time than that in some previous studies.

The spectral sensitivity graphs obtained in the present study are similar to those previously calculated for *Calliphora vicina* (see review in Goldsmith 1961) and for other red-eyed Diptera such as *Musca domestica* L. (Diptera: Muscidae) (Goldsmith 1965), and *Glossina morsitans morsitans* Westwood (Diptera: Glossinidae) (Green and Cosens 1983), which also show three peaks in their responses. Intracellular recordings in *Calliphora* have located an ultraviolet peak at approximately 360nm, and a blue/green peak at approximately 490nm (Horridge and Mimura 1975; Hardie 1979), which correspond to two different chromophores, 3-hydroxy retinol and 3-hydroxy retinal. The latter is associated with the bi-stable visual pigment, xanthopsin (Vogt 1983; Vogt and Kirschfeld 1984), and the former with a photostable pigment which transfers the energy of the absorbed light to the bi-stable pigment in a sensitisation process (Kirschfeld 1981; see review in Hardie 1986). In the present study. the differences between the responses to wavelengths between 400nm and 560nm are not significant. However, all four of the spectral sensitivity graphs show the maximum response in this range to be either at 529nm or at 559nm, and this suggests that the xanthopsin in *Lucilia* species has its peak absorbance at a higher wavelength than that in *Calliphora*. Although minor differences exist between the spectral sensitivity curves calculated for *Lucilia caesar* and those of *L. sericata*, the results of these electrophysiological experiments did not suggest that any significant difference exists between the spectral responses of the two species. More precise

equipment, and a substantially larger number of experimental insects would be required in order to isolate any minor variation between the members of this genus.

It appears from the spectral sensitivity curves that there is a difference between male and female flies in their sensitivity in the ultraviolet, with the males showing higher physiological responses in this part of the spectrum. Additional experimentation would be required to confirm that this is a real phenomenon, but it is apparent on the graphs for both *Lucilia caesar* and *L. sericata*. In the females of both species, the mean sensitivity at 300nm is less than that at 380nm, whereas in the male flies sensitivity at 300nm is considerably higher. Differences between the visual systems of male and female flies have been identified in the housefly, *Musca domestica* (see review in Hardie 1979). The males of this species possess a region of specialised visual cells which are used for the location of mates. It is possible that a mate-finding adaptation is also present in the males of *Lucilia* species.

The third peak, present in both sexes of *Lucilia caesar* and *L. sericata,* is located in the red, at about 620nm. This feature is also found in spectral sensitivity graphs of other red-eyed flies, but does not appear when measurements are taken from individual R1-6 cells. This is not due to the presence of a specific red receptor, but is caused by the presence of screening pigments between the ommatidia. These pigments are transparent at wavelengths in excess of 600nm, and so leak off-axis light to the photoreceptors at red wavelengths, resulting in an increased response. When the *chalky* mutant of *C. vicina,* which has white eyes containing no ommochrome, was used in place of the wild-type, the additional red peak was not present, and the sensitivity curve closely resembled that obtained from individual R1-6 cells (Goldsmith 1965; Paul *et al.* 1986).

Previous research into the relationship between physiological responses and behavioural responses of insects to light of particular wavelengths has often found a difference between the two. The horse fly *Tabanus nigrovittatus* Macquart (Diptera: Tabanidae) was found to be attracted in the field to blue and red colouration, but less so to green and yellow, and it avoided objects which reflect ultraviolet (Allan and Stoffolano 1986). However electrophysiological studies have shown that, like other flies, this species has high spectral sensitivity in the ultraviolet and green (Allan *et al.* 1991). Similarly, the attraction of the tsetse fly *Glossina morsitans morsitans* has been found to be substantially lower at wavelengths between 450nm and 500nm than at those between 400nm and 450nm, both in laboratory studies (Green and Cosens 1983), and in the field (Green 1986), while no such decline appeared on the spectral sensitivity curve for this species (Green and Cosens 1983). The present study also revealed differences between the spectral sensitivity and

behavioural responses of *Lucilia caesar*, particularly regarding the relative attraction of green and blue.

Studies of the responses of sheep blowflies to colour in the field have produced a variety of results. The responses of *Lucilia caesar* in the present study differ from those of *L. sericata* recorded in the field by Hall *et al.* (1995), but are similar to those found in a study of *L. sericata* by Wall *et al.* (1992c). In both cases, yellow and white proved to be the most attractive colours. Although their order of attractiveness is reversed, with yellow proving the most attractive in the present study, the catches using these two colours do not differ significantly in either case. It should also be noted that objects appearing "white" to human eyes may vary substantially from each other in their reflectivity in certain parts of the spectrum. Blue traps performed well in the present study, not differing significantly from yellow and white, and performing significantly better than green and black. Wall *et al.* (1992c) found blue to be the least attractive colour of those tested, and it attracted significantly lower numbers of flies than the two most attractive colours. This contrast may be at least partly due to differences between the blue colours used. The blue used in the present case showed maximum reflectivity at 460nm, while that used by Wall *et al.* (1992c) had its peak at 420nm. It is notable that the dark blue colour used in a laboratory study of *L. sericata* by Wall and Smith (1996) had its peak at about 445nm, and that this colour, in contrast to that used by Wall *et al.* (1992c), proved more attractive than red. The order of attraction of red and black differed between the two studies, with red proving significantly more attractive in the present case. It appears unlikely that this is due to differences between the colours used, as their reflectivity curves are very similar. The colour green was not included in the experiment conducted by Wall *et al.* (1992c). Overall, despite the differences between the results of the two experiments, *L. caesar* responds to colour in a similar way to *L. sericata*, although minor differences are not excluded.

Wall *et al.* (1992c), proposed a model in which the performance of coloured targets for the capture of *Lucilia sericata* was related negatively to reflectivity in the 300-450nm (ultraviolet/blue) area of the spectrum, and positively to reflectivity in the 450-580nm (blue/green/yellow) band. This model provided a good explanation of the experimental results in the same study, but subsequent experiments have suggested that the first component of the model was insignificant, and that positive attraction to wavelengths between 450nm and 580nm was the important factor in determining the response to coloured traps (Wall and Smith 1996). The results of the field experiment in the present study are generally in agreement with this revised model. Although the model does not explain the apparent superiority of blue over

green, it is possible that this was due to the lack of contrast between the green target and the surrounding grass, and further research would be required to clarify this point.

Neither the physiological data nor the behavioural data collected in the present study suggest that any important differences exist between the visual systems of *Lucilia caesar* and *L. sericata*. It is therefore probable that no distinction will need to be made between the colouration of traps designed to capture these two species of sheep blowfly.

5. Olfactory Responses

5.1. Introduction

5.1.1. Olfactory Physiology

Insects posses two main types of chemoreceptor: those responsible for the detection of volatile substances, and those responsible for the detection of substances in aqueous solution. These two types of reception correspond to senses of smell (olfaction) and taste (gustation). The principal site of the olfactory receptors responsible for distance chemoreception in blowflies is the antennae, and in the absence of these organs olfactory responses are greatly reduced. Although the antennae also carry some contact chemoreceptors, these are found primarily on the ventral and ventro-lateral surfaces of the tarsi (Cragg and Cole 1956; Monita and Shiraishi 1985). Specialised contact receptors are also found on the ovipositor of female blowflies (Wallis 1962).

Olfactory chemosensilla have porous cuticles with thin (0.1-0.3μm) or thick (0.2-1.0μm) walls, and the distal part of the sensory cilium branches in some cases (Monita and Shiraishi 1985). They occur both on the surface of blowfly antennae, (Boeckh *et al.* 1965), and in pits below the surface level (Kaib 1974). Insect chemoreceptors are of many types, some of which are highly specialised to detect specific chemicals, while others are more general, and respond to a wider range of substances (Monita and Shiraishi 1985). Kaib (1974) identified nine distinct types of olfactory sensilla in pits on the antennae of *Calliphora vicina*, six of which responded to "meaty" odours, and three to "flowery" odours. The sensilla were insensitive to odours outwith their specialisation.

5.1.2. Fleece chemistry and susceptibility to blowfly strike

The principal component of the sheep fleece is the wool fibre, which consists of keratin, a protein which has a high sulphur content due to the presence of cystine. The fibre is coated with wool wax and suint. The wax contains cholesterol and lanosterol and various other organic compounds including carboxylic, fatty and

hydroxy-fatty acids, while suint is a water-soluble mixture of electrolytes such as potassium carbonate and sulphates, nitrogenous compounds such as ammonia and urea, and organic compounds including carboxylic, fatty, and amino acids. The fleece also contains epithelial debris, moisture and extraneous matter such as dirt, fungi and bacteria (Emmens and Murray 1982). Hydrogen sulphide has also been detected as a component of the fleece atmosphere of some living sheep. Additionally, the gas was found in weathered wool samples after incubation at 37°C, which suggests that it is produced as a result of bacterial activity (Cragg 1950b).

Hobson (1936b) found that there was no significant link between the parts of sheep particularly susceptible to blowfly strike, and the suint and grease content, and pH, of the fleece in those areas. Another study, however, has shown that female blowflies are attracted to some factor associated with wool (Cragg and Cole 1956). The factor did not disappear during storage and it was not completely removed by washing.

Although little research has been carried out to identify the attractive volatiles released by faecally soiled sheep, several experiments have looked at the release of such attractants by bacteria normally present in the fleece. Cragg (1956) incubated wool clippings at 38°C, and exposed them to blowflies, but recorded no oviposition on the incubated wool. Cragg therefore suggested that if bacterial odours are important as an oviposition stimulus then they must be associated with the skin of the sheep rather than the wool, but he also admitted that the quantity of wool used (approximately 6g per beaker) might produce insufficient quantities of the relevant volatiles to induce oviposition (Cragg 1956). Emmens and Murray (1982) developed cultures of several species of bacteria which had been found to be widespread in the fleeces of Australian Merino sheep, incorporated them into nutrient agar, and exposed them to captive populations of *Lucilia cuprina*. The blowflies often laid eggs in response to odours emanating from all four bacterial species used. *Enterobacter cloacae* and *Pseudomonas aeruginosa* did not appear to make use of fleece components in the production of oviposition stimulants, while *Bacillus subtilis* utilised compounds such as palmitic acid and *Proteus mirabilis* was found to degrade wool fibres to produce sulphurous compounds. In a further experiment, it was found that although extracts from unsterile sheep fleeces seeded with any of these four species of bacteria elicited very similar levels of oviposition after incubation for 24 hours, differences emerged as the length of incubation was increased (Emmens and Murray 1983). The highest levels of oviposition were observed on cultures of *E. cloacae* and *P. mirabilis* incubated for 96 hours, after which time these cultures had been

significantly contaminated by *P. aeruginosa*. Pure cultures of *P. aeruginosa* did not elicit high responses, but this species appeared to enhance the attractiveness of the other cultures to *L. cuprina* females.

Eisemann and Rice (1987), in another study using *L. cuprina*, also found a high degree of oviposition attraction associated with bacteria, in this case those involved in the degradation of meat. Their experiments showed that the presence of blowfly larvae in a bacterial culture provides substantial additional attraction, although larvae reared in sterile media had only a very small attractive effect. The attractive volatiles involved are kairomones rather than pheromones, as their effect was not restricted to *L. cuprina* larvae, but was also produced, with approximately equal effect, by larvae of the calliphorid species *Chrysomya megacephala* and *Ch. rufifacies*, and of the sarcophagid *Boettcherisca peregrina*. Larvae of *Calliphora augur* proved less attractive, and this may be due to the presence of different micro-organisms in the larval gut which produce less attractive, or even repellent, volatiles. There was no evidence that fly larvae actually secrete compounds attractive to gravid female blowflies, but they can enhance the attractive effect produced by micro-organisms acting on proteinaceous media. It has been found that oviposition kairomones for the screwworm fly *Cochliomyia hominivorax* are produced by micro-organisms in wounds, and these are also accentuated by the action of larvae (Hammack and Holt 1983).

5.1.3. Olfactory responses of *Lucilia sericata* and *Lucilia caesar*

A review of the olfactory responses of *Lucilia sericata* was published by Ashworth and Wall (1994). Some of the earliest investigations into the responses of *Lucilia sericata* to olfactory stimuli were carried out by Hobson (1935). It was demonstrated that various putrefying substances (particularly excreta of *Lucilia* larvae, but also faeces from scouring sheep, stale urine, and various bacterial cultures) caused *L. sericata* to oviposit on live sheep in the field, despite being unable to elicit oviposition when tested in the absence of sheep. Neither sheep skin, wool, nor other live animals could take the place of the sheep in initiating oviposition. Further experimental work showed that the use of indole, 3-methyl indole and ammonium carbonate could achieve a similar effect to the putrefying substances used previously (Hobson 1936a). Hobson postulated that the stimulus required for *L. sericata* to oviposit on sheep required a combination of two factors, one provided by the sheep itself, and the other by products of putrefaction. These were referred to, respectively, as the S-factor, and the P-factor. Hobson proposed that the S-factor caused attraction

over a distance while the P-factor stimulated oviposition by short-distance olfactory and tactile responses (Hobson 1936a, 1938). Cragg and Ramage (1945) found that blowflies were attracted to a moist clipped fleece, demonstrating that the "S-factor" was associated with some component of the fleece, and did not require a live animal. They suggested that the attractive effect could be due to the release of compounds containing sulphur, as breakdown products of cystine.

Cragg and Ramage (1945) also performed a chemical analysis on the substances found by Hobson to be attractive to blowflies. It was found that the most attractive substances were characterised by high levels of ammonia, sulphydryl groups (hydrogen sulphide), and in some cases indole and 3-methyl indole. In field trials on sheep, a solution of ammonium carbonate (0.1%) and ethanethiol (ethyl mercaptan) (0.002%) elicited oviposition from blowflies, while neither of these compounds alone could elicit oviposition at the concentrations used. Traces of hydrogen sulphide (0.0001%) increased the efficacy of the solution, allowing a halving of the ethanethiol concentration. Further field experiments using cylindrical traps baited with sheep wool and chemical attractants demonstrated that various mixtures of ammonium carbonate and hydrogen sulphide (some also containing indole) were successful in attracting females of *Lucilia caesar*, although very little oviposition took place. *L. sericata* was virtually absent from these field experiments, and the researchers suggest that this was due to differing responses between the two species. However, catches of *L. caesar* during simultaneous trapping with animal carcass bait were more than 20 times higher than those of *L. sericata*, suggesting that the *L. sericata* population in the area was very low.

Due to the prevalence of *Lucilia caesar* in the British Isles, this species was included in many studies of the olfactory responses of blowflies in the field. Cragg (1950b) investigated the attraction of various substances placed on pads attached to sheep, drawing a clear distinction (unlike Hobson) between those compounds which attracted flies to their source and those which elicited oviposition. Blowflies did not respond either to cystine or to cystine hydrochloride, but seven probable breakdown products of cystine all showed some attraction to females of *L. sericata* and *L. caesar*. The most attractive of the compounds were ethanethiol (ethyl mercaptan) and dimethyl disulphide, but none were able to induce oviposition unless ammonium carbonate was present. Tests with other ammonium compounds showed that ammonia itself acted as an attractant, but only elicited oviposition when combined with carbon dioxide (as ammonium carbonate or bicarbonate) (Cragg 1950b). It was later shown that ammonium carbonate and indole could induce a similarly large oviposition response when used with sheep wool while heating in a water bath

(Cragg 1956). A subsequent study of the chemosensilla on the ovipositor of *Phormia regina* showed that oviposition was stimulated when they came in contact with sodium chloride, sodium carbonate and ammonium carbonate (Wallis 1962).

The same seven organic compounds containing sulphur were tested in the field for attractancy to blowflies (Cragg and Thurston 1950). Two of them, ethanethiol (ethyl mercaptan) and dimethyl disulphide, proved to be powerful attractants for both *Lucilia caesar* (including *L. illustris*) and *L. sericata,* although only when mixed with each other or with hydrogen sulphide (which neither attracts flies when used alone, nor induces oviposition, but enhances the attractiveness of other compounds (Cragg and Ramage 1945)) or carbon dioxide. A combination of 0.2% ethanethiol solution and freshly prepared (saturated) hydrogen sulphide solution was shown to be a much stronger attractant than a combination of ammonium carbonate (20%), indole (0.12%) and hydrogen sulphide (saturated), which was used previously by Cragg and Ramage (1945). However, even this new chemical attractant was less effective than a meat bait in attracting *L. sericata, L. caesar, Calliphora vomitoria* and *C. vicina.* A range of other compounds, including several carbonates, ammonium hydroxide and indole, were found not to enhance the attractive effect of the organic compounds, although indole elicited oviposition, which was not achieved by any of the other substances tested (Cragg and Thurston 1950).

Cragg (1956) counted the number of *Lucilia sericata* and *L. caesar* attracted to mixtures of ammonium carbonate/indole and ethanethiol/hydrogen sulphide, which were exposed alternately. Although the learning responses of the flies (which will return to a site which was previously attractive) make interpretation of the results difficult, the experiment indicated that *L. sericata* had a preference for ammonium-type attractants and *L. caesar* for the sulphydryl mixture.

Cragg and Cole (1956) found that female (but not male) *Lucilia* were attracted to sheep wool. The highest degree of attraction was observed with fertilised females which had daily access to meat, but even in the absence of both fertilisation and meat some attraction still took place. The attraction was strongest for the British strain of *Lucilia sericata,* followed by *L. cuprina,* and a strain of *L. sericata* from the Danish countryside. Australian and urban Danish strains of *L. sericata* showed less attraction, and *L. illustris, L. caesar* and *Calliphora vomitoria* demonstrated little or no response. The authors suggested that a 'wool factor' exists, to which only certain strains of *L. sericata* and *L. cuprina* are specially sensitive.

5.1.4. Olfactory responses of *Lucilia cuprina*

Studies on the ovipositional responses of *Lucilia cuprina* to indole and ammonium carbonate showed that indole was an oviposition stimulant, except in the complete absence of carbon dioxide. Higher concentrations proved inhibitory in some circumstances. Oviposition responses were also observed to aqueous solutions of ammonium carbonate, reaching a peak with concentrations of 1-2%, and declining thereafter. The response to mixtures of carbon dioxide and air was independent of carbon dioxide concentration over a wide range (Barton Browne 1965).

Caged groups of gravid females of *Lucilia cuprina* flew upwind in response to sheep placed upwind of the cage, whereas no downwind flight was observed when the sheep were placed downwind of the cage. Sheep suffering from flystrike elicited the largest accumulation of flies on the upwind cage wall (46% of total), compared with infestation-free wet sheep (29%), and dry sheep (19%). Sheep proved to be considerably more attractive than man (which elicited a 14% response), and a bait-free response. Flies responded to struck sheep at a distance of 20 metres, whereas dry sheep were only attractive at 10 metres. It was concluded that *L. cuprina* is able to orient from a distance to volatile sheep kairomones, which are augmented by wetting or by the presence of an infestation of larval blowflies (Eisemann 1988).

5.1.5. Natural attractants as trap baits

The most commonly used attractant for blowfly traps is beef liver, or similar offal, which is often used with sodium sulphide solution (Mackerras *et al.* 1936; Norris 1966; Wall *et al.* 1992c). The sodium sulphide supplements the natural odour of the liver, acts as a preservative for the meat, and also prevents the development of blowfly larvae, should any eggs be laid on the bait.

A comparison of various natural baits as attractants for *Lucilia cuprina* found that sheep offal (liver and small intestine) resulted in the highest catches, followed by portions of sheep carcass and blended goat carcass. A solution of decomposing fish performed even more poorly. It was also found that the attractiveness of both sheep offal and blended goat declined when baits were used between 2 and 4 weeks of age rather than less than two weeks (Dymock and Forgie 1995).

5.1.6. Synthetic attractants as trap baits

A synthetic chemical attractant for the New World screwworm fly, *Cochliomyia hominivorax*, was developed by Jones *et al.* (1976). The formulation was based on earlier work by Grabbe and Turner (1973), who isolated the attractive components from decomposing blood previously prepared by DeVaney *et al.* (1973). Of the 35 components thus identified, 30 were compared in the field by Jones *et al.* (1976), and ten of the most attractive mixed as a chemical attractant, which became known as swormlure. This attractant was found to be better than liver for the attraction of male *C. hominivorax*, but not as good for the attraction of females. However, swormlure was much less attractive to other Diptera than liver, giving improved selectivity. Subsequently, an improved mixture, swormlure-2, was made by Coppedge *et al.* (1977), and this proved a more effective attractant than liver. Mackley and Brown (1984) formulated swormlure-4 by varying the proportions of the various components, further improving the performance of the attractant. The current formulation of swormlure consists of butan-2-ol (*sec*-butyl alcohol), 2-methylpropan-1-ol (*iso*-butyl alcohol), dimethyl disulphide, ethanoic acid (acetic acid), butanoic acid (butyric acid), pentanoic acid (valeric acid), phenol, 4-hydroxytoluene (*p*-cresol), benzoic acid, and 1-benzopyrrole (indole) (Mackley and Brown 1984).

Swormlure has also been used to bait traps for capture of the Old World screwworm fly *Chrysomya bezziana* (Spradbery 1981), and has recently been tested against the wound myiasis fly, *Wohlfahrtia magnifica* and the sheep blowfly *Lucilia sericata* in Hungary (Hall *et al.* 1995). The latter work showed swormlure-4 to have a highly significant positive effect on the catch of *L. sericata*, but no significant effect on the catch of *W. magnifica*. Traps baited with swormlure-4 caught 72 times as many *L. sericata* as unbaited traps. However, a field trial carried out in southwestern England subsequently showed that swormlure-4 was inferior as a trap bait to liver and sodium sulphide (Wall and Smith 1996). Targets baited with approximately 0.25-0.3 kilogrammes of liver with 10% (w/v) sodium sulphide solution showed very significantly higher catches than those baited with 10ml of swormlure-4 (dispensing at approximately 0.25ml per day).

5.1.7. Electrophysiological measurement of olfactory responses

Electrophysiological methods were first used for the measurement of olfactory responses in insects by Schneider (1957), who developed a procedure for measuring the responses of the silkworm moth *Bombyx mori* L. (lepidoptera: Bombycidae) to pheromones. Air containing the volatile compound was blown over an antenna to which an electrode had been connected, and the voltage changes between this electrode and a second, indifferent electrode connected to another part of the insect were measured. The technique, generating a signal known as a electroantennogram (EAG), measures changes in the potential difference between the two electrodes. In the same manner as an electroretinogram (ERG), the EAG includes the summed responses of a number of cells.

A study of electroantennograms of the New World screwworm fly, *Cochliomyia hominivorax*, showed that pentanoic acid elicited stronger responses than other straight-chain aliphatic carboxylic acids (given in doses of 1μg, followed by butanoic acid, and 4-methylpentanoic acid. Of other compounds tested, 3-methylindole elicited the highest responses when doses of 1μg were used, followed by 1-octen-3-ol, 3-methylphenol, 1-benzopyrrole (indole), phenol, and dimethyldisulphide. At doses of 1ng, the order of responses was 3-methylphenol, 3-methylindole, 1-octen-3-ol, dimethyldisulphide, and phenol (Cork 1994).

5.1.8. Aims and objectives

The aim of the present olfactory research was to investigate the responses of sheep blowflies to a variety of odour stimuli, both in the laboratory and in the field. The objective of the laboratory study was to record the electroantennogram responses of both *Lucilia caesar* and *L. sericata* to a variety of organic and inorganic compounds. Although a similar method has been used to investigate the responses of *Cochliomyia hominivorax* (Cork 1994), there is no published record of such electroantennographic studies having previously been conducted on *Lucilia* species. The objective of the field study was to compare the effectiveness of alternative baits with that of the standard bait, liver and sodium sulphide solution. The organic compounds tested in the electrophysiological study included the most volatile components of swormlure-4, which were chosen because of the findings of Hall *et al.* (1995) that the mixture was attractive to *L. sericata* in the field. For the same reason, swormlure-4 was one of the potential trap baits tested in the field.

5.2. Materials and Methods

5.2.1. Experimental Animals

The insects used in the physiological experiments were *Lucilia sericata* and *L. caesar* taken from the laboratory colonies described in section 4.2.1. However, no liver was supplied for at least three days immediately prior to the experiments, in order to ensure that oviposition did not take place, and that female flies therefore remained gravid when the experiments were carried out. Only female flies were used in the physiological experiments, because these are the main targets of control strategies, and because a study of *Cochliomyia hominivorax* had previously found no significant differences between the EAG responses of female and male flies (Cork 1994).

5.2.2. Preparation and dilution of potential stimulants

The preparation of swormlure-4 was carried out in advance of experimentation. All ten of the components were classified as irritants and as harmful. Additionally, phenol, 4-hydroxytoluene and butanoic acid were toxins, and phenol, 4-hydroxytoluene, and 1-benzopyrrole were carcinogens or suspected carcinogens. Protective clothing and equipment were therefore required. A laboratory coat with a disposable covering, nitrile gloves, safety glasses and a respirator (4251, 3M) were worn, and a fume cupboard was used for the pouring and mixing of the volatile substances. Those constituents of the mixture which were solid at room temperature: 1-benzopyrrole, benzoic acid, and 4-hydroxytoluene, were measured first, and placed in a large glass jar with a secure lid. The liquid components were then added: butan-2-ol, 2-methylpropan-1-ol, ethanoic acid, butanoic acid, pentanoic acid, phenol and dimethyl disulphide. The dimethyl disulphide was measured last, and the jar was then sealed and agitated to fully mix the contents and dissolve the solids. The mixture was then dispensed into small bottles (capacity 1l and 0.5l) for storage until required.

The dilution of potential stimulants was carried out in a laboratory, immediately prior to the recording of EAGs. Three dilutions: 10^{-1}, 10^{-3}, and 10^{-5}, were made of each compound. Solvent was first measured out into Eppendorf tubes, 360µl into one, and 396µl into each of two more, using a Gilson pipette. Using a new pipette tip, 40µl of the test chemical was removed from its container and placed in the first

Eppendorf tube. A fume cupboard and protective clothing were used for this procedure when necessary. The solution was then mixed well by repeated gentle removal and replacement of some of the contents using the pipette. A second Gilson pipette was used to place 4μl of the contents of the first tube into the second, and then 4μl of the contents of the second into the third, mixing thoroughly on each occasion. New pipette tips were used for each dilution, and this procedure was repeated for each test chemical. When not in use, the Eppendorf tubes were closed and refrigerated to prevent any evaporation of the contents.

5.2.3. Equipment used to stimulate and measure EAGs

A diagrammatic representation of the equipment used for the recording of EAGs is shown in Figure 5.1. The site at which the biological preparation was mounted was surrounded by a Faraday cage, a metal frame with wire mesh attached on top and on three sides. This was intended to reduce electrical interference.

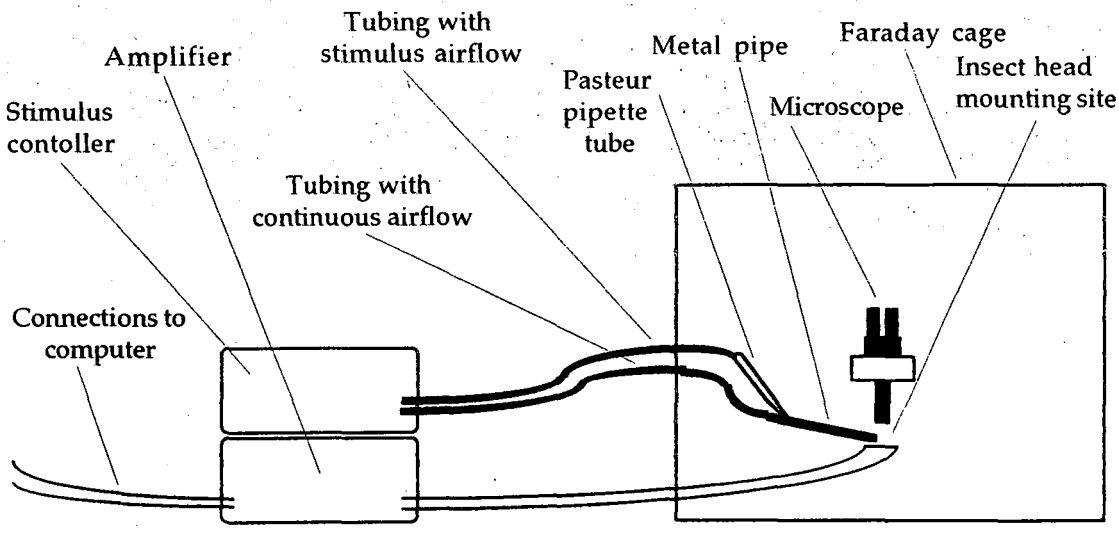


Figure 5.1: Diagram showing apparatus for stimulation of EAGs

The stimulation of electroantennograms (EAGs) was carried out by a Stimulus Controller (Syntech CS-05). This provided a continuous airflow through rubber tubing and, when activated by a foot pedal or button, diverted some of the air through a second piece of tubing, to which a glass Pasteur pipette tube (John Poulteen Ltd., Barking, Essex) was attached. The tip of the pipette tube was inserted into a hole in a metal pipe (about 100mm in length and 8mm in external diameter) through which the continuous airflow passed. The airflow at the end of the metal pipe remained constant, regardless of whether some air was being diverted through the pipette tube. This mechanism theoretically allowed vaporised chemicals in the

pipette tube to be blown onto a biological preparation placed at the end of the metal pipe, without the overall rate of airflow being affected. Any electrical response recorded could therefore be interpreted as a response to the vaporised chemicals rather than to mechanical stimulation due to changes in the airflow.

Two glass electrodes, formed by pulling a capillary tube (as described in Section 4.2.2) to produce a fine point, were used in these experiments. Both were filled, using a hypodermic syringe, with Beadle-Ephrussi Ringer solution, which had been prepared in advance in a glass flask. This solution consisted of 0.75g of sodium chloride, 0.035g of potassium chloride, and 0.29g of calcium chloride, dissolved in 100ml of water. It was kept stoppered in a refrigerator when not in use, and replaced every 1-2 days.

Recording of EAGs was facilitated by an AC/DC amplifier (Syntech UN-05), which was connected to the electrodes. The amplified signal was then supplied to a Personal Computer and processed by the Syntech EAG analysis program. Use of the foot pedal or button to deliver the potential stimulus simultaneously initiated the recording procedure. The program displayed the signal initially as a graph of the changes in potential difference between the two electrodes over time, and could also show the maximal responses in histogram form, either unadjusted or adjusted with regard to a standard. This latter form of display enabled account to be taken of declining responses over time.

5.2.4. Experimental procedure

Before starting an experiment, an individual female fly was removed from its cage and placed in a small plastic container which was then cooled in the freezer compartment of a refrigerator for 3-4 minutes in order to anaesthetise the fly. Following this the fly's head was removed using a scalpel, and mounted on one of the glass electrodes, with the tip of the electrode positioned in the wound caused by decapitation. The microscope was used to accurately position the electrodes. Using micromanipulators, the second electrode was manipulated into position so that the tip of the first flagellomere of one antenna was in contact with the electrolyte. Figure 5.2 illustrates a typical calliphorid antenna, and Figure 5.3 shows the attachment of a fly head to the apparatus. The end of the metal air pipe was positioned to point directly at the preparation, at a distance of about 10mm from it.

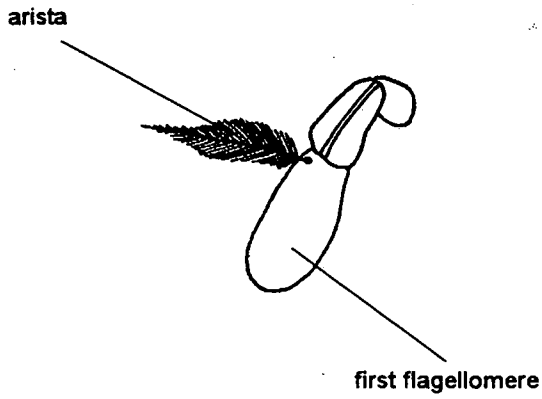


Figure 5.2: A typical calliphorid antenna.

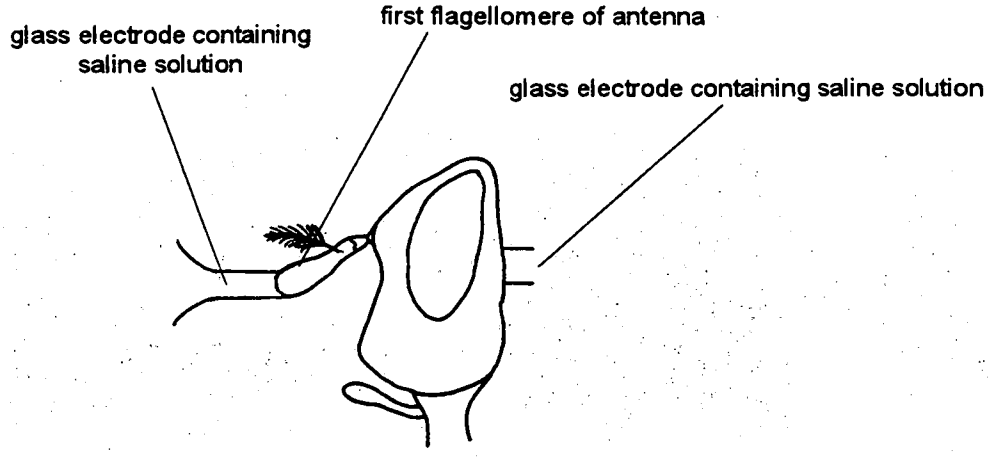


Figure 5.3: A fly head attached to the EAG apparatus.

The preparation was then left for at least three minutes to allow it to stabilise. If after that time an approximately steady baseline with little noise had not been obtained, the preparation was abandoned, and a new fly used. An empty Pasteur pipette tube was then attached, and the foot pedal depressed to record the response of the preparation to air alone. Although the design of the apparatus theoretically prevented any change in airflow, in practice some change, resulting in a response by the insect, was always recorded.

A predetermined sequence of potential stimulants was then used. In each experiment the first used was the solvent alone, followed by three concentrations of a chemical or mixture: 10^{-5}, 10^{-3}, and 10^{-1}. Other test chemicals then followed, with the same three concentrations used for each, and in each case preceded by the

solvent. A small piece of glassfibre (GF/C, Whatman, Maidstone, Kent), cut with scissors to measure approximately 12x4mm, was placed in each Pasteur pipette tube using forceps, and 10µl of solvent or diluted chemical was applied to it using a Gilson pipette. The same volume was used in each case, and a different Pasteur pipette tube was used for each concentration of each chemical. The pipette tube was attached to the rubber tubing, as rapidly as possible in order to minimise loss of volatiles, and its tip placed in the metal pipe. Following a time period of about 40 seconds, to give the contents time to vaporise, the foot pedal was depressed to initiate stimulation and recording. The resulting graph was then inspected on the monitor. If the maximum response appeared to have been distorted by other electrical signals from the fly, such as those caused by movement of the antennae, the size of the maximum was adjusted using the computer program. Occasionally, where the graph had been so severely distorted that the correct level of the response to the stimulus could not be accurately determined, the recording was discarded, and the stimulus repeated.

Tests were carried out using several potential solvents. The responses of six female *Lucilia sericata* to three solvents suitable for organic compounds: hexane, ethanol (80%), and paraffin oil, were tested, by following the experimental procedure described above with 10µl of the test solvent in each case. A fourth solvent, water, was also tested in the same way. The responses of the flies are recorded in Table A4.1 of Appendix 4, which shows the initial response to an air pulse, the response to a pulse containing the solvent, given 40 seconds later, and the response to a second pulse containing the solvent, given 160 seconds after that, in order that any general decline in the responses of the fly could be adjusted for. After adjustment (see below), hexane was found to elicit a mean response of 133.1%, relative to the pure air pulse, ethanol 96.7%, paraffin oil 101.0%, and water 104.3%. The response to hexane was regarded as unacceptably high, so this was discarded. Paraffin oil was also discarded, with one exception described below, due to the low solubility of several of the organic compounds in this substance. Ethanol was therefore chosen as the solvent for the experiments involving organic compounds, and water for the experiment involving inorganic compounds.

In the first two laboratory experiments the substances tested were eight organic compounds, and the mixture swormlure-4. Seven of the compounds tested were the most volatile of the constituents of swormlure-4: butan-2-ol (*sec*-butyl alcohol), 2-methylpropan-1-ol (*iso*-butyl alcohol), dimethyl disulphide, ethanoic acid (acetic acid), butanoic acid (butyric acid), pentanoic acid (valeric acid), and phenol (Mackley and Brown 1984), and the eighth was 2-mercaptoethanol (2-hydroxyethyl

mercaptan). The compounds were assigned at random to the two experiments, 5.1 and 5.2, which were each conducted six times, and ethanol was used as the solvent in both cases. Because dimethyl disulphide was incompletely soluble in ethanol, an additional test was carried out using dimethyl disulphide in paraffin oil.

Experiment 5.3 included beef liver extract, and two inorganic compounds: sodium sulphide and ammonium sulphide. Each was tested alone, and then the two sulphide compounds were tested in turn in combination with the liver extract (using 5µl of sulphide plus 5µl of liver extract). Water was used as the solvent, and the experiment was conducted six times.

5.2.5. Data analysis

All three experiments (and the test of solvents which preceded them) were analysed by adjusting the electroantennogram measurements for the decline in the overall responses of the flies to stimuli. The use in these experiments of blowfly heads, with the thorax and abdomen removed, resulted, in most cases, in a rapid decline in responses over the course of each experimental replicate. The effect of this decline on the data was removed as far as possible, by adjusting each figure by a factor proportional to the difference between two successive measurements for pulses of solvent in the absence of other stimuli. The formula for the calculation of such an adjusted figure, a, is shown below:

$$a = n\left(\frac{x}{f(x-y)+y}\right)$$

where: n = unadjusted EAG response
x = preceding response to solvent
y = subsequent response to solvent

and f = time between readings x and n, as a proportion of time between x and y. For example, $f = 0.75$ for the third of a set of three readings.

This method of adjustment is the same as that used by the by the Syntech EAG analysis program, but in this case was carried out by a spreadsheet created in Claris Works 2.0, running on an Apple Macintosh LC475, in order to allow the calculation of standard errors. All the adjusted data were then expressed as proportions of the first response measured to solvent. Finally, the adjusted data were analysed by

ANOVA using GENSTAT 5 (Release 3.3 for Windows), with replicate number as a blocking factor and substance and concentration as treatment factors. For the purposes of this analysis, the data from Experiments 5.1 and 5.2 were pooled.

5.2.6. Field experimentation

Two field experiments were carried out to compare the responses of *Lucilia caesar* to various olfactory stimuli used as trap baits. Experiment 5.4 included three different baits, the standard attractant: liver and sodium sulphide solution, a vegetable protein mixture supplied with the Fly City® commercial trap, and the chemical mixture swormlure-4. Each bait was tested using both a horizontal adhesive target, and Fly City® (as described in sub-section 3.2.1), giving six combinations of bait and trap in total. All traps were mounted on fenceposts, at a height of approximately 400mm. In the case of traps baited with swormlure-4, the standard plastic bait containers were replaced with narrow glass containers (capacity 150ml), to avoid the possibility of a plastic container being dissolved by the organic compounds in the mixture. Safety precautions were taken while dispensing swormlure-4 in the field, including the wearing of nitrile gloves and safety glasses. One replicate of this experiment was conducted, in August and September 1995.

Experiment 5.5 was a comparison of the response to liver and sodium sulphide solution with that to liver alone, liver with ammonium sulphide solution, and to both sulphides in the absence of liver. In every case, the sulphides were used at concentrations of approximately 10% w/v, and horizontal adhesive targets, at ground level, were used as described in sub-section 3.2.1. Two replicates were used, and the experiment was conducted during August and September 1996.

Both experiments were carried out at the site detailed in sub-section 3.2.2, using Latin square designs as described in sub-section 3.2.4. The trap arrangements are shown in Appendix 4. The results were analysed by ANOVA using GENSTAT 5 (Release 3.2 for Windows), and target means compared using Duncan's new multiple-range test (sub-section 3.2.5).

5.3. Results

5.3.1. Electroantennograms

A typical electroantennogram (EAG) is illustrated in Figure 5.4. This was recorded from a female *Lucilia sericata* stimulated with ammonium sulphide solution at a concentration of 10^{-3}. Electroantennogram data for all three experiments is tabulated in Appendix 4. The mean response of *L. caesar* females to three concentrations of butan-2-ol is shown in Figure 5.5, in order to illustrate the change in response with increasing concentration.

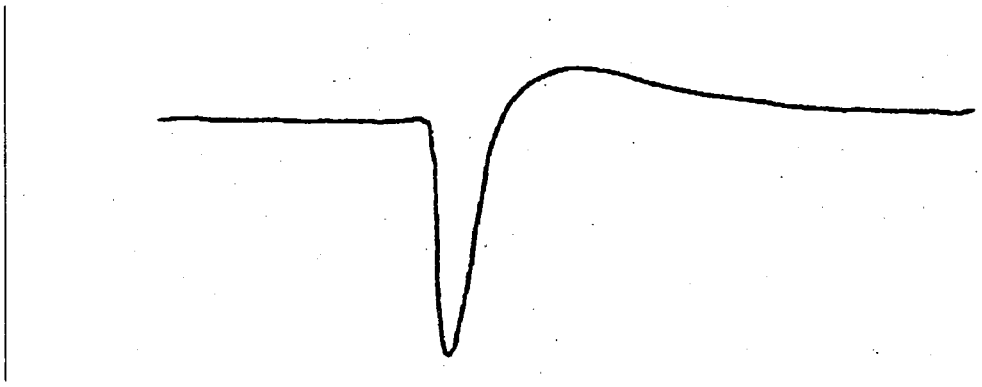


Figure 5.4: A typical electroantennogram (EAG), recorded from a female *Lucilia sericata* stimulated with ammonium sulphide solution at a concentration of 10^{-3}.

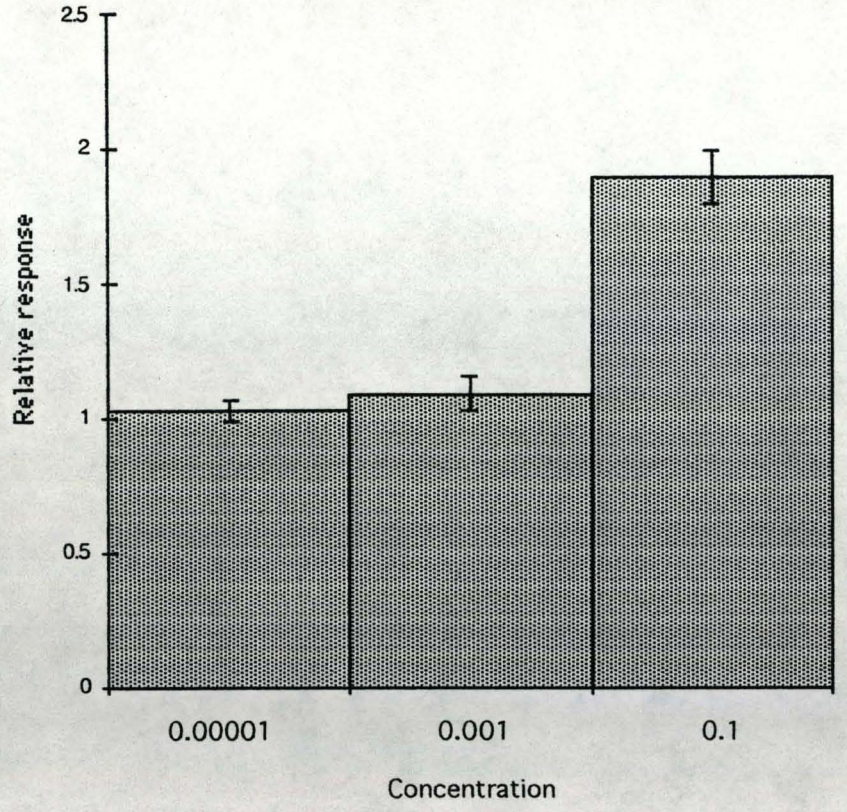


Figure 5.5: Mean electroantennogram (EAG) responses of six *Lucilia caesar* females to butan-2-ol at three different concentrations as adjusted proportions of the response to solvent (ethanol) alone.

The means of the adjusted results of experiments 5.1 and 5.2 are tabulated, with standard errors, in Tables 5.1 (*Lucilia caesar*) and 5.2 (*L. sericata*). Some of the results are also presented graphically: Figures 5.5 and 5.6 show the mean responses of both species to stimuli of the highest concentration (10^{-1}). The differences between the resposes to the various compounds and mixtures tested were shown by ANOVA to be highly significant, both for *L. caesar* ($n=162$; $F=40.69$; $P<0.001$) and for *L. sericata* ($n=162$; $F=22.8$; $P<0.001$). Among the individual organic compounds, at every concentration the highest response in both species was to dimethyl disulphide. At 10^{-5}, this was followed in *L. caesar* by butanoic acid, phenol, pentanoic acid, and 2-mercaptoethanol; the remaining compounds not eliciting significant responses. In *L. sericata*, the next highest responses were produced by ethanoic acid (although this

result was not significant), pentanoic acid, and phenol. At 10^{-3}, all the compounds except ethanoic acid resulted in a significant response from *L. caesar*, with the order remaining similar. *L. sericata* responded at a significant level to all stimuli except butan-2-ol and 2-mercaptoethanol, with butanoic acid producing the second largest mean electroantennogram. At the highest concentration, all of the compounds evoked a significant response in *L. caesar*, with the responses to butan-2-ol and 2-methylpropan-1-ol following dimethyl disulphide in magnitude. Butanoic acid and 2-methylpropan-1-ol hold the equivalent positions with regard to *L. sericata*, which responded significantly in every case, although negatively in the case of 2-mercaptoethanol.

Swormlure-4 produced a significant response in both species at every concentration, and at 10^{-1} (and at the 10^{-3} in the case of *Lucilia caesar*), the mixture evoked a greater response than that to dimethyl disulphide alone, although this difference was not significant.

Compound/ Mixture	Concentration					
	10^{-5}	S.E.	10^{-3}	S.E.	10^{-1}	S.E.
butan-2-ol	1.031	0.036	1.093	0.062	1.892	0.098
2-methylpropan-1-ol	1.030	0.031	1.131	0.091	1.619	0.091
dimethyl disulphide	1.275	0.064	1.668	0.153	2.999	0.324
ethanoic acid	1.050	0.059	1.009	0.044	1.124	0.100
butanoic acid	1.161	0.075	1.343	0.115	1.289	0.115
pentanoic acid	1.078	0.030	1.250	0.034	1.298	0.031
phenol	1.138	0.032	1.192	0.054	1.406	0.060
2-mercaptoethanol	1.078	0.055	1.107	0.051	1.282	0.075
swormlure-4	1.144	0.053	1.737	0.099	3.522	0.231

Table 5.1: Mean electroantennogram (EAG) responses of six *Lucilia caesar* females to eight organic compounds and swormlure-4 (Experiments 5.1 and 5.2) as adjusted proportions of the response to solvent alone. The solvent was ethanol in each case.

Compound/ Mixture	Concentration					
	10^{-5}	S.E.	10^{-3}	S.E.	10^{-1}	S.E.
butan-2-ol	0.986	0.021	1.009	0.022	1.129	0.081
2-methylpropan-1-ol	0.968	0.031	1.157	0.066	1.255	0.103
dimethyl disulphide	1.159	0.037	1.376	0.103	1.908	0.103
" " *	1.299	0.041	1.771	0.053	2.554	0.141
ethanoic acid	1.060	0.085	1.127	0.058	1.120	0.054
butanoic acid	1.029	0.087	1.265	0.055	1.297	0.035
pentanoic acid	1.056	0.026	1.175	0.027	1.203	0.025
phenol	1.041	0.035	1.054	0.046	1.094	0.047
2-mercaptoethanol	1.020	0.066	0.986	0.038	0.895	0.033
swormlure-4	1.061	0.055	1.364	0.086	2.182	0.210

Table 5.2: Mean electroantennogram (EAG) responses of six *Lucilia sericata* females to eight organic compounds and swormlure-4 (Experiments 5.1 and 5.2) as adjusted proportions of the response to solvent alone. The solvent was ethanol except for * where paraffin oil was used.

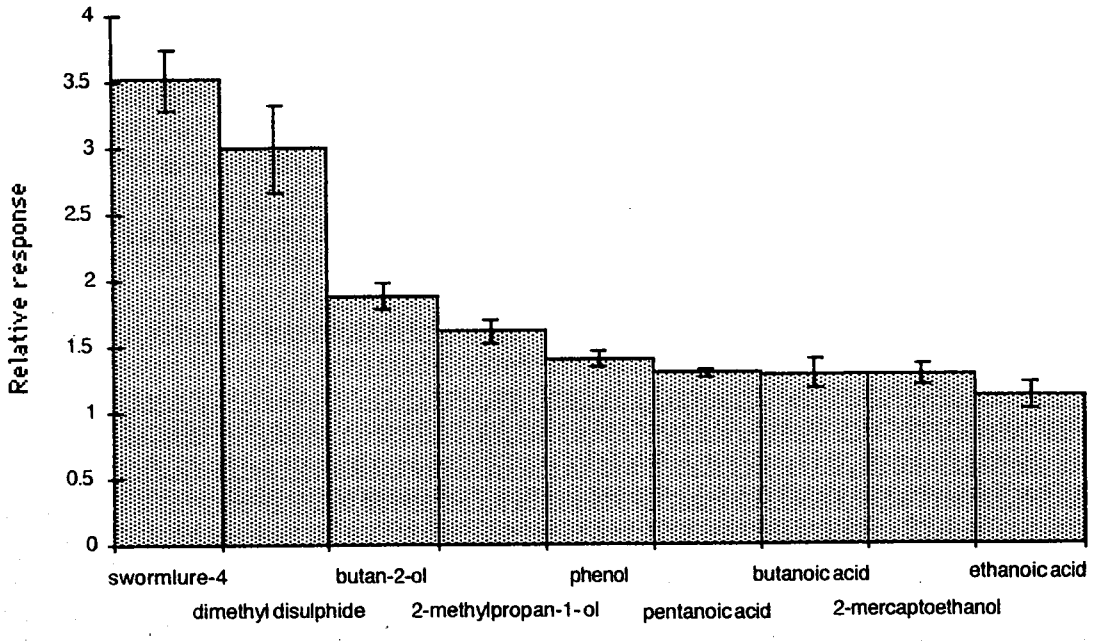


Figure 5.6: Mean electroantennogram (EAG) responses of six *Lucilia caesar* females to eight organic compounds and swormlure-4 as adjusted proportions of the response to solvent alone. Solute concentration 10^{-1} in each case.

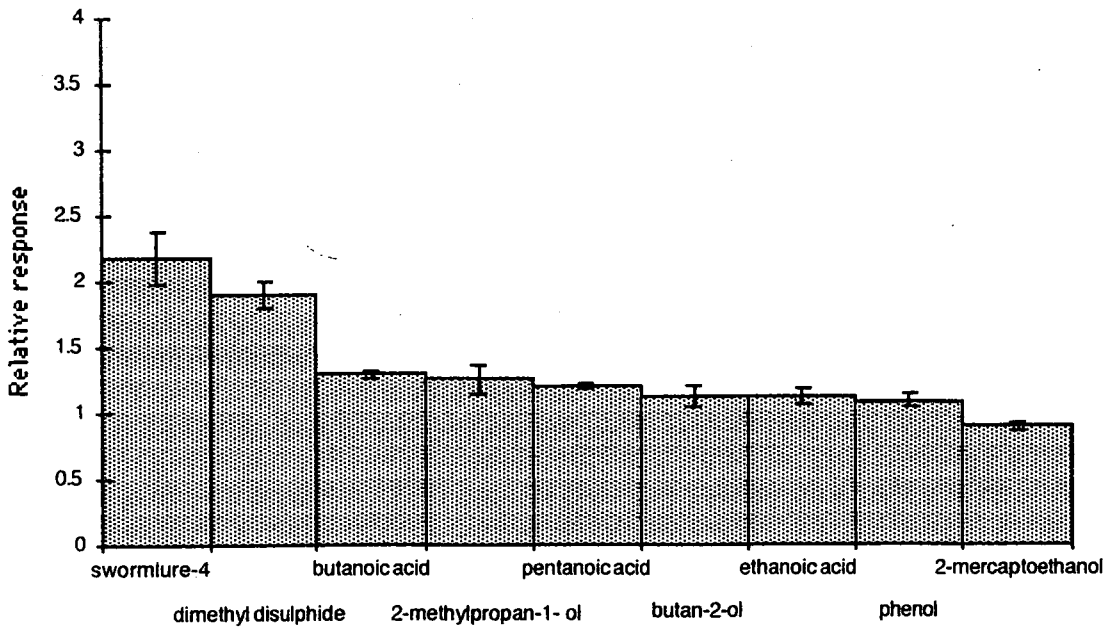


Figure 5.7: Mean electroantennogram (EAG) responses of six *Lucilia sericata* females to eight organic compounds and swormlure-4 as adjusted proportions of the response to solvent alone. Solute concentration 10^{-1} in each case.

The mean responses recorded in Experiment 5.3, with standard errors, are contained in Tables 5.3 (*Lucilia caesar*) and 5.4 (*L. sericata*). Figures 5.8 and 5.9 show the mean responses of both species to stimuli of the highest concentration (10^{-1}) in a graphical form. The differences between the resposes to the various compounds and mixtures tested were shown by ANOVA to be highly significant, both for *L. caesar* (n=90; F=5.19; *P*=0.001) and for *L. sericata* (n=90; F=41.61; *P*<0.001). At the lowest concentration used, *L. caesar* females gave the greatest responses to liver extract with ammonium sulphide, followed by liver extract with sodium sulphide, and then by sodium sulphide alone. The greatest responses by *L. sericata* females were to liver extract with sodium sulphide, followed by liver extract with ammonium sulphide, and then by ammonium sulphide alone. At the highest concentration, the two species show a much more similar pattern of responses, with ammonium sulphide eliciting the highest responses, followed by liver extract with ammonium sulphide, and then by liver extract with sodium sulphide.

Compound/ Mixture	Concentration					
	10^{-5}	S.E.	10^{-3}	S.E.	10^{-1}	S.E.
liver extract	1.019	0.070	1.297	0.156	1.745	0.181
sodium sulphide	1.087	0.076	1.185	0.120	1.498	0.194
ammonium sulphide	1.027	0.046	2.204	0.598	4.140	1.465
liver extract + sodium sulphide	1.202	0.079	1.242	0.053	1.887	0.288
liver extract + ammonium	1.298	0.101	1.644	0.216	3.929	0.806

Table 5.3: Mean electroantennogram (EAG) responses of six *Lucilia caesar* females to liver extracts and sulphides (Experiment 5.3) as adjusted proportions of the response to solvent alone. The solvent was water in each case.

Compound/ Mixture	Concentration					
	10^{-5}	S.E.	10^{-3}	S.E.	10^{-1}	S.E.
liver extract	0.983	0.041	1.041	0.044	1.148	0.032
sodium sulphide	0.980	0.023	1.015	0.031	1.168	0.040
ammonium sulphide	1.063	0.022	1.125	0.035	1.680	0.098
liver extract + sodium sulphide	1.127	0.032	1.112	0.028	1.424	0.057
liver extract + ammonium	1.097	0.034	1.132	0.026	1.583	0.068

Table 5.4: Mean electroantennogram (EAG) responses of six *Lucilia sericata* females to liver extracts and sulphides (Experiment 5.3) as adjusted proportions of the response to solvent alone. The solvent was water in each case.

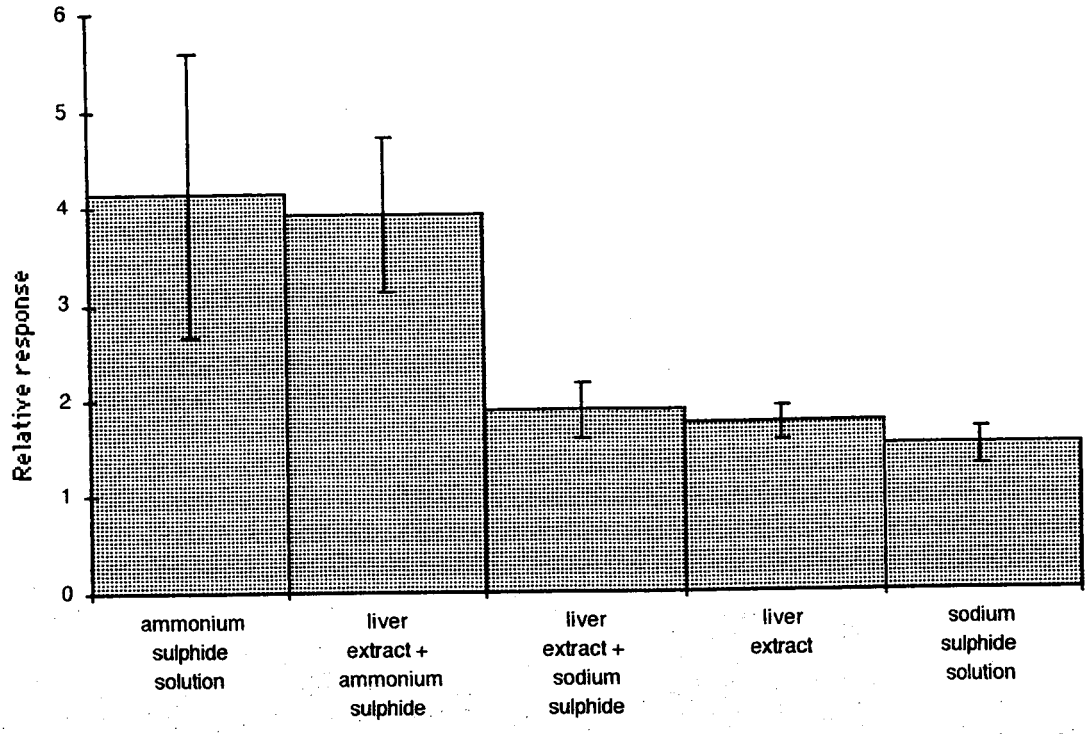


Figure 5.8: Mean electroantennogram (EAG) responses of six *Lucilia sericata* females to liver extracts and sulphides as adjusted proportions of the response to solvent alone. Solute concentration 10^{-1} in each case.

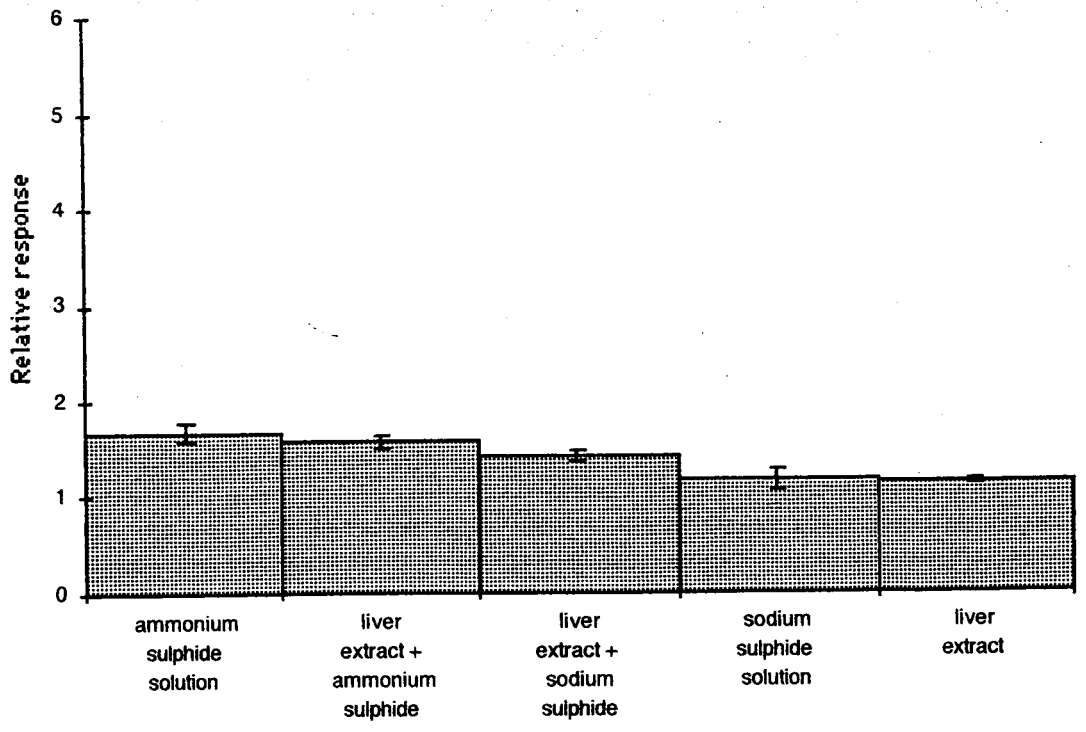


Figure 5.9: Mean electroantennogram (EAG) responses of six *Lucilia sericata* females to liver extracts and sulphides as adjusted proportions of the response to solvent alone. Solute concentration 10^{-1} in each case.

5.3.2. Field experiments

Experiment 5.4 showed highly significant differences between the attractive powers of the baits used, for both female *Lucilia caesar* group ($F=14.77$, residual $df=20$, $P<0.001$) and male *L. caesar* ($F=6.42$, residual $df=20$, $P=0.001$). Trap means are shown in Table 5.5 The horizontal adhesive target produced significantly higher catches than any other trap and bait combination, both of *L. caesar* group females, and of *L. caesar* males ($P<0.01$).

Trap type and bait	Females			Males		
	detransformed	transformed		detransformed	transformed	
Horizontal adhesive Liver+sodium sulphide	25.5	1.424	b	1.8	0.448	b
Horizontal adhesive Protein bait	0.4	0.159	a	0.0	0.000	a
Horizontal adhesive Swormlure-4	0.9	0.280	a	0.0	0.000	a
Fly City® Liver+sodium sulphide	1.6	0.421	a	0.0	0.000	a
Fly City® Protein bait	0.6	0.209	a	0.0	0.000	a
Fly City® Swormlure-4	0.0	0.000	a	0.0	0.000	a

Table 5.5: Mean catches of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets with five different baits. Standard Errors of Difference (for transformed data) 0.189 (females) and 0.102 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

Experiment 5.5 also demonstrated a significant effect of trap bait on catches. *Lucilia caesar* group ($F=32.02$, residual $df=28$, $P<0.001$) and male *L. caesar* ($F=3.07$, residual $df=28$, $P=0.032$). Target means are shown in Table 5.6. In the case of *L. caesar* group females, targets baited with liver and sodium sulphide solution captured

significantly higher numbers than any other bait ($P<0.05$). Those baited with liver alone, and with liver and ammonium sulphide performed significantly better than those baited with sulphide solutions in the absence of liver ($P<0.05$). The results for male *L. caesar* showed a similar pattern, although the only significant difference was that catches using ammonium sulphide solution only were lower than those using all other baits ($P<0.05$).

bait	Females			Males		
	detransformed	transformed		detransformed	transformed	
Liver	14.1	1.180	b	1.1	0.324	b
Sodium sulphide	2.5	0.543	a	0.5	0.186	ab
Ammonium sulphide	1.3	0.358	a	0.2	0.090	a
Liver + sodium sulphide	21.3	1.348	c	1.2	0.348	b
Liver +ammonium sulphide	7.2	0.912	b	0.7	0.243	ab

Table 5.6: Mean catches per square metre of *Lucilia caesar* (*L. caesar* group in the case of females) on horizontal targets with five different baits. Standard Errors of Difference (for transformed data) 0.104 (females) and 0.085 (males). Means marked with the same letter are not significantly different (Duncan's new multiple-range test, $P<0.05$).

5.4. Discussion

5.4.1. Electroantennograms

Some caution must be exercised in the interpretation of electroantennographic data, because the responses which are measured are purely physiological, and are not necessarily directly related to the behaviour of the insect under investigation. The same experimental procedure can be used to investigate repellent compounds (for example, Ntebela 1994), and the measurement of EAGs alone only reveals the relative size of the physiological response, not whether a particular compound is attractant or repellent. Nevertheless, electrophysiological studies have proved useful in the identification of attractant compounds in other types of insect, particularly pheromones in Lepidoptera (for example, Moorhouse *et al.* 1969), and Coleoptera (Cork *et al.* 1991), and kairomones in Diptera such as tsetse flies (Hall *et al.* 1984; Bursell *et al.* 1988).

Of the organic compounds tested in the present study, the largest responses of both species of *Lucilia* were to dimethyl disulphide. This is a volatile compound which was added to the original swormlure formulation to produce swormlure-2, which proved more attractive to New World screwworm fly, *Cochliomyia hominivorax*, than its predecessor (Coppedge *et al.* 1977), and the compound remains part of the present mixture, swormlure-4 (Mackley and Brown 1984). At the highest concentration, the two most volatile components of swormlure-4, the isomers butan-2-ol and 2-methylpropan-1-ol, also elicited high response levels in *L. caesar*. Swormlure-4 itself proved to be highly stimulatory for both species, and at the highest concentration evoked higher responses than any of its components.

This study included three aliphatic carboxylic acids: ethanoic acid (C2), butanoic acid (C4), and pentanoic acid (C5). Of these, butanoic acid elicited the highest responses in most cases, and at certain concentrations this compound (and to a lesser extent, pentanoic acid) proved highly stimulatory relative to the other organic compounds tested. Ethanoic acid was found to elicit comparatively low responses. These findings are similar to those of Cork (1994), who found that *Cochliomyia hominivorax* produced responses to pentanoic acid and butanoic acid which were significantly higher than those to other straight-chain carboxylic acids.

At high concentrations, ammonium sulphide was found to result in much higher responses than sodium sulphide, liver extract, or either of the combinations containing liver extract and sulphides. At the lowest concentration, however, the liver extract appeared to enhance the response to the sulphides, with the two combinations of liver extract and sulphides providing the greatest stimulus to both species. As concentrations of wind-borne odours detected by blowflies in the field are likely to be relatively low, the results suggest that the inclusion of liver may be of importance for trap baits.

The relative levels of response to the various test compounds was different at each concentration used. This phenomenon has also been recorded in *Cochliomyia hominivorax* (Cork 1994), and may be related both to the characteristics of individual sensory cells, and to the number of cells adapted for the detection of a particular substance. A cell may have a range of concentrations resulting in corresponding levels of stimulation, beyond the upper threshold of which the cell either 'fires' at a maximal level, or ceases to respond at all. Chemicals which a relatively low number of cells are adapted to detect may not produce increases in response proportional to increases in concentration once a certain saturation point has been reached. The responses of *Lucilia sericata* to 2-mercaptoethanol, which were found to decline as the concentration increased, may be an extreme example of such activity. Another factor to be considered is that the potential stimulants were always supplied to the flies in order of increasing concentration, and therefore the insects might have become habituated to substances which normally elicit responses at low concentrations.

The choice of solvents for this study was made by preliminary testing of several available compounds. Previous studies of insect EAG responses have often used a volatile solvent such as hexane, which is often removed from the test compound prior to experimentation by the use of a preliminary pulse (for example, Cork 1994). It was not possible to use this procedure in the present study because there would inevitably be some loss of the test compound at the same time, and this could not be quantified without the availability of gas chromatography equipment. The alternative is to use a non-volatile solvent such as paraffin oil (Den Otter *et al.* 1991), but this proved unsuitable for general use, due to the insolubility in it of certain of the organic test compounds. Ethanol (80%) was chosen as it did not elicit any significant response from the experimental insects, and fully dissolved all the organic compounds except dimethyl disulphide. Despite the solubility problem with dimethyl disulphide in ethanol, the responses to the compound proved to be similar when tested in paraffin oil. In the case of the inorganic compounds, water, a relatively non-volatile solvent, was used. There is no record of this compound

having previously been employed in experiments of this type, but it did not elicit a significant electroantennographic response in *Lucilia*, and was successfully used in the present study.

The technique used in these experiments for the supply of potential stimulants to experimental insects is similar to that used in other electroantennographic studies (for example, Evans and Allen-Williams 1992). One potential problem with the method is that some evaporation takes place before testing, and that the rate of this evaporation is greater in the case of more volatile compounds. When gas chromatography can be conducted, the extent of any loss can be measured, and adjustments made to eliminate it (Cork 1994), but this facility was not available during the present study. However, the loss of test compounds is much greater when a preliminary pulse is given to remove solvent prior to the exposure of an experimental insect (for example, Cork 1994), but this procedure was not carried out in the present study, and the loss of volatile substances was minimised by the rapid connection of the Pasteur pipette to the rubber tubing.

5.4.2. Relationship between physiological and behavioural responses

Field studies of the responses of *Cochliomyia hominivorax* (for example, Jones *et al.* 1976) to potential attractants produced results which differed in some respects from those obtained using EAGs (Cork 1994). Similarly, the turnip moth *Agrotis segetum* (Schiff.) (Lepidoptera: Noctuidae), has been found to respond differently in behavioural experiments than in those involving electroantennograms (Van der Pers and Löfstedt 1986). One compound which has been found to be vital for good attraction of female moths elicited almost no response in an EAG recording from males. One explanation of this discrepancy appeared to be the relatively low number of sensory cells responding to the compound. Although the sensitivity of these cells was not low, their scarcity resulted in a minimal effect on the EAG, and the compound concerned would not have been proposed as a pheromone component on the basis of EAG measurements. In contrast, two other compounds evoked substantial EAG responses, due to the presence of relatively large numbers of receptor cells, despite causing inhibition of male moths in behavioural experiments. Electroantennograms therefore have some limitations in predicting the behavioural responses of an insect.

Further complication in the use of physiological data to predict insect behaviour is interactions occur between the responses to different attractant components

(Priesner 1986). The responses of *Polia pisi* L. (Lepidoptera: Noctuidae) to four pheromonal compounds was found to vary greatly depending on the relative levels of the chemicals (Priesner 1980). In certain situations attractive compounds can even become inhibitory. Palaniswamy *et al.* (1983) found that the pheromone component (Z)-9-dodecenyl acetate was synergistic for the red-backed cutworm moth, *Euxoa ochrogaster* (Gunee) (Lepidoptera: Noctuidae), at levels of 0.2-0.3% relative to the major pheromone component. However, at the level of 1% the compound proved inhibitory.

Inhibitory effects of attractants when used at high concentrations have also been observed in blowflies. A study of the ovipositional responses of *Lucilia cuprina* in response to the oviposition stimulants indole and ammonium carbonate found that both compounds could inhibit oviposition once a certain concentration was reached (Barton Browne 1965).

Previous research has also illustrated the importance of considering the relative volatility of compounds used to stimulate electroantennograms. A comparison of the behavioural and electrophysiological responses of the moth *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) found that phytol, while an important behavioural stimulant, nevertheless failed to elicit large electroantennograms (Anderson *et al.* 1993). The explanation for this appeared to be the low volatility of the compound, and it was suggested that a more correct comparison would attempt to equalise the number of molecules emitted in each stimulatory pulse, rather than simply applying the same volume of each compound.

Although the present electrophysiological study provided indications of potential attractants, the complex relationship between physiological and behavioural responses necessitated the subsequent use of field studies. The electrophysiological data suggested that swormlure-4, and its components, particularly dimethyl disulphide, were potential attractants for both *Lucilia caesar* and *L. sericata.* Ammonium sulphide, either alone or with liver, was also identified as a potential attractant. However, the behavioural studies in the field would determine whether any of these substances and mixtures provided a level of attraction greater than or comparable to that of the standard attractant, liver with sodium sulphide solution.

5.4.3. Behavioural responses in the field

Experiment 5.4 showed liver and sodium sulphide to be a significantly better attractant than either of the other. That the vegetable protein bait supplied with Fly City® proved ineffective is unsurprising, as this bait was not formulated for the attraction of carrion-feeding flies such as *Lucilia*, and would be expected to be more attractive to flies with a preference for decaying vegetable matter. Indeed, during the course of the experiment, this bait was observed to attract other types of fly, particularly those of genus *Muscina* (Diptera: Muscidae). Swormlure-4 was developed for the screwworm fly, *Cochliomyia hominivorax*, another calliphorid, and it is now the standard attractant for that species. However, one of the aims during the formulation of swormlure was to reduce catches of other dipteran species, known as "trash" flies, and this includes blowflies such as *Lucilia* (Jones *et al.* 1976; Mackley and Brown 1984). Although swormlure-4 has been shown to attract *L. sericata* in conjunction with electric grid traps in Hungary (Hall *et al.* 1995), a comparative study involving the same species in England found that liver and sodium sulphide bait resulted in much higher catches (Wall and Smith 1996). The results of the present study suggest that swormlure-4 is also a comparatively poor trap bait for *L. caesar*.

The results of Experiment 5.5 show that none of the potential alternative trap baits attracted such large numbers of *Lucilia caesar* group blowflies as the standard attractant, liver and sodium sulphide solution. Catches using liver and ammonium sulphide solution did not differ significantly from those using liver alone. In contrast, in the case of female flies, catches using liver and sodium sulphide are significantly higher than those without the sulphide, suggesting that the sodium sulphide solution enhances the attractancy of the liver. Sulphide solutions used in the absence of liver proved to be very poor attractants.

A previous study has found dimethyl disulphide to be a good attractant for *Lucilia caesar* in the field, but only in combination with other substances (Cragg and Thurston 1956). Ammonium carbonate, which decomposes to produce ammonia gas, is an oviposition stimulant for *L. sericata* (Cragg 1950b) and *L. cuprina* (Barton Browne 1965), and has been found to be attractive to *L. caesar* females in combination with indole and hydrogen sulphide (Cragg and Ramage 1945). Ammonia itself is also an attractant for *L. sericata* (Cragg 1950b).

5.4.4. Conclusion

An attempt to formulate a chemical bait for blowfly species did not produce any mixture which was more attractive than a meat bait (Cragg and Thurston 1950). However, swormlure-4, the present formulation used for *Cochliomyia hominivorax*, is the result of a series of extensive trials involving a large number of candidate mixtures (Jones *et al.* 1976; Coppedge *et al.* 1977; Mackley and Brown 1984). It is now both more attractive and more selective than liver bait, and it is probable that a similar process could identify a suitable chemical attractant for *Lucilia* species. Such an attractant would be desirable if blowfly traps were to be used on farms as a method of blowfly control, as, unlike liver-based baits, it could be manufactured in bulk, and stored for long periods of time. If a bait could be developed which was selectively attractive to *Lucilia* over other blowflies, this would have the additional advantage of prolonging the life of the traps, reducing the need for labour-intensive servicing. The results of the present study show that the components of swormlure-4 are potential components of a chemical attractant for *Lucilia*, but that they do not form an efficient attractant in their present ratio. Further testing of an extensive range of mixtures will be required if such a bait is to be formulated.

6. Ecological Impact of Adhesive Traps

6.1. Introduction

6.1.1. Specificity of adhesive traps

Although adhesive traps of various designs have been tested for use against sheep blowflies (Wardhaugh *et al.* 1984; Glen 1992; Wall *et al.* 1992c), no previous study has examined the impact of such traps on other sections of the insect fauna. The targets used in the present study, like those in previous investigations, are used with baits which have a relatively high level of specificity to calliphorids. However, the colouration of the targets could potentially prove attractive to members of other insect groups, and virtually any insect species could be captured by alighting on the target at random. It is therefore possible that adhesive targets could, in addition to capturing blowflies, also prove useful by reducing numbers of other species of insect pest. Alternatively, they could prove detrimental if numbers of beneficial insects were affected.

6.1.2. Beneficial insects

Beneficial insects fall into several different categories. Some are of importance as pollinators of flowering plants, while others are significant because they feed on pests of agricultural and horticultural importance. Pollinators include many species of bee (Hymenoptera: Apidae), including honeybees, *Apis mellifera* L., and bumblebees, *Bombus* species, which are important for the fertilisation of a wide variety of plants, both wild and cultivated (reviews in Free 1970; Prys-Jones 1987). Hoverflies (Diptera: Syrphidae) are also known as pollinators of certain plant species (Gilbert 1986).

Among the most important of the predaceous beneficial insects are the predators of aphids (Hemiptera: Aphididae and Pemphigidae). There are five major groups of obligatory aphid predators (Rotheray 1989). About 100 British species of hoverfly (Diptera: Syrphidae) have predaceous larvae. Most of these are members of subfamily Syrphinae, whose larvae pierce aphids and suck out the contents. Aphid

midges, *Aphidoletes* and *Monobremia* (Diptera: Cecidomyiidae) also have larvae which predate aphids, injecting them with a paralysing venom prior to feeding. Ladybirds (Coleoptera: Coccinellidae) feed on aphids both as larvae and adults. Ladybird larvae can inject digestive fluids into their prey, and then suck out the partially digested contents. Flower bugs, *Anthocoris* (Hemiptera: Anthocoridae), are the most important of many hemipteran aphid predators, and consume aphids both as larvae and as adults. Finally, the those larvae of lacewings (Neuroptera: Chrysopidae and Hemerobiidae) which are non-aquatic are of significance, as are some adult hemerobriids which will also eat aphids.

In addition to the obligate predators, a large number of insect groups feed facultatively on aphids, as well as on other sources of food (Rotheray 1989). These include earwigs (Dermaptera: Forficulidae), ground beetles (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae), and ants (Hymenoptera: Formicidae), which may 'milk' aphids for honeydew or eat them depending on the availability of food.

Several hymenopteran families of parasitoid wasps are also considered to be beneficial, due to their use of pest insects as larval hosts. The most important of these are the Braconidae, Chalcidae, and Ichneumonidae.

6.1.3. Insect pests of field crops

Aphids (Hemiptera: Aphididae) are among the most economically important plant pests in the British Isles, and can cause substantial damage to a wide variety of crop plants. Certain moths and butterflies (Lepidoptera) are also pests of field crops, as are some beetles (Coleoptera), particularly flea beetles (Coleoptera: Chrysomelidae), and weevils (Coleoptera: Curculionidae). Some capsid bugs (Hemiptera: Miridae) are locally significant pests of many crop species, although others are beneficial as predators of aphids and red spider mites. Dipteran families which contain important pest species include the Tipulidae (craneflies), Chloropidae (which includes the frit fly), Psilidae (in particular the carrot fly), and Anthomyiidae (including the cabbage root fly and onion fly). Insects of minor economic importance as pests of field crops in Britain include springtails (Collembola), earwigs (Dermaptera), and thrips (Thysanoptera) (Jones and Jones 1974).

6.1.4. Aims and Objectives

The aim of this experiment was to examine the entire catch of invertebrates from a number of horizontal adhesive traps over a period of time, in order to identify any significant catches of beneficial insects or of pests other than *Lucilia* species.

6.2. Method

6.2.1. Experimental design

Three horizontal adhesive targets, as described in sub-section 3.2.1, were mounted on fenceposts at a height of approximately 400mm. The experiment was carried out between August and October 1996 at the site detailed in sub-section 3.2.2. The traps were deployed for two periods, each of 20 days. The first of these, in late August and early September, was considered to be a time of high abundance of *Lucilia* species, while the second, in late September and early October, was considered to be a time of low abundance of *Lucilia* species. A long period duration was chosen in order to simulate the use of adhesive traps as a blowfly control method on farms, which would be unlikely to be serviced as frequently as those in an experimental situation.

6.2.2. Identification of invertebrates

All invertebrates measuring over 4mm in length were examined in the laboratory using a binocular microscope, and identified to the level of order. Additionally, insects belonging to the following orders were identified to the level of family: Coleoptera; Dermaptera; Hemiptera; Hymenoptera; and Lepidoptera. Members of the following dipteran families were also isolated: Calliphoridae; Muscidae; Sarcophagidae; Scatophagidae; Syrphidae; Tabanidae; and Tipulidae. Within the Calliphoridae, *Calliphora* species; *Lucilia* species; and *Protophormia* species were identified to the level of genus, and syrphids were divided into members of subfamily Syrphinae and members of other subfamilies.

6.3. Results

Counts for each grouping of invertebrates collected are shown in Appendix 5. The counts are summarised in Tables 6.1 (Diptera) and 6.2 (other groups), which show the total numbers of each group collected in each of the two periods.

Order	Family	Subgrouping	Total Count Period 1	Total Count Period 2
Diptera	Calliphoridae	*Calliphora*	209	579
		Lucilia	964	158
		Protophormia	1	1
		Other	65	73
	Muscidae		419	558
	Sarcophagidae		4	3
	Scatophagidae		4	0
	Syrphidae	Syrphinae	110	18
		Other	5	5
	Tabanidae		1	0
	Tipulidae		3	1
	Other		91	110

Table 6.1: Total catches of Diptera on three adhesive targets during two periods of 1996.

Order	Family	Total Count Period 1	Total Count Period 2
Coleoptera	Scarabaeidae	0	2
	Staphylinidae	1	0
Dermaptera	Forficulidae	0	1
Hemiptera	Cicadellidae	0	1
Hymenoptera	Apidae	5	1
	Ichneumonidae	0	1
	Sphecidae	3	1
	Vespulidae	4	4
Lepidoptera	Notodontidae	1	0
	Noctuidae	3	0
	Nymphalidae	3	3
Isopoda		1	0
Opiliones		2	0

Table 6.2: Total catches of invertebrates other than Diptera on three adhesive targets during two periods of 1996.

A total of 1899 invertebrates over 4mm in length were collected during Period 1, of which 1876 (98.8%) were dipteran species. Calliphorids accounted for 1239 specimens (65.2% of the total), and muscids for a further 419 (22.1%). The only other individual family of significance was the Syrphidae, with 115 specimens (6.1%), within which 110 (5.9% of the total) were members of subfamily Syrphinae. During Period 2, 1520 specimens were collected, of which 1506 (99.1%) were dipteran. In this case, 811 (53.4% of the total) were calliphorids, and 558 (36.7%) were muscids. Only 23 specimens (1.5%) collected during this period were syrphids.

Within the Calliphoridae, the percentage of *Lucilia* species fell from 77.8% (50.8% of the total) in Period 1 to 19.5% (10.4% of the total) in Period 2, and there was a corresponding rise in the percentage of *Calliphora* species from 16.9% (11.0% of the total) to 71.4% (38.1% of the total).

6.4. Discussion

Considerable variation was found between the catches on different traps exposed during the same period, and caution must therefore be exercised in the interpretation of the results of this experiment. Nevertheless, the results demonstrate that a very high proportion of the invertebrates captured on horizontal adhesive targets were members of Order Diptera. Calliphorid species accounted for an overall majority of catches during both periods. During Period 1, at a time when many cases of sheep strike are recorded, catches of *Lucilia* species exceeded 50% of the overall total, representing a very high level of trap specificity. In Period 2, the proportion of *Lucilia* specimens collected fell significantly, but this was partially compensated for by an increase in the catches of *Calliphora* species. Even at this time, which coincides with a steep decline in the population of *Lucilia* adults, the catches from this genus remained at a significant level, in excess of 10% of the total.

Neither the Calliphoridae nor the Muscidae, which together accounted for a substantial majority of the invertebrates collected, contain any species regarded as important beneficial insects. The only significant catches of beneficial insects were of hoverflies (Diptera: Syrphidae) of subfamily Syrphinae, many of which are notable aphid predators. It is not known whether such a level of catches could make a significant impact on the hoverfly population, but the catches are low relative to those of blowflies. Members of several families of Diptera were not distinguished, and these accounted for 4.8% and 7.2%, of the total catch in Periods 1 and 2, respectively. It is possible that these specimens may have included beneficial insects, but a wide variety of species were included, and it is therefore highly unlikely that any were present in significant numbers. While it is unfortunate that butterflies (Lepidoptera: Nymphalidae) were captured by the traps, those collected were relatively common species (the red admiral, *Vanessa atlanta*, and the small tortoiseshell, *Aglais urticae*), and were not caught in high numbers. Similarly, although honey bees, *Apis mellifera* (Hymenoptera: Apidae), were identified among the catches, their numbers were low.

It does not appear that the adhesive traps are effective in the capture of any significant pests other than the target species. Potential pests which were identified from the traps included craneflies, *Tipula* species (Diptera: Tipulidae), and an earwig, *Forficula* species (Dermaptera: Forficulidae), but only very small numbers of these were collected.

In conclusion, it appears that the horizontal adhesive traps designed for the capture of sheep blowflies have a relatively high level of specificity, particularly at times when the adult population of the target species is high. With the possible exception of some hoverfly species, the traps do not capture significant numbers of any invertebrates which are regarded as beneficial, and their use on farms is therefore not anticipated to have any detrimental effect on the local invertebrate ecology.

7. Conclusion

Sheep blowfly strike is a longstanding agricultural problem in the British Isles, and a considerable volume of research has been published regarding the condition, its agents, and their control. The need for ongoing investigation is due to the changing nature of the chemical control methods available, and the public attitude towards them. The withdrawal of organochlorine compounds such as dieldrin has been followed by recent concerns over the effects of organophosphate compounds on human users (for example, Stephens *et al.* 1995), and on the wider environment (for example, Littlejohn and Melvin 1991). These have led to tightened controls on the supply and use of organophosphates and have resulted in the use of treatments containing other classes of active ingredient (French *et al.* 1992; 1994b). However, these preparations, particularly those containing synthetic pyrethroids, also have the potential to cause significant environmental damage. The subject of sheep blowflies, and especially non-insecticidal methods for their control, is therefore of particular interest at the present time. There is a potential role for an effective design of trap for sheep blowfly control.

Traps have been shown to be capable of reducing fly populations; a notable example being tsetse fly control programmes in southern Africa (Hargrove and Vale 1979), which have proved effective in reducing fly populations. However, the reproductive biology of tsetse flies (see review in Tobe and Langley 1978), and the resulting low population density (Glasgow 1963) makes them particularly susceptible to such a control strategy (Weidhaas and Haile 1978). In contrast, flies with a high reproductive capability, such as blowflies (Wall 1993), require to be trapped in much greater proportions in order to have a significant impact on a population.

A refinement of any process of control is to use knowledge of the population biology of the insects involved in order to target control methods at particular points within a season or life-cycle. Models of *Lucilia sericata* populations have been developed with this aim (Wall *et al.* 1993b; Fenton *et al.* 1997), and these have shown that the use of control methods early in the blowfly season has the potential to significantly reduce the population throughout the remainder of the season. An evaluation of this strategy was carried out in the field using the larvicide cyromazine (Wall *et al.* 1995). Although problems were identified, including immigration of blowflies into the control areas from the surrounding countryside, the application of the treatment at an early stage did have a significant impact on the *L. sericata* population, and also

reduced the prevalence of sheep strike in the control areas. The potential for traps to be used in place of the larvicide is clear. Indeed, the trapping of *L. cuprina* in Australia has previously been shown to reduce both blowfly populations and the incidence of sheep strike in areas where trapping was carried out (Mackerras *et al.* 1936; Anderson and Simpson 1991).

The study of sheep blowfly control in Scotland, as distinct from the rest of the British Isles, is important because of the differing nature of myiasis agents in this country. The higher incidence of alternative species (those other than *Lucilia sericata*) in sheep strike cases in Scotland was first revealed by research in the 1930s and 1940s (Haddow and Thomson 1937; MacLeod 1943a), and the present study has revealed even higher levels of alternative species than those found previously. The incidence of these alternative species is highest in western Scotland, and the most important is *L. caesar*. This species is common throughout Great Britain (MacLeod and Donnelly 1956b), and the reason why it is only an important agent of myiasis in certain areas is still not completely clear. However, MacLeod (1943b) found strong associations between the incidence of alternative species in ovine myiasis cases, and several ecological factors: the breed of sheep involved; the grazing type; and the vegetation type. Hill breeds of sheep, mountain and moorland grazing, and the presence of bracken and heather were shown to be associated with higher levels of alternative species, and the analysis suggested that the presence of bracken was the most important of these. Although the present study was smaller, and could therefore not be analysed in such great detail, the results are consistent with those of MacLeod (1943b), and significantly higher levels of alternative species were found to be associated with altitudes in excess of 200m, hill breeds of sheep, rough grazing and moorland grazing (as opposed to permanent pasture), and the presence of bracken. There was a significant difference between the incidence of alternative species in strike cases from western Scotland and those from eastern Scotland. However, this is likely to have resulted from the geographical distribution of the factors identified.

Although research has previously been published regarding the use of adhesive traps for the capture of *Lucilia sericata* (Wall *et al.* 1992c), no such work had hitherto been undertaken involving *L. caesar*. As *L. caesar* is important as an agent of myiasis in Scotland, any trapping programme in this country would have to consider this species in addition to *L. sericata*. Furthermore, the two species are regarded as belonging to different sub-sections of the genus (Stevens and Wall 1996a), which probably evolved the myiasis habit separately from each other (Stevens and Wall 1997). It is therefore possible that differences exist between the responses of the two species to olfactory or visual stimuli, or to other factors which could influence the

optimum design of trap for their capture. Previous research had suggested the existence of such differences, with reference to odour responses (Cragg 1956; Cragg and Cole 1956). It was in the light of these considerations that the trapping experiments in the present study were conducted.

Catches of *Lucilia caesar* group flies were found to be significantly higher with adhesive trap designs than with the enclosed Fly City® trap or a water trap. Furthermore, it was found that blowfly catches were maximised at a height of approximately 200mm. Although the highest catches were obtained using targets angled at 45°, these were not significantly different from those taken from horizontal targets. Vertical targets, such as the design developed by Wall *et al.* (1992c) captured significantly lower numbers of the target species. Trap shape was found to be relatively unimportant, although lower catches were collected from highly elongate targets, and while larger targets captured more sheep blowflies, there was no increase in the catch per unit area. It is concluded that square horizontal adhesive targets mounted approximately 200mm above ground level and of similar size to the standard targets used in the present study ($410mm^2$) will provide the best compromise of catch size and ease of use for future studies.

The electrophysiological studies of the responses of *Lucilia caesar* and *L. sericata* to light of various wavelengths are of interest because the spectral sensitivities of these species have not previously been published. It was found that their spectral sensitivities were broadly similar to those of other Diptera used in previous research (for example, Green and Cosens 1983). However, the results indicate that the xanthopsin visual pigment in *Lucilia* may differ from that in *Calliphora* in having its peak absorbance at a higher wavelength. The results for the two species of *Lucilia* were very similar to each other, and did not suggest any significant difference between their visual systems. Both species showed three major peaks in their spectral sensitivity, in the ultraviolet, green/yellow, and red, although as explained in chapter 4, the red peak does not represent the activity of a specific receptor. Caution must be exercised in drawing conclusions about behaviour from physiological data, as the interactions between the two are complex. In the present study, therefore, the measurement of electroretinograms was supplemented by a field study of the responses of *L. caesar* group flies to targets of various colours. The results, which showed the highest responses to yellow and white targets, proved similar to those obtained with *L. sericata* by Wall *et al.* (1993c), and are in agreement with the revised behavioural model proposed for *L. sericata* by Wall and Smith (1996), in which trap catches were related positively to reflectivity in the 450-580nm

(blue/green/yellow) band. The present study therefore provides no evidence for any significant differences in the responses to colour of different species of *Lucilia*.

Although the results of the electroantennographic experiments suggested that some differences exist between the responses of *Lucilia caesar* and *L. sericata*, the general pattern of results was similar. Dimethyl disulphide elicited the largest responses of the individual organic compounds, with the mixture swormlure-4 producing even greater responses in flies of both species. Ammonium sulphide evoked a higher level of stimulus than sodium sulphide, liver extract, or either of the liver and sulphide combinations tested. However, field experiments using swormlure-4 and ammonium sulphide (both with and without liver) as trap baits found that in both cases a greater number of *Lucilia* was attracted by the traditional bait of liver and sodium sulphide solution. It appears to be difficult to draw conclusions regarding the attractiveness of a particular substance through the use of electroantennograms. Further field studies will therefore be required in order to develop a useful synthetic attractant for sheep blowflies.

The experimental work in the present study suggests that the responses of *Lucilia caesar* and *L. sericata* to trap variables, with the possible exception of some olfactory stimuli, are broadly similar. It therefore seems probable that traps developed for use against one of these species will also prove effective for the other. Whether trapping has the potential to control *L. caesar* as effectively as it is predicted to control *L. sericata* (Wall *et al.* 1993b) depends on how similar are the population dynamics of the two species. *L. caesar* was found to be a much more abundant species, both in the present study and in previous research (MacLeod and Donnelly 1957b; Wall *et al.* 1992c). Based on low relative emergence levels of *L. sericata* from carcases (Cragg 1955), it has been proposed that this species is a poor competitor in carrion when compared to *L. caesar*, and that it therefore maintains its population primarily through infestation of living sheep (Wall *et al.* 1992c). However, competition studies by Prinkkilä and Hanski (1995) do not provide evidence for this, and further research is needed into the relative importance of carrion and live hosts for both of these species.

A further important consideration, if adhesive targets are to be considered for general use as a control measure for sheep blowflies, is their impact on other species of invertebrate. Large adhesive traps are potentially somewhat indiscriminate, as although the bait may only be attractive to blowflies and their close relatives, the colouration of the targets may also prove attractive to other species, and others may be caught at random when they alight on the adhesive surface. If beneficial insects were captured by the traps in significant numbers, this could be an argument

against their use on a large scale. However, the present study suggests that the targets exhibit a relatively high level of specificity, particularly at times of peak populations of *Lucilia* adults. The only beneficial insects which were trapped in significant numbers were hoverflies (Diptera: Syrphidae), and even in this case, the numbers were low relative to those of blowflies.

Due to the high reproductive potential of blowflies, it seems unlikely that trapping could completely replace insecticides as a control method, particularly as many synthetic treatments are used against a wide range of sheep ectoparasites. Nevertheless, it could be used as a supplement to chemical agents. In order for the use of traps to become widespread on farms, designs would be required which were neither expensive nor labour-intensive in their operation. The present study suggests that a mass-produced adhesive target should be coated in advance with non-setting adhesive, and should either be lightweight, or have a heavy base with disposable surfaces attached. The development of a synthetic bait to replace traditional meat-based attractants must also be a priority, as this would make the traps much easier to service, and would require much less frequent attention. If these criteria can be met, adhesive traps have the potential to play a significant part in the control of sheep blowflies in the future.

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Appendix 1

Sample Ref.	Date	Farm Ref.	Sheep type	*Lucilia sericata*		*Lucilia caesar*		*P. terraenovae*		Other species
				F	M	F	M	F	M	
1	7/93	1	L	1	6	1	6			
2	7/93	1	L	2	8					
3	8/93	2	L	7	13					*M. pabulorum* 1F
4	7/94	1	L	75	151					
5	7/94	3	L	3	4	2	1	1	2	
6	7/94	3	L	1	1					
7	7/94	1	L	8	13					
8	8/94	1	L	17	5					*C. vicina* 17F 12M
9	6/95	1	L	3	3					
10	7/95	4	X	22	21					
11	7/95	1	L	25	20				1	*L. illustris* 1M
12	7/95	5	H	374	187			13	8	
13	7/95	1	L	11	15					
14	7/95	1	L					7	2	
15	7/95	5	H	1	1	16	8			
16	8/95	6	L	5	2					
17	6/96	1	L	17	9					
18	6/96	1	L	10	6					
19	6/96	1	L	10	7					
20	6/96	1	L	5	4					

Table A1.1: Details of dipteran larval samples collected from sheep. Sheep types: L = Lowland; X = Cross-breed; H = Hill breed. *C.* =*Calliphora*; *L.* = *Lucilia*; *M.* = *Muscina*; *P.* = *Protophormia*.

Sample Ref.	Date	Farm Ref.	Sheep type	*Lucilia sericata*		*Lucilia caesar*		*P. terraenovae*		Other species
				F	M	F	M	F	M	
21	6/96	1	L	3	3					
22	6/96	1	L	7	10					
23	7/96	1	L	6	7					
24	7/96	1	L	1	1					
25	7/96	1	L	2	1					
26	7/96	7	H	88	99		1			
27	8/96	8	X			7	1			
28	8/96	9	H			31	19			
29	8/96	10	H	63	73					
30	8/96	11	H			73	36			
31	8/96	7	H	23	12		1			
32	8/96	12	H	2	1					
33	8/96	13	H	1		4	4			
34	9/96	1	L	3						
35	9/96	14	H			18	3	2	3	
36	9/96	14	H				2	2		
37	9/96	14	H			3	1	2	1	
38	9/96	9	H							*C. vomitoria* 66F 49M
39	9/96	9	H							*C. vomitoria* 57F 41M

Table A1.2: Details of dipteran larval samples collected from sheep. Sheep types: L = Lowland; X = Cross-breed; H = Hill breed. *C.* =*Calliphora; L.* = *Lucilia; M.* = *Muscina; P.* = *Protophormia.*

Farm Ref.	Location		Approx. altitude (m)	Grazing type	Trees	Bracken	Heather	Gorse
	OS Ref.	Former Region						
1	NT63	Border	100	P	D	N	N	N
2	NS32	Strathclyde	50	P	C	N	N	N
3	NT33	Border	150	P	N	N	N	N
4	NX75	Dumfries& Galloway	100	R	D	N	N	N
5	NX65	Dumfries& Galloway	200	M	C	Y	Y	N
6	NJ66	Grampian	100	P	N	N	N	N
7	NX26	Dumfries& Galloway	150	R	N	Y	N	N
8	NS87	Central	200	R	N	N	Y	N
9	NN29	Highland	235	M	N	Y	Y	N
10	NG83	Highland	110	M	N	Y	Y	N
11	NN00	Strathclyde	150	P	N	Y	N	N
12	NS86	Central	245	R	N	Y	N	N
13	NT32	Border	275	R	N	Y	Y	N
14	NN51	Central	245	R	D	N	N	N

Table A1.3: Details of the farms from which samples were collected (Grazing types: P=Permanent pasture; R=Rough grazing; M=Moorland. Trees: C=Coniferous; D=Deciduous; N=None).

Appendix 2

Period Dates	*Lucilia caesar* *		I *	*Lucilia sericata*		*Calliphora vicina*		*Calliphora vomitoria*		*P. terraenovae*		*Cynomya mortuorum*	
	F	M	M	F	M	F	M	F	M	F	M	F	M
10-17	3	0	0	0	0	13	8	1	1	1	2	0	0
10-17	14	0	1	0	0	12	6	1	1	0	0	0	0
10-17	4	0	1	0	0	5	2	0	0	0	0	0	0
10-17	0	0	0	0	0	2	2	1	0	0	0	0	0
10-17	0	1	0	0	0	2	4	0	2	0	2	0	0
21-24	2	1	0	0	0	1	2	0	0	1	0	0	0
21-24	2	2	1	0	0	0	1	0	0	0	0	0	0
21-24	9	1	0	0	0	9	1	2	1	0	0	0	0
21-24	13	2	2	0	0	2	1	0	3	0	0	0	0
21-24	63	31	3	1	0	8	7	9	7	1	0	0	0
24-28	3	0	0	0	0	0	0	1	0	1	0	0	0
24-28	49	6	1	0	0	2	6	1	0	3	0	0	1
24-28	70	10	1	0	0	3	1	6	2	0	0	0	0
24-28	67	6	0	0	0	3	3	3	2	3	2	1	0
24-28	45	5	0	0	0	2	0	2	0	8	2	0	0
25-26	7	2	0	0	0	3	1	4	3	4	0	0	0
25-26	119	15	2	0	0	7	2	40	32	9	3	0	0
25-26	36	2	0	0	0	14	7	51	42	9	2	0	0
25-26	56	11	0	0	0	9	3	25	21	17	5	0	0
25-26	24	1	0	0	0	21	8	38	22	4	0	0	0
26-27	9	1	0	0	0	0	1	0	0	3	0	0	0
26-28	120	2	0	0	0	8	0	10	6	0	0	0	0
26-28	106	3	0	0	0	6	3	9	0	0	0	0	0
26-28	112	0	0	0	0	17	1	25	5	0	0	0	0
26-28	117	2	0	0	0	6	0	2	0	0	0	0	0
26-28	37	0	0	0	0	2	0	3	1	0	0	0	0
26-31	38	1	1	0	0	7	2	5	0	1	2	0	0
26-31	88	6	0	0	0	10	1	6	3	4	1	0	0
26-31	279	17	7	0	0	29	13	20	14	5	0	0	0
TOTAL	1492	128	20	1	0	203	86	264	168	75	21	1	1

Table A2.1: Catches on horizontal adhesive traps during July 1995 showing numbers of each species of necrophagous calliphorid (Part 1). F = Female; M = Male.

* I= *L. illustris*. Figures for *L. caesar* females include *L. illustris* (see text for details).

Period Dates	*Lucilia caesar* *		I *	*Lucilia sericata*		*Calliphora vicina*		*Calliphora vomitoria*		*P. terraenovae*		*Cynomya mortuorum*	
	F	M	M	F	M	F	M	F	M	F	M	F	M
A2.1	1492	128	20	1	0	203	86	264	168	75	21	1	1
26-31	13	0	0	0	0	2	4	2	0	2	0	0	0
26-31	25	2	0	0	0	9	3	3	0	0	0	0	0
27-31	114	3	2	0	0	9	4	10	8	3	0	0	0
28-30	190	8	0	0	0	12	21	46	3	1	4	0	0
28-30	202	4	0	0	0	22	16	51	18	3	0	0	0
28-30	198	6	2	0	0	12	13	34	7	1	0	0	0
28-30	35	0	0	0	0	6	2	7	2	0	0	0	0
28-30	20	1	0	0	0	5	1	7	1	0	0	0	0
28-31	0	0	0	0	0	0	0	0	0	0	0	0	0
28-31	21	0	0	0	0	1	0	0	0	0	0	0	0
28-31	13	1	0	0	0	0	1	0	0	1	0	0	0
28-31	24	3	1	0	0	1	0	0	0	2	0	0	0
28-31	52	9	2	0	0	1	0	1	0	4	0	0	0
TOTAL	2399	165	27	1	0	282	151	425	207	92	25	1	1

Table A2.2: Catches on horizontal adhesive traps during July 1995 showing numbers of each species of necrophagous calliphorid (Part 2). F = Female; M = Male.

* I= *L. illustris*. Figures for *L. caesar* females include *L. illustris* (see text for details).

Period Dates	*Lucilia caesar* *		I *	*Lucilia sericata*		*Calliphora vicina*		*Calliphora vomitoria*		*P. terraenovae*		*Cynomya mortuorum*	
	F	M	M	F	M	F	M	F	M	F	M	F	M
1-1	120	4	0	0	0	3	1	2	2	5	2	0	0
2-3	29	0	0	0	0	10	3	3	2	0	0	0	0
2-3	16	1	0	0	0	3	4	2	2	0	0	0	0
2-3	196	2	0	0	0	10	5	7	1	0	1	0	0
2-3	22	2	1	0	0	19	4	6	0	0	0	0	0
2-3	75	0	0	0	0	12	7	4	4	0	0	0	0
2-4	19	1	0	0	0	0	0	0	0	1	0	0	0
2-4	32	1	1	0	0	0	1	1	0	1	1	0	0
2-4	11	1	1	0	0	2	2	0	1	4	1	0	0
2-4	18	5	0	0	0	0	3	0	1	4	1	0	0
2-4	1	0	0	2	0	1	0	0	0	2	0	0	0
2-4	31	3	0	0	0	4	1	0	1	1	1	0	0
2-4	287	19	1	0	0	6	4	6	2	5	0	0	0
2-4	17	2	1	0	0	4	1	0	1	2	0	0	0
2-4	42	15	1	0	0	11	2	5	6	2	0	0	0
2-4	23	5	0	0	0	2	0	1	3	3	0	0	0
3-4	34	3	1	0	0	11	10	3	7	0	0	0	0
3-4	13	0	0	0	0	2	1	0	1	0	0	0	0
3-4	52	4	0	0	0	4	4	3	3	0	0	0	0
3-4	138	4	0	0	0	10	3	6	3	0	0	0	0
3-4	15	1	1	0	0	2	2	1	1	0	0	0	0
4-7	133	12	0	0	0	2	1	3	1	0	0	0	0
4-7	13	4	1	0	0	0	1	0	0	0	1	0	0
4-7	66	12	1	0	0	1	1	1	1	0	0	0	0
4-7	58	10	1	0	0	1	2	2	4	0	0	0	0
4-7	20	7	0	0	0	7	0	1	2	0	0	0	0
7-8	19	0	0	0	0	1	2	3	2	0	0	0	0
7-8	35	2	0	0	0	1	3	4	3	0	0	0	0
7-8	32	1	0	0	0	4	4	13	5	0	0	0	0
7-8	179	6	0	0	0	5	3	9	7	0	0	0	0
TOTAL	1746	127	11	2	0	138	75	86	65	30	8	0	0

Table A2.3: Catches on horizontal adhesive traps during August 1995 showing numbers of each species of necrophagous calliphorid (Part 1). F = Female; M = Male.

* Figures for *L. caesar* females include *L. illustris* (see text for details).

Period Dates	*Lucilia caesar* *		I *	*Lucilia sericata*		*Calliphora vicina*		*Calliphora vomitoria*		*P. terraenovae*		*Cynomya mortuorum*	
	F	M	M	F	M	F	M	F	M	F	M	F	M
A2.3	1746	127	11	2	0	138	75	86	65	30	8	0	0
7-8	20	0	0	0	0	1	1	1	1	0	0	0	0
7-9	30	2	0	0	0	0	0	0	0	0	0	0	0
7-9	196	22	4	0	0	3	3	11	4	2	0	0	0
7-9	10	2	0	0	0	0	0	0	0	0	0	0	0
7-9	2	0	0	0	0	2	0	1	1	0	0	0	0
7-9	1	0	0	0	0	0	0	0	0	0	0	0	0
8-8	67	7	1	0	0	0	0	0	0	0	0	0	0
8-8	23	1	0	0	0	0	1	0	0	0	0	0	0
8-8	4	0	0	0	0	0	0	0	0	0	0	0	0
8-8	36	3	3	0	0	1	0	0	0	0	0	0	0
8-8	82	9	1	0	0	0	1	1	0	3	1	0	0
11-12	14	2	0	0	0	0	0	0	0	0	0	0	0
15-15	200	2	0	0	0	2	0	12	3	0	0	0	0
15-16	4	0	0	0	0	0	1	1	0	2	1	0	0
16-16	267	5	1	0	0	1	0	3	4	0	1	0	0
17-17	166	0	0	0	0	0	0	2	0	0	1	0	0
18-18	382	8	0	0	0	0	0	35	22	0	0	0	0
30-31	82	8	0	2	0	0	0	11	0	0	0	0	0
31-31	198	8	0	0	0	0	0	10	2	0	0	0	0
TOTAL	3530	206	21	4	0	148	82	174	103	37	12	0	0

Table A2.4: Catches on horizontal adhesive traps during August 1995 showing numbers of each species of necrophagous calliphorid (Part 2). F = Female; M = Male.

Period Dates	*Lucilia caesar* *		I *	*Lucilia sericata*		*Calliphora vicina*		*Calliphora vomitoria*		*P. terraenovae*		*Cynomya mortuorum*	
	F	M	M	F	M	F	M	F	M	F	M	F	M
10-12	10	0	0	0	0	1	0	17	1	0	0	0	0
12-13	10	0	0	0	0	0	0	19	2	0	0	0	0
15-16	10	2	1	0	0	1	0	9	1	0	0	0	0
18-20	15	1	0	0	0	29	3	38	6	0	0	0	0
TOTAL	45	3	1	0	0	31	3	83	10	0	0	0	0

Table A2.5: Catches on horizontal adhesive traps during September 1995 showing numbers of each species of necrophagous calliphorid. F = Female; M = Male.

* I= *L. illustris*. Figures for *L. caesar* females include *L. illustris* (see text for details).

	Replicate	1	1	1	1	1	1	1	1
Period	Position	1	2	3	4	1	2	3	4
1		D	C	B	A	C	D	B	A
2		A	B	D	C	D	A	C	B
3		B	A	C	D	B	C	A	D
4		C	D	A	B	A	B	D	C

Table A2.6: Latin square design for two replicates of experiment 2.1. Trap Heights: A = Water Trap; B = Fly City; C = Horizontal adhesive; D = Vertical adhesive.

Period			Trap Type							
No.	Start Date	Finish Date	Water Trap		Fly City		Horizontal adhesive		Vertical adhesive	
			F	M	F	M	F	M	F	M
1	11/8/95	12/8/95	4	1	45	0	14	2	16	3
2	15/8/95	15/8/95	0	0	0	0	200	2	3	1
3	15/8/95	16/8/95	1	0	4	0	267	6	49	2
4	16/8/95	17/8/95	0	0	0	0	166	0	70	1
1	25/9/96	26/9/96	1	0	2	0	32	3	35	2
2	26/9/96	27/9/96	1	1	5	0	23	1	13	0
3	27/9/96	2/10/96	0	0	13	0	61	3	8	0
4	2/10/96	8/10/96	0	0	26	0	31	2	13	1

Table A2.7: Catches of *Lucilia caesar* from two replicates of experiment 2.1 comparing four types of trap. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

	Replicate	1	1	1	1	1	2	2	2	2	2
Period	Position	1	2	3	4	5	1	2	3	4	5
1		A	C	B	D	E	E	D	A	C	B
2		E	B	D	A	C	D	C	E	B	A
3		B	A	E	C	D	C	B	D	A	E
4		D	E	C	B	A	A	E	B	D	C
5		C	D	A	E	B	B	A	C	E	D

Table A2.8: Latin square design for two replicates of experiment 2.2.
Trap Heights: A = 0.0m; B = 0.2m; C = 0.4m; D = 0.6m; E = 0.8m.

Period			Trap Height (m)									
No.	Start Date	Finish Date	0.0		0.2		0.4		0.6		0.8	
			F	M	F	M	F	M	F	M	F	M
1	25/7/95	26/7/95	7	2	119	15	36	2	56	11	24	1
2	28/7/95	31/7/95	38	1	88	0	279	17	13	0	25	2
3	2/8/95	4/8/95	31	3	287	19	17	2	42	15	23	5
4	4/8/95	7/8/95	133	12	13	4	66	12	58	10	20	7
5	7/9/95	9/8/95	30	2	196	22	10	2	2	0	1	0
1	1/7/96	8/7/96	68	3	23	6	59	2	19	1	2	1
2	8/7/96	17/7/96	12	1	82	6	61	2	6	0	4	0
3	17/7/96	20/7/96	12	4	175	19	10	4	2	0	4	0
4	20/7/96	26/7/96	49	9	121	42	66	15	39	8	21	5
5	26/7/96	29/7/96	3	2	10	3	59	17	29	10	17	5

Table A2.9: Catches of *Lucilia caesar* from two replicates of experiment 2.2 comparing horizontal adhesive targets at five different heights. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

	Replicate	1	1	1	1	1	2	2	2	2	2
Period	Position	1	2	3	4	5	1	2	3	4	5
1		C	E	B	D	A	C	E	B	A	D
2		A	C	E	B	D	E	B	D	C	A
3		D	A	C	E	B	B	D	A	E	C
4		B	D	A	C	E	A	C	E	D	B
5		E	B	D	A	C	D	A	C	B	E

Table A2.10: Latin square design for two replicates of experiment 2.3.
Trap Sizes: A = 0.21x0.21m; B = 0.31x0.31m; C = 0.41x0.41m; D = 0.51x0.51m; E = 0.61x0.61m.

Period			Trap Size(m)									
No.	Start Date	Finish Date	0.21x0.21		0.31x0.31		0.41x0.41		0.51x0.51		0.61x0.61	
			F	M	F	M	F	M	F	M	F	M
1	21/7/95	24/7/95	2	1	2	2	9	1	13	2	63	31
2	24/7/95	28/7/95	3	0	49	6	70	10	67	6	45	5
3	28/7/95	31/7/95	0	0	21	0	13	1	24	3	52	9
4	2/8/95	4/8/95	19	1	32	1	11	1	18	5	31	9
5	8/8/95	8/8/95	67	7	23	1	4	0	36	3	82	9
1	19/6/96	8/7/96	1	0	4	1	10	0	9	2	37	7
2	8/7/96	19/7/96	10	0	43	11	68	13	38	6	53	11
3	19/7/96	23/7/96	12	2	29	9	53	23	59	10	87	21
4	23/7/96	29/7/96	12	3	17	6	62	32	12	3	34	10
5	29/7/96	31/7/96	16	2	13	1	79	15	60	10	183	31

Table A2.11: Catches of *Lucilia caesar* from two replicates of experiment 2.3 comparing horizontal adhesive targets of five different sizes. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

	Trap Size (m)									
No.	0.21x0.21		0.31x0.31		0.41x0.41		0.51x0.51		0.61x0.61	
	F	M	F	M	F	M	F	M	F	M
1	45.4	22.7	20.8	20.8	53.5	6.0	50.0	7.7	169.3	83.3
2	68.0	0.0	509.9	62.4	416.4	59.5	257.6	23.1	120.9	13.4
3	0.0	0.0	218.5	0.0	77.3	5.9	92.3	11.5	139.7	24.19
4	430.8	22.7	331.0	10.4	65.4	5.9	69.2	19.2	83.3	24.2
5	1519.3	158.7	239.3	10.4	23.8	0.0	138.4	11.5	220.4	24.2
1	22.7	0.0	41.6	10.4	59.5	0.0	34.6	7.7	99.4	18.8
2	226.8	0.0	447.5	114.5	404.5	77.3	146.1	23.1	142.4	29.6
3	272.1	45.4	301.8	93.7	315.3	136.8	226.8	38.4	233.8	56.4
4	272.1	68.0	176.9	62.4	368.8	190.4	46.1	11.5	91.4	26.8
5	362.8	45.4	135.3	10.4	470.0	89.2	230.7	38.4	491.8	83.3

Table A2.12: Catches of *Lucilia caesar* from two replicates of experiment 2.3 expressed as catch per unit area (square metre). Period dates as shown in Table A2.11. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

	Replicate	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3
Period	Position	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
1		D	A	E	C	B	E	D	A	B	C	D	C	E	A	B
2		B	C	A	D	E	C	A	D	E	B	C	B	D	E	A
3		C	E	B	A	D	D	E	B	C	A	A	E	B	C	D
4		A	B	D	E	C	A	B	C	D	E	E	D	A	B	C
5		E	D	C	B	A	B	C	E	A	D	B	A	C	D	E

Table A2.13: Latin square design for three replicates of experiment 2.4.
Trap Angles: A = 0°; B = 22.5°; C = 45°; D = 67.5°; E = 90°.

Period			Trap Angle to the horizontal									
No.	Start Date	Finish Date	0°		22.5°		45°		67.5°		90°	
			F	M	F	M	F	M	F	M	F	M
1	8/7/94	12/7/94	0	0	0	0	0	0	0	0	0	0
2	13/7/94	18/7/94	0	0	0	0	0	0	0	0	0	0
3	18/7/94	20/7/94	3	1	1	0	0	0	2	0	1	0
4	20/7/94	22/7/94	0	0	0	0	2	0	0	0	0	0
5	22/7/94	25/7/94	2	0	3	0	4	0	1	0	0	0
1	26/7/95	27/7/95	9	1	11	1	103	7	56	4	6	0
2	31/7/95	31/7/95	114	3	50	1	150	14	7	3	26	2
3	1/8/95	1/8/95	120	4	6	0	33	0	92	1	15	3
4	15/8/95	16/8/95	4	0	44	2	133	4	206	7	162	3
5	17/8/95	18/8/95	89	*	147	*	116	*	217	*	43	*
1	17/7/96	22/7/96	103	17	71	11	40	16	26	5	86	11
2	22/7/96	1/8/96	16	9	34	19	33	18	18	9	2	0
3	1/8/96	8/8/96	167	44	10	2	43	8	75	16	14	4
4	8/8/96	12/8/96	76	26	140	45	210	67	32	9	5	2
5	12/8/96	14/8/96	201	33	227	41	178	25	180	24	19	2

Table A2.14: Catches of *Lucilia caesar* from three replicates of experiment 2.4 comparing horizontal adhesive targets at five different angles of orientation. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

* = missing value.

	Replicate	1	1	1	1	1	2	2	2	2	2
Period	Position	1	2	3	4	5	1	2	3	4	5
1		C	D	E	A	B	E	D	A	B	C
2		B	C	D	E	A	D	C	E	A	B
3		D	E	A	B	C	C	B	D	E	A
4		A	B	C	D	E	B	A	C	D	E
5		E	A	B	C	D	A	E	B	C	D

Table A2.15: Latin square design for two replicates of experiment 2.5.
Length of longest sides: A = 0.41m; B = 0.55m; C = 0.68m; D = 0.82m; E = 0.96m.

	Period		Length of longest sides (m)									
No.	Start Date	Finish Date	0.41		0.55		0.68		0.82		0.96	
			F	M	F	M	F	M	F	M	F	M
1	27/7/95	28/7/95	120	2	106	3	112	0	117	2	37	0
2	28/7/95	30/7/95	190	8	202	4	198	6	35	0	20	1
3	2/8/96	3/8/96	29	0	16	1	196	2	22	2	75	0
4	3/8/96	4/8/96	34	3	13	0	52	4	138	4	15	1
5	7/8/96	8/8/96	19	0	35	2	32	1	179	6	20	0
1	5/8/96	8/8/96	40	13	214	71	37	12	39	13	55	20
2	8/8/96	12/8/96	41	11	77	24	73	19	75	21	10	4
3	12/8/96	13/8/96	19	3	37	0	151	15	79	4	53	5
4	13/8/96	14/8/96	65	12	89	16	53	10	209	36	152	20
5	14/8/96	15/8/96	55	9	24	6	69	13	114	25	15	3

Table A2.16: Catches of *Lucilia caesar* from two replicates of experiment 2.5 comparing horizontal adhesive targets of five different shapes. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

Appendix 3

% transmission	Central wavelength of bandpass filter (nm)								
	300.0	331.6	359.0	379.7	408.6	440.4	469.6	489.0	500.0
0.09	0.04	0.04	0.04	0.04	0.15	0.17	0.29	0.18	0.23
0.54	0.04	0.04	0.07	0.11	0.57	0.7	1.3	0.9	1.07
1.0	0.04	0.05	0.13	0.2	1.37	1.57	2.8	1.8	2.1
2.2	0.04	0.06	0.26	0.53	2.9	3.4	6.5	4.2	5
5.0	0.05	0.08	0.54	1.05	6	6.9	13.6	9.1	10.4
6.4	0.05	0.09	0.63	1.29	8	9.4	17.7	11.8	13.7
19.8	0.07	0.17	1.7	3.1	19.6	23	46	30	35
30.2	0.09	0.22	2.5	5	32	38	75	49	57
40.3	0.11	0.28	3.4	6.7	42	51	100	66	78
63.0	0.15	0.4	5.1	9.9	68	77	150	100	118
100.0	0.19	0.61	7.8	15.3	105	117	230	154	177

Table A3.1: Light intensity readings from Tektronix J16 photometer (mWm^{-2}) using nine bandpass filters of various wavelengths and a variety of neutral density filters in identical conditions to those used for recording of ERGs.

% transmission	Central wavelength of bandpass filter (nm)							
	529.6	559.2	590.1	620.5	650.1	679.5	705.0	White
0.09	0.26	0.37	0.34	0.38	0.3	0.34	3	1
0.54	1.28	1.88	1.79	2	1.66	1.92	15.5	6
1.0	2.5	3.6	3.2	3.7	2.9	3.5	29	11
2.2	5.7	8.6	7.8	8.8	6.8	8.1	60	24
5.0	11.8	17.2	16.3	18.3	14.5	17	125	50
6.4	15.8	23	21	23	19.2	22	164	68
19.8	41	63	59	67	55	64	510	200
30.2	67	102	93	106	83	96	740	300
40.3	89	136	123	142	111	132	1060	420
63.0	134	200	184	210	167	198	1550	620
100.0	210	320	290	330	260	310	2200	920

Table A3.2: Light intensity readings from Tektronix J16 photometer (mWm^{-2}) using seven bandpass filters of various wavelengths plus white light and a variety of neutral density filters in identical conditions to those used for recording of ERGs.

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	Central wavelength of bandpass filter (nm)							
%	300.0	331.6	359.0	379.7	408.6	440.4	469.6	489.0
0.09			0.03	0.06	0.41	0.37	0.79	0.52
0.23			0.03	0.06	0.31	0.31	0.58	0.43
0.54			0.06	0.14	0.77	0.77	1.5	1.09
0.403			0.06	0.12	0.7	0.74	1.45	1.1
0.63			0.08	0.2	1.12	1.13	2.2	1.59
0.796			0.12	0.27	1.5	1.55	2.9	2.1
1		0.01	0.13	0.29	1.58	1.66	3	2.2
2.2	0.01	0.02	0.27	0.63	3.5	3.6	7	5
5	0.01	0.04	0.58	1.32	7.1	7.5	14.2	10.2
9.9	0.02	0.06	1.03	2.2	13	14.9	27	20
19.8	0.04	0.13	1.98	4	23	25	49	36
30.2	0.05	0.19	2.88	6.6	37	41	79	58
40.3	0.08	0.26	3.88	8.6	49	53	104	76
63	0.13	0.38	5.77	12.7	74	81	158	116
79.6	0.16	0.53	7.86	17.4	100	110	210	157
97.2	0.18	0.53	7.96	17.7	103	114	220	166
100	0.19	0.60	8.56	18.7	108	118	230	168

Table A3.3: Light intensity readings from Tektronix J16 photometer (mWm^{-2}) using eight bandpass filters of various wavelengths and a variety of neutral density filters in conditions used for calibration.

%	Central wavelength of bandpass filter (nm)							
	500.3	529.6	559.2	590.1	620.5	650.1	679.5	White light
0.09	0.6	0.65	0.94	0.86	1.01	0.83	0.99	145
0.23	0.46	0.47	0.69	0.64	0.74	0.55	0.71	124
0.54	1.16	1.23	1.79	1.66	1.9	1.45	1.78	300
0.403	1.18	1.28	1.91	1.8	2.1	1.64	2	350
0.63	1.69	1.7	2.5	2.4	2.7	2.1	2.5	430
0.796	2.2	2.3	3.5	3.2	3.7	2.8	3.3	560
1	2.4	2.5	3.7	3.3	3.9	3.1	3.7	600
2.2	5.4	5.6	8.2	7.6	8.7	6.8	8.3	1290
5	11	11.6	17	15.4	18.3	14.3	17.1	2600
9.9	22	23	34	31	36	28	34	5200
19.8	39	41	61	57	67	53	65	10300
30.2	62	66	98	90	103	80	96	15100
40.3	82	88	130	120	139	111	135	
63	125	132	195	180	200	166	200	
79.6	170	182	270	250	290	220	270	
97.2	178	190	290	260	300	240	280	
100	182	193	290	270	310	250	300	

Table A3.4: Light intensity readings from Tektronix J16 photometer using eight bandpass filters of various wavelengths and a variety of neutral density filters in conditions used for calibration.

	Central wavelength of bandpass filter (nm)							
%	300.0	331.6	359.0	379.7	408.6	440.4	469.6	489.0
0.09		0.0002	0.0006	0.0006	0.002	0.003	0.005	0.004
0.23		0.0004	0.0012	0.0014	0.005	0.006	0.012	0.01
0.54	0.0002	0.0008	0.0031	0.0036	0.012	0.013	0.033	0.027
0.403	0.0002	0.0008	0.0029	0.0032	0.011	0.013	0.032	0.027
0.63	0.0003	0.0012	0.0045	0.005	0.018	0.02	0.05	0.04
0.796	0.0003	0.0017	0.005	0.007	0.022	0.022	0.067	0.054
1	0.0004	0.002	0.007	0.007	0.023	0.024	0.072	0.057
2.2	0.0007	0.004	0.012	0.017	0.057	0.066	0.163	0.136
5	0.0014	0.011	0.029	0.035	0.122	0.141	0.327	0.264
9.9	0.0019	0.019	0.056	0.065	0.223	0.293	0.685	0.542
19.8	0.005	0.04	0.107	0.119	0.399	0.527	1.2	0.98
30.2	0.007	0.054	0.156	0.184	0.629	0.85	1.91	1.57
40.3	0.011	0.072	0.211	0.242	0.812	1.11	2.54	2.1
63	0.016	0.11	0.316	0.355	1.23	1.7	3.83	3.15
79.6	0.022	0.154	0.42	0.485	1.691	2.31	5.17	4.3
97.2	0.023	0.149	0.423	0.488	1.712	2.42	5.41	4.53
100	0.026	0.183	0.453	0.522	1.799	2.46	5.64	4.64

Table A3.5: Unadjusted meter readings from photodiode (RS 303-674) using eight bandpass filters of various wavelengths and a variety of neutral density filters in conditions used for calibration.

Multiplication factors for conversion to volts: unmarked=985.51; *= 99.97; **= 1.

%	Central wavelength of bandpass filter (nm)							
	500.3	529.6	559.2	590.1	620.5	650.1	679.5	White light
0.09	0.014	0.016	0.01	0.01	0.025	0.011	0.016	0.28*
0.23	0.011	0.013	0.021	0.02	0.038	0.022	0.031	0.509*
0.54	0.031	0.036	0.055	0.053	0.08	0.058	0.083	1.256*
0.403	0.03	0.036	0.06	0.057	0.086	0.065	0.088	1.473*
0.63	0.046	0.053	0.082	0.078	0.11	0.085	0.115	1.756*
0.796	0.062	0.071	0.109	0.104	0.141	0.114	0.152	2.35*
1	0.066	0.075	0.114	0.112	0.151	0.121	0.161	2.49*
2.2	0.148	0.17	0.263	0.254	0.32	0.274	0.34	0.052**
5	0.297	0.351	0.52	0.51	0.65	0.55	0.7	0.106**
9.9	0.622	0.72	1.09	1.07	1.38	1.18	1.43	0.22**
19.8	1.1	1.28	2.02	1.92	2.46	2.2	2.73	0.442**
30.2	1.79	2.07	3.13	3.07	3.9	3.31	4.05	0.63**
40.3	2.36	2.74	4.1	4.08	5.2	4.54	5.66	0.89**
63	3.58	4.12	6.42	6.17	0.772	6.86	0.836*	1.38**
79.6	4.87	5.65	0.84*	0.823*	1.036*	0.914*	1.119*	1.82**
97.2	5.13	5.98	0.89*	0.859*	1.106*	0.973*	1.192*	1.91**
100	5.26	6.12	0.92*	0.89*	1.12*	0.999*	1.233*	1.97**

Table A3.6: Unadjusted meter readings from photodiode (RS 303-674) using eight bandpass filters of various wavelengths and a variety of neutral density filters in conditions used for calibration.

Multiplication factors for conversion to volts: unmarked=985.51; *= 99.97; **= 1.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09					0.09	12	13.5	12.5	10.5
0.54					0.54	22	23	24.5	21.5
1	1.5	1.5	1.5	1.5	1	27.5	30	33.5	31.5
2.2	3	4	4	4	2.2	40	38	39	38
5	7.5	8	7	7	5	48	48	44.5	50
6.4	11.5	12	11	11	6.4	52.5	49	52	56
19.8	23	20	22	22	19.8	73.5	68	71	71
30.2	19	17.5	19	19	30.2	85.5	84.5	81	79.5
40.3	21	21.5	22	22	40.3	86	81	88	89
63	31	31.5	33	33	63	96	97	89	97
100	64.5	58	57.5	57.5	100	107	99	99.5	101
331.6nm					440.4nm				
0.09	8	8	9	8.5	0.09	13	12.5	13	11.5
0.54	19	20.5	16.5	17	0.54	22.5	24	25.5	24
1	28	24.5	26.5	27	1	28.5	36	32.5	32.5
2.2	36	37	36	33	2.2	47	40	42	41
5	50	53.5	51	47.5	5	51.5	51	54.5	52
6.4	48	48.5	50	40.5	6.4	49	54.5	55	55.5
19.8	66	59	59	58	19.8	71	68	69	72
30.2	58.5	64.5	66	66	30.2	86.5	81.5	78	73.5
40.3	74	67.5	64	67	40.3	87.5	92.5	94	86
63	73	76	77	79	63	100	101.5	94	92
100	93	91.5	99	86.5	100	113	105	101	104
359.0nm					469.6nm				
0.09	17.5	16	16	16	0.09	18	16.5	14.5	16.5
0.54	27.5	28	29.5	31	0.54	29	30.5	28	31
1	39	32.5	35	38	1	38	35.5	34.5	35
2.2	49	47	43	44	2.2	52	47	46	47.5
5	58	54.5	57	55	5	60	61	61	64
6.4	59	70	54	53	6.4	65.5	62	61	61
19.8	74.5	74	71	69	19.8	81	82	83	84
30.2	72	75	82	80	30.2	88.5	89	89	90.5
40.3	88.5	86	84	79.5	40.3	100	98	96	103
63	92.5	91.5	92.5	86	63	106	106	107	106.5
100	95.5	92	97	97.5	100	116	119	121	119
379.7nm					489.0nm				
0.09	11.5	12	11	11	0.09	19	20.5	20	19
0.54	21	22	22.5	22	0.54	29	30	30	29
1	31	28.5	31	30	1	37	36.5	38.5	39
2.2	42.5	36	39	40	2.2	48	47	45.5	48
5	50	52	46	50	5	56	62	61.5	60.5
6.4	54	55.5	52.5	48	6.4	62	60	60	62
19.8	70.5	68	62	68.5	19.8	75.5	76.5	77	79
30.2	73.5	76	79	81	30.2	83	83	89.5	92.5
40.3	77	78.5	78	80	40.3	90	95.5	95	89
63	86	82.5	81.5	87.5	63	106	99	102	100
100	98	99	93.5	100	100	115	111.5	110	104.5

Table A3.7: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 1, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	17	17.5	16.5	17.5	0.09	5	6	6	7
0.54	32	28	30	29.5	0.54	23	23	23	23.5
1	38	40	43	40	1	34	33	33.5	37.5
2.2	52	47.5	47	55	2.2	59.5	59	54	65.5
5	65	65.5	69	63.5	5	81	66	71	78
6.4	65.5	66	60.5	62.5	6.4	88	78	79	78
19.8	77	77.5	81.5	85	19.8	99	101	105	106
30.2	92	94	92	86	30.2	112	110	109	105
40.3	99.5	96.5	93	96	40.3	121	126	124.5	120
63	113	107.5	104	100	63	121	127	128.5	120.5
100	119.5	113.5	112	108.5	100	145.5	137	138	130
529.6nm					650.1nm				
0.09	17	17.5	16.5	17.5	0.09	7	7	6	6
0.54	32	28	30	29.5	0.54	28	26	31	28
1	38	40	43	40	1	46	38	40	40
2.2	52	47.5	47	55	2.2	64	61	65	63.5
5	65	65.5	69	63.5	5	83.5	87	92	89
6.4	65.5	66	60.5	62.5	6.4	95	90	86	87
19.8	77	77.5	81.5	85	19.8	112	113	116	115.5
30.2	92	94	92	86	30.2	132	122.5	126	118
40.3	99.5	96.5	93	96	40.3	130	127	125	135
63	113	107.5	104	100	63	137	129	140	142
100	119.5	113.5	112	108.5	100	145	133	147	148
559.2nm					679.5nm				
0.09	14.5	14.5	14.5	13	0.09	2	1.5	1.5	2
0.54	28	25.5	27.5	25.5	0.54	6	9	7	8
1	36	35	36.5	34	1	14	13	13.5	14
2.2	41.5	49.5	48.5	48.5	2.2	32.5	27.5	26.5	27
5	56.5	58	57	55.5	5	42	49	49	46
6.4	65	65.5	67	58.5	6.4	51	49	52	55
19.8	78	79.5	76	81	19.8	81	85	88	81
30.2	96.5	85.5	86.5	80.5	30.2	90	88.5	87	91
40.3	98	101.5	92	92.5	40.3	106	101	103	94
63	106	107	108.5	107	63	99	104.5	104.5	111
100	113	114	107	104.5	100	116	118	120	113
590.1nm									
0.09	4.5	7.5	6	6					
0.54	12	13	16	14.5					
1	17	17	18	17					
2.2	31	29.5	27	28.5					
5	36.5	36.5	45	38					
6.4	44	44	45	44					
19.8	62.5	61	61.5	58.5					
30.2	71	72	72.5	69					
40.3	71.5	76.5	68.5	75.5					
63	81.5	85.5	81.5	81					
100	86	91	80	92					

Table A3.8: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 1, a female *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09					0.09	0	0	0	0
0.54					0.54	5.5	5.5	5.5	5
1					1	7.5	6.5	7.5	6.5
2.2					2.2	12	10.5	10	9
5					5	13	15	14	15.5
6.4					6.4	16	16	17.5	17
19.8	6.5	6	5	5	19.8	25.5	22.5	23.5	25
30.2	5	7	5	5	30.2	27.5	28	26	26.5
40.3	6	8	5.5	5.5	40.3	30	29.5	29.5	29.5
63	7.5	8	8	8	63	35.5	33.5	34	34.5
100	20.5	17	19.5	19.5	100	40.5	37.5	41.5	38.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5.5	5.5	6.5	6	0.54	7.5	7	6.5	7
1	8.5	7	7	6	1	9.5	11	9	9
2.2	11	11	9	11	2.2	13	11.5	11.5	10
5	17	15.5	15	15	5	14	15	15	16.5
6.4	17	15	17.5	16.5	6.4	14.5	17	17.5	18
19.8	27.5	26	23.5	26	19.8	24.5	24	22.5	24.5
30.2	29.5	28.5	29	30	30.2	27	27	25.5	28
40.3	30.5	31	31.5	29.5	40.3	30	30.5	28	28
63	34.5	33	35	33.5	63	32	32.5	30.5	32.5
100	40.5	40.5	41.5	42.5	100	41.5	37.5	35.5	36
359.0nm					469.6nm				
0.09	5.5	4.5	5	5.5	0.09	5.5	5	7	6
0.54	8.5	6	6.5	7.5	0.54	7	9.5	9.5	7.5
1	9	10.5	8.5	10	1	10	10	9	8.5
2.2	12.5	13	13.5	12.5	2.2	14	12.5	13	15
5	17.5	18	18	18	5	19	16.5	18	16.5
6.4	18.5	19	19	19.5	6.4	18	18.5	17.5	16
19.8	26.5	25	25	24	19.8	26	27	22	25
30.2	30	30	31	30	30.2	29	28.5	28	28.5
40.3	35.5	32.5	30	30	40.3	30	30	32	30
63	40	37	36	36.5	63	36	36	34	33.5
100	39	40.5	40	41.5	100	37.5	38	38	37
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5.5	5	5.5	5	0.54	9	8	8.5	7.5
1	8	7	6.5	7	1	9	8.5	9.5	10
2.2	10	9	9.5	10	2.2	15.5	14	13	13.5
5	14	14	13.5	12	5	17	18.5	17	18
6.4	15	15	15.5	16	6.4	18	18	17.5	20
19.8	22.5	22	20.5	20	19.8	23	28	26.5	25
30.2	25.5	27.5	25	23.5	30.2	30	30	30	29
40.3	30.5	27.5	28	29.5	40.3	33	32.5	32	32
63	34	33	34.5	33	63	36	34.5	34	33.5
100	37.5	37.5	38	39.5	100	40	39	43.5	40.5

Table A3.9: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 2, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	8	7	8	8
0.54	7	5.5	4.5	6.5	0.54	24	24.5	23.5	26
1	9	8	8.5	7	1	34	34	32.5	35
2.2	13	12	10.5	10.5	2.2	45.5	44	44	42.5
5	15	16	16.5	16.5	5	63	56.5	58.5	52
6.4	18.5	18	17	16.5	6.4	61.5	61	59	58.5
19.8	28	26	26.5	26	19.8	78	71	73.5	74
30.2	31	30	33	28	30.2	82.5	80.5	85	80.5
40.3	35	31.5	31.5	34.5	40.3	88	87	81	84
63	37.5	37.5	36	37.5	63	99	92	92	91.5
100	46.5	40.5	39	39.5	100	96	98	96	95
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	5	4.5	5	6
0.54	7	5.5	4.5	6.5	0.54	16.5	15.5	16	18.5
1	9	8	8.5	7	1	23	22	21	27
2.2	13	12	10.5	10.5	2.2	42.5	35.5	37	34
5	15	16	16.5	16.5	5	47.5	44	46	46.5
6.4	18.5	18	17	16.5	6.4	50.5	47.5	50.5	48.5
19.8	28	26	26.5	26	19.8	72.5	65.5	65	66
30.2	31	30	33	28	30.2	79	72	73.5	70.5
40.3	35	31.5	31.5	34.5	40.3	87	75	79	81
63	37.5	37.5	36	37.5	63	86.5	87.5	87.5	86
100	46.5	40.5	39	39.5	100	97	92	90	91
559.2nm					679.5nm				
0.09	6.5	6	6	6	0.09	0	0	0	0
0.54	9	8.5	9.5	9	0.54	6	5.5	7	5
1	12	13.5	14	14.5	1	7	7	5	5.5
2.2	18	15.5	16	16.5	2.2	14.5	15	13	13
5	24	22.5	22.5	22.5	5	18.5	19.5	23	19.5
6.4	25	29.5	24.5	25	6.4	23	23.5	22	24.5
19.8	38.5	34	35.5	36	19.8	41.5	37.5	36.5	37.5
30.2	40	40	42	38	30.2	44.5	45.5	42	42.5
40.3	41	43	43	42.5	40.3	54	52.5	56.5	50
63	48.5	49.5	48	44	63	61	57	57	54
100	52.5	51.5	54.5	54	100	70	64.5	65	62
590.1nm									
0.09	0	0	0	0					
0.54	9	8.5	7.5	7.5					
1	10	12	11	11.5					
2.2	17.5	17.5	18	18					
5	26.5	24	24	25					
6.4	28	30	29.5	29					
19.8	43.5	41.5	40.5	41					
30.2	51	46.5	47	47					
40.3	53	50	49	52.5					
63	55.5	52.5	55	55.5					
100	56.5	59	62	60.5					

Table A3.10: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 2, a female *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	13.5	13.5	13	13
0.54	0	0	0	0	0.54	23.5	24	24	23.5
1	5	5	5.5	5.5	1	28.5	29.5	28.5	29.5
2.2	8	8	8.5	8.5	2.2	35	41	39	37.5
5	15.5	14.5	16	16	5	41.5	44.5	43	41.5
6.4	17	17.5	19	19	6.4	42.5	42.5	41.5	43
19.8	27	26.5	26	26	19.8	56.5	57.5	56	55
30.2	24	22.5	25	25	30.2	56	55.5	60	62.5
40.3	25.5	25.5	24	24	40.3	62	63.5	60.5	58.5
63	37.5	35	33.5	33.5	63	68.5	72.5	73.5	71
100	56.5	54	53.5	53.5	100	72	70.5	68	67
331.6nm					440.4nm				
0.09	12.5	11.5	9.5	9.5	0.09	0	0	0	0
0.54	23	20	20.5	20	0.54	8	8	9.5	11
1	28	26.5	30	29.5	1	17	17	18	17
2.2	34.5	34	33	32.5	2.2	23.5	24	23.5	23
5	47.5	47.5	45	43	5	28.5	32	32.5	34
6.4	46.5	49	48	45	6.4	37.5	36.5	35.5	35.5
19.8	51.5	53.5	55.5	58	19.8	39	42	44	43
30.2	57	56	53	52.5	30.2	50.5	48	49	47
40.3	61	66	63	61	40.3	54	56.5	58.5	56.5
63	65	60.5	61	60.5	63	55.5	56	54.5	53.5
100	70	74	73	71.5	100	63	66.5	66	59.5
359.0nm					469.6nm				
0.09	13.5	13.5	16.5	13.5	0.09	18.5	17.5	17.5	18.5
0.54	26	27.5	24.5	24.5	0.54	33	31	29.5	29.5
1	31.5	31.5	32	33.5	1	35.5	33.5	35	36
2.2	39.5	39.5	39.5	39.5	2.2	44.5	44	44	42
5	47	50.5	53	50	5	48	47.5	46	46
6.4	49.5	48.5	46.5	48	6.4	48.5	50.5	52.5	51
19.8	57.5	61	63	66.5	19.8	60.5	57	61	55
30.2	66	65	62.5	60.5	30.2	63	64.5	62	60.5
40.3	64.5	63.5	65	68.5	40.3	64.5	66	67.5	66.5
63	75	69.5	69	65	63	70.5	69	66.5	69.5
100	73.5	71	71	75	100	81	76	74	72.5
379.7nm					489.0nm				
0.09	11	13	12.5	11.5	0.09	16	14.5	15	17.5
0.54	18.5	19.5	21.5	20	0.54	27	27	26.5	26.5
1	25.5	27.5	30.5	31	1	34.5	34.5	33.5	33.5
2.2	34	34.5	35	35	2.2	39	39.5	39	38.5
5	44	43	42.5	39.5	5	42.5	43	43.5	41.5
6.4	43	45.5	47	46	6.4	48.5	49	47	44.5
19.8	54.5	53	52	52	19.8	56	55.5	57	61.5
30.2	57	60.5	64	58.5	30.2	64.5	62.5	60	60
40.3	58.5	58	60	56	40.3	65.5	69	71	73
63	65	71	67.5	64	63	69	68	66	67
100	66.5	65	65	68.5	100	74.5	77	78	74.5

Table A3.11: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 3, a female *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	15.5	16	16	16	0.09	5.5	6	8	7.5
0.54	22.5	23.5	22.5	22.5	0.54	25	24.5	24	24
1	31	28.5	28.5	32	1	37	40	36.5	38
2.2	43.5	44	41	39	2.2	51	51	48.5	49
5	43	45	42.5	44.5	5	69.5	73.5	68.5	65
6.4	52	49	48	47.5	6.4	67	67	64	63
19.8	58	56	59	63	19.8	83.5	86.5	88	89
30.2	64	62.5	61	62	30.2	87	86.5	84.5	82.5
40.3	65.5	67.5	71	73	40.3	87.5	92	95	92
63	71.5	68.5	70.5	69	63	92.5	90	92.5	88
100	80	73.5	74	70.5	100	101	103	106.5	104.5
529.6nm					650.1nm				
0.09	15.5	16	16	16	0.09	0	0	0	0
0.54	22.5	23.5	22.5	22.5	0.54	7.5	9.5	8.5	7.5
1	31	28.5	28.5	32	1	15	14	12.5	12
2.2	43.5	44	41	39	2.2	18.5	18	19	17.5
5	43	45	42.5	44.5	5	32	34.5	32	29.5
6.4	52	49	48	47.5	6.4	33.5	36	38.5	38
19.8	58	56	59	63	19.8	52	57.5	59.5	57
30.2	64	62.5	61	62	30.2	56.5	60	65	68
40.3	65.5	67.5	71	73	40.3	65	62.5	64	68
63	71.5	68.5	70.5	69	63	81	77	72	67.5
100	80	73.5	74	70.5	100	72.5	73	78.5	78
559.2nm					679.5nm				
0.09	12	12.5	12	11	0.09	0	0	0	0
0.54	22	26	26	25	0.54	0	0	0	0
1	27	28	30	29.5	1	4	2.5	3	2.5
2.2	36	36	35.5	34.5	2.2	8	8	10.5	10
5	44	46	44.5	44.5	5	14.5	15	15.5	14
6.4	46.5	49	49.5	55	6.4	18	20.5	21	19.5
19.8	61.5	58	57.5	57	19.8	36.5	35	36	36.5
30.2	68	72	68	68	30.2	50	50.5	47	43.5
40.3	66	63.5	62	64	40.3	52	50.5	52	55
63	77	72.5	70.5	69.5	63	68.5	65.5	63	63
100	72	77	80	80	100	68.5	68	65.5	67.5
590.1nm									
0.09	5.5	6.5	8.5	8					
0.54	21.5	22	23.5	21.5					
1	30.5	32.5	36	36					
2.2	45	42	42	41.5					
5	53	55.5	57.5	56					
6.4	56.5	54.5	51	51					
19.8	66.5	69.5	71.5	70					
30.2	70.5	71.5	68	66.5					
40.3	82	82	77.5	74					
63	78	76.5	75	78.5					
100	85.5	85	81	80					

Table A3.12: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 3, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	3	4	3	4
0.54	0	0	0	0	0.54	5.5	6.5	7.5	6
1	0	0	0	0	1	8.5	10	7	8
2.2	0	0	0	0	2.2	13.5	13	14	13
5	0	0	0	0	5	15.5	16.5	17.5	18
6.4	0	0	0	0	6.4	18.5	18.5	19.5	18
19.8	3.5	2	2.5	2.5	19.8	27.5	26.5	27.5	28.5
30.2	4	3	3	3	30.2	35.5	31.5	23	29.5
40.3	3.5	3	5.5	5.5	40.3	32	33.5	33	34
63	7.5	5.5	5.5	5.5	63	38.5	36.5	34.5	35.5
100	14	13.5	14.5	14.5	100	37	40.5	40	37
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	6.5	6	6.5	7
1	7	9.5	8	8.5	1	10.5	7	8.5	10
2.2	11	11.5	12	12	2.2	15.5	15.5	14.5	15.5
5	12.5	14	12.5	12	5	22	22	20.5	21
6.4	12.5	11.5	14	13.5	6.4	24	23.5	23	23.5
19.8	22	21	21	19.5	19.8	34	33	33	35
30.2	28.5	22.5	21	20.5	30.2	34.5	38	40	39
40.3	30	21.5	23	23	40.3	38.5	40.5	38	38
63	27	29.5	27	25	63	44	46	43.5	41.5
100	30	32.5	27.5	29.5	100	51	50	48.5	47.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5	7	4.5	5	0.54	7	7.5	6.5	6.5
1	10.5	11	10	7.5	1	17.5	13.5	13	12.5
2.2	16	14.5	14.5	15	2.2	16	18	19.5	17.5
5	19.5	19.5	21.5	17.5	5	20.5	25	22	25.5
6.4	25	20	21	22	6.4	24	27	25	26
19.8	31	34.5	33.5	30.5	19.8	33.5	37.5	34	36.5
30.2	33.5	35.5	34.5	35	30.2	37.5	40.5	37.5	39
40.3	37.5	40	40.5	36	40.3	45.5	43	41	42
63	40.5	42.5	42	40	63	46.5	44	46.5	49.5
100	44	41.5	41.5	45.5	100	47.5	45.5	48	48
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	5.5	5	5	0.54	9.5	13	10	10.5
1	10	9	9.5	9.5	1	14.5	17	14.5	18.5
2.2	17	18.5	16	17.5	2.2	19	24	18.5	18.5
5	20	23.5	22	24	5	32	29	26	25.5
6.4	27	25.5	24	30.5	6.4	27.5	30.5	33	26
19.8	34.5	33.5	32.5	34.5	19.8	37.5	36.5	35.5	43.5
30.2	38	37	36.5	40.5	30.2	42	42	41.5	45.5
40.3	41	42.5	41	40	40.3	45.5	44	44.5	44
63	47	48	45.5	46	63	44	51	49.5	44.5
100	50	51	50.5	53	100	51.5	49.5	49	51.5

Table A3.13: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 4, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	2	2.5	2.5	2.5	0.09	0	0	0	0
0.54	5.5	5	6.5	6.5	0.54	0	0	0	0
1	9	12.5	9.5	9.5	1	5	5.5	6	4.5
2.2	20	14.5	16	14	2.2	7	6.5	7.5	7.5
5	22	22.5	26	21.5	5	11.5	13.5	13.5	13.5
6.4	30	25	24	23.5	6.4	24	20	19.5	16.5
19.8	39	34	31.5	30.5	19.8	23.5	26.5	25	23.5
30.2	40.5	39	39.5	39	30.2	35.5	38.5	41.5	41
40.3	43	42	43.5	51.5	40.3	47.5	44.5	41.5	46
63	49	46.5	46.5	54.5	63	47.5	54	49	49
100	52	51.5	51.5	61	100	53	50.5	51.5	52.5
529.6nm					650.1nm				
0.09	2	2.5	2.5	2.5	0.09	0	0	0	0
0.54	5.5	5	6.5	6.5	0.54	5	6	6	5
1	9	12.5	9.5	9.5	1	7	8.5	7.5	5.5
2.2	20	14.5	16	14	2.2	7.5	8	7.5	8.5
5	22	22.5	26	21.5	5	19	15.5	16	14.5
6.4	30	25	24	23.5	6.4	21	18.5	17	18.5
19.8	39	34	31.5	30.5	19.8	34	36	36.5	37.5
30.2	40.5	39	39.5	39	30.2	43	43	40.5	41
40.3	43	42	43.5	51.5	40.3	52.5	50.5	50.5	50.5
63	49	46.5	46.5	54.5	63	53	51.5	52.5	53
100	52	51.5	51.5	61	100	63	63.5	59	59.5
559.2nm					679.5nm				
0.09	3.5	4.5	4	4.5	0.09	0	0	0	0
0.54	8.5	8	6	8	0.54	0	0	0	0
1	12	11.5	11.5	10.5	1	0	0	0	0
2.2	20	22	17	16	2.2	0	0	0	0
5	25.5	25	24.5	23	5	0	0	0	0
6.4	22.5	27	27.5	28.5	6.4	6	6	7	6.5
19.8	42	38.5	38	37	19.8	8	10.5	7.5	11.5
30.2	39.5	43	47	45	30.2	17	14	14.5	14
40.3	45.5	46.5	45	40.5	40.3	17	18	19.5	20.5
63	50	53	53	50.5	63	24	22.5	20.5	24.5
100	59	56.5	53	50.5	100	28.5	26.5	29	31
590.1nm									
0.09	0	0	0	0					
0.54	3.5	4.5	3	3					
1	5.5	5.5	6.5	6					
2.2	10.5	11	15.5	11.5					
5	18.5	21	15.5	21.5					
6.4	16	19.5	17.5	19					
19.8	34	30.5	32	28					
30.2	33.5	34.5	37.5	37					
40.3	38.5	37	38.5	41					
63	42	41	42.5	40					
100	48.5	49.5	51	51					

Table A3.14: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 4, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	3	2.5	2.5	3
0.54	0	0	0	0	0.54	9	8.5	9.5	7
1	0	0	0	0	1	15	17	17	15
2.2	0	0	0	0	2.2	25	28.5	27	27
5	0	0	0	0	5	37	39.5	42.5	42
6.4	4	5.5	5	5	6.4	43.5	43	43	42.5
19.8	9	8	9	9	19.8	67.5	63	63	62
30.2	7	8	10	10	30.2	75	75.5	79	77
40.3	9	10	8.5	8.5	40.3	83.5	80.5	79.5	84
63	15	15	16	16	63	85	88	86.5	87.5
100	40.5	40	39	39	100	95	92.5	94.5	95
331.6nm					440.4nm				
0.09	3.5	3.5	3	3	0.09	3.5	3.5	3	3.5
0.54	10	8.5	7	8	0.54	11	11	12.5	14.5
1	15	16	14	14.5	1	19	19	21	19
2.2	23	25	27	23.5	2.2	31	27	30	33
5	41	41	40	36.5	5	47	47.5	43	43.5
6.4	45	48	42.5	40.5	6.4	50.5	50	50	51
19.8	62.5	61	61.5	65	19.8	73	73	72	69
30.2	69	72	69	69	30.2	82.5	78	75.5	76
40.3	77.5	73	71	71.5	40.3	81.5	83	87	82
63	80	81.5	80	78	63	95.5	98	95	95
100	93.5	88.5	95	87.5	100	99	97.5	90.5	96
359.0nm					469.6nm				
0.09	2.5	3	4	3	0.09	10	8.5	10	10
0.54	8	9.5	9	9	0.54	11.5	15	14.5	14
1	16	16.5	17	17	1	27	22.5	24.5	24.5
2.2	27	28.5	28	27	2.2	29	34	30	34
5	46.5	47	42.5	41.5	5	48	47	46	46
6.4	50	46.5	46.5	42	6.4	54	53	52.5	53
19.8	68	62	61	61.5	19.8	78	71	69	70
30.2	77	75.5	70.5	71	30.2	88	89	85	80
40.3	80.5	82	73	73.5	40.3	88	83	85	88.5
63	89	92	87	81.5	63	96.5	97.5	95	93
100	93	88.5	89.5	90.5	100	106.5	105	108	102
379.7nm					489.0nm				
0.09	9	7.5	7.5	6.5	0.09	0	0	0	0
0.54	11	11	13.5	11.5	0.54	6.5	6	6	6
1	22	19.5	19.5	19	1	16	16	16	15.5
2.2	31.5	31.5	32	31.5	2.2	27	25	24.5	24.5
5	47.5	48	50	45.5	5	38	40	39.5	40
6.4	51	51.5	52	55	6.4	57	55.5	51	52.5
19.8	73	70	74	71.5	19.8	60.5	61.5	59	63.5
30.2	84.5	88.5	80.5	81.5	30.2	83	78	80	85
40.3	86	87	89	83	40.3	93	91	92.5	93
63	97	97.5	94	93	63	96.5	91.5	98	108
100	101.5	104	105.5	104	100	109.5	103	101	105

Table A3.15: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 5, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	7.5	7	6	5.5	0.09	10	11	7.5	8
0.54	16.5	18	18	19	0.54	36.5	39	36.5	40
1	28	26.5	25.5	27	1	54.5	54	53.5	55
2.2	43	42.5	36	38	2.2	84.5	79	72	78
5	60	61	62.5	59	5	93	95	95.5	95
6.4	67	75.5	62.5	64	6.4	97	95.5	99	98
19.8	83	76.5	82	80.5	19.8	116	113	113	113
30.2	100	94	95	94.5	30.2	118	119	114	116
40.3	97	102	104	92	40.3	120.5	125	120	120.5
63	109	108	105	105	63	124	125	125	117
100	108.5	110	107	115	100	130.5	130	122.5	129.5
529.6nm					650.1nm				
0.09	7.5	7	6	5.5	0.09	3	3	3	4.5
0.54	16.5	18	18	19	0.54	19	20	20	19.5
1	28	26.5	25.5	27	1	33	33.5	33	32.5
2.2	43	42.5	36	38	2.2	56	55	56.5	54
5	60	61	62.5	59	5	77	77	77.5	77
6.4	67	75.5	62.5	64	6.4	87	86	82.5	82.5
19.8	83	76.5	82	80.5	19.8	102	105.5	107	107
30.2	100	94	95	94.5	30.2	111.5	111	108	106
40.3	97	102	104	92	40.3	114.5	116.5	115	110
63	109	108	105	105	63	115	120.5	119	122.5
100	108.5	110	107	115	100	121	123	133.5	120
559.2nm					679.5nm				
0.09	6	6	8	8	0.09	0	0	0	0
0.54	20	22.5	24	22.5	0.54	3.5	3	3	3.5
1	33.5	32.5	29.5	29.5	1	6	7	6	6
2.2	52	51	50	49.5	2.2	15	16.5	20.5	16.5
5	66.5	63	64	68	5	28	31.5	28.5	29
6.4	75.5	71	70.5	70.5	6.4	36	41.5	41.5	37.5
19.8	97	101	100	93.5	19.8	66.5	68	71	69
30.2	103	105.5	108	106.5	30.2	79	86	87.5	81.5
40.3	109	108	110	109	40.3	87	89.5	93.5	90.5
63	117	111	114	109	63	99	96.5	99	101.5
100	116	118.5	120	117.5	100	110.5	108	106	104
590.1nm					705.0nm				
0.09	3	2.5	3	3	0.09	0	0	0	0
0.54	18.5	15	13	15	0.54	0	0	0	0
1	22	20	20.5	19.5	1	0	0	0	0
2.2	40	37	37	37.5	2.2	0	0	0	0
5	56.5	55.5	57.5	55	5	0	0	0	0
6.4	56	61.5	58.5	61	6.4	0	0	0	0
19.8	87	92	86	86.5	19.8	0	0	0	0
30.2	95.5	92	88	88	30.2	0	0	0	0
40.3	106.5	106	99	100	40.3	0	0	0	0
63	106.5	104	103.5	110	63	0	0	0	0
100	117	113.5	109.5	104	100	0	0	0	0

Table A3.16: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 5, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	2.5	1.5	1	1.5
0.54	0	0	0	0	0.54	3	3	3	3
1	0	0	0	0	1	4.5	4	4	3.5
2.2	0	0	0	0	2.2	5.5	5.5	5	5
5	0	0	0	0	5	6.5	7.5	7.5	6.5
6.4	3	3.5	3.5	3.5	6.4	8	7.5	7.5	6
19.8	5	5	4.5	4.5	19.8	12	11.5	12	12
30.2	5	4.5	5	5	30.2	16	15	15	15.5
40.3	6.5	6	5	5	40.3	17.5	16.5	17.5	16.5
63	6	5.5	6.5	6.5	63	20.5	20	20	20
100	18.5	18	18.5	18.5	100	22.5	23	22.5	22.5
331.6nm					440.4nm				
0.09	3	2.5	3.5	2.5	0.09	0	0	0	0
0.54	4.5	4.5	4.5	4	0.54	4.5	4.5	5.5	4
1	5	5.5	5.5	6.5	1	5.5	6.5	4.5	5
2.2	6.5	9	9	7	2.2	7	7.5	8	7.5
5	10.5	12	13	13	5	11.5	12.5	13	12.5
6.4	12	12.5	12	14	6.4	13	14.5	15.5	14
19.8	20.5	21.5	22	21.5	19.8	23.5	23.5	25	25
30.2	23.5	24.5	23.5	25	30.2	28.5	29.5	29.5	29.5
40.3	26	26.5	26.5	27	40.3	33.5	33.5	31	33.5
63	29.5	30.5	28.5	31	63	39.5	41	42.5	40
100	36.5	35	30.5	33	100	46	45	46.5	47.5
359.0nm					469.6nm				
0.09	3	3	3	3	0.09	0	0	0	0
0.54	5	5.5	5.5	5	0.54	4	3.5	3	3
1	8	7.5	7.5	7.5	1	4	5	4	5
2.2	10.5	10	11	9.5	2.2	7	7.5	7.5	7.5
5	17.5	16.5	16.5	17.5	5	11	11	11.5	11
6.4	17	18.5	18	18	6.4	12.5	12	12	11.5
19.8	30	29	30	28	19.8	19	18.5	19	18
30.2	35.5	37.5	35.5	36.5	30.2	23	23	23	22.5
40.3	39.5	40.5	40.5	41.5	40.3	25.5	25.5	26	25
63	46	46.5	44.5	45	63	31	30	29.5	30
100	57	55	54	54	100	35	34	33.5	33
379.7nm					489.0nm				
0.09	2.5	3	3	2.5	0.09	2.5	2.5	3	3.5
0.54	4	6	5	5	0.54	4.5	4.5	6	4.5
1	8	7	8	8.5	1	6.5	5.5	5.5	7.5
2.2	9.5	10	10	9.5	2.2	9.5	10.5	11	9.5
5	14	14	13.5	13.5	5	13	13.5	14.5	13.5
6.4	15.5	16	16	15	6.4	15.5	16.5	16	18
19.8	23	23	23.5	22.5	19.8	26.5	27.5	26	26.5
30.2	28.5	29	28.5	28.5	30.2	31.5	32.5	31.5	32
40.3	31	30.5	30	31	40.3	37.5	42.5	39	39.5
63	37	37.5	41	37.5	63	44	43	42.5	41.5
100	42	41.5	42	40.5	100	48.5	48.5	47.5	47

Table A3.17: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 6, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	2	1.5	2	1.5	0.09	0	0	0	0
0.54	3.5	3.5	4	3.5	0.54	0	0	0	0
1	5	5	5.5	5.5	1	1.5	2	1.5	1
2.2	8.5	7.5	7	7.5	2.2	3	3.5	3	3.5
5	9.5	9	9	9	5	5.5	6	6.5	6
6.4	9	9.5	9.5	9.5	6.4	7	6.5	6.5	7
19.8	13	10.5	11.5	12.5	19.8	16	15.5	16	16
30.2	12.5	13.5	13	12.5	30.2	20	20	20	19.5
40.3	15	16.5	14	13	40.3	24	22.5	23.5	22
63	14.5	15	15.5	15	63	28.5	28.5	28.5	28.5
100	15.5	16	17.5	16.5	100	34.5	35.5	33.5	33
529.6nm					650.1nm				
0.09	2	1.5	2	1.5	0.09	0	0	0	0
0.54	3.5	3.5	4	3.5	0.54	0	0	0	0
1	5	5	5.5	5.5	1	3.5	3	3	3.5
2.2	8.5	7.5	7	7.5	2.2	7.5	8	7	7.5
5	9.5	9	9	9	5	16	16.5	16.5	17
6.4	9	9.5	9.5	9.5	6.4	19	19.5	20	19
19.8	13	10.5	11.5	12.5	19.8	37.5	43.5	42.5	39.5
30.2	12.5	13.5	13	12.5	30.2	47.5	47	47	47.5
40.3	15	16.5	14	13	40.3	52.5	57.5	61	57
63	14.5	15	15.5	15	63	62	65	62	60.5
100	15.5	16	17.5	16.5	100	70.5	68	68.5	72.5
559.2nm					679.5nm				
0.09	1	1.5	1.5	1.5	0.09	0	0	0	0
0.54	2	3	2.5	2.5	0.54	0	0	0	0
1	2.5	2	3.5	2.5	1	0	0	0	0
2.2	2.5	2.5	2.5	2.5	2.2	0	0	0	0
5	3	3.5	3	3	5	0	0	0	0
6.4	3.5	3	3.5	4	6.4	3.5	3	3.5	3
19.8	5	5.5	5	5.5	19.8	5	6.5	6.5	6
30.2	6.5	6	6	7	30.2	9.5	8.5	9.5	9
40.3	7	7	7	7	40.3	12.5	14	13	12
63	9	9	9	9	63	19.5	18	19.5	18
100	12	11.5	13	14	100	28	26.5	26	27.5
590.1nm									
0.09	0	0	0	0					
0.54	0	0	0	0					
1	0	0	0	0					
2.2	1.5	2	1.5	1.5					
5	3	3	2.5	3					
6.4	3.5	4	3.5	3					
19.8	8	7	7.5	7.5					
30.2	10	9	9	9					
40.3	12	11.5	11	11					
63	15.5	14	15.5	14.5					
100	18.5	21.5	20	19					

Table A3.18: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 6, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	0	0	0	0	2.2	0	0	0	0
5	0	0	0	0	5	4.5	5	4	4
6.4	0	0	0	0	6.4	6	5.5	6.5	6
19.8	0	0	0	0	19.8	8.5	10	10	9.5
30.2	0	0	0	0	30.2	11	12.5	11	11.5
40.3	0	0	0	0	40.3	12.5	13.5	13	13
63	3.5	3	3	3	63	14.5	13	12.5	12
100	6	6	7	7	100	15	15.5	16.5	16.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	1.5	1	1.5	1
2.2	0	0	0	0	2.2	3.5	3	3	2.2
5	0	0	0	0	5	4	3.5	4	4
6.4	0	0	0	0	6.4	4.5	4	4	4
19.8	3	4.5	5	4.5	19.8	7.5	6.5	6.5	7
30.2	6	5	5.5	6	30.2	9	8.5	9	9
40.3	7	7.5	8.5	6.5	40.3	10.5	10	10	9.5
63	10	8.5	8	8.5	63	13	12.5	12	12
100	11.5	11.5	11	11	100	15.5	14.5	15	14.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	2	2	2.5	2
0.54	0	0	0	0	0.54	4	3	3	3
1	3.5	3	3.5	3	1	5.5	5.5	5	5
2.2	5.5	5	5	5	2.2	9	9.5	11	10.5
5	9	10	9.5	9.5	5	14	15	15.5	15.5
6.4	11.5	11	9	10	6.4	18.5	18	17.5	17.5
19.8	15.5	14	14.5	15.5	19.8	27	30	27.5	27.5
30.2	19.5	18.5	19	19.5	30.2	35.5	35.5	35.5	36.5
40.3	22	22.5	23.5	23	40.3	38.5	38.5	36.5	38.5
63	27.5	25.5	24.5	25	63	46.5	49	46.5	48
100	31	30	30	32	100	53.5	55	52.5	53.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	2.5	3	2.5	2.5
1	1.5	1	1.5	1	1	4	3	3	3
2.2	3	3	3	3.5	2.2	5	5.5	5.5	5.5
5	4.5	4	4	4	5	9	10	10.5	10
6.4	4.5	4	4	4	6.4	13	14	13.5	14
19.8	7.5	6.5	6.5	7	19.8	17.5	16.5	15	15.5
30.2	9.5	8	8.5	8.5	30.2	23.5	26	26.5	25.5
40.3	9.5	9.5	9	9	40.3	33.5	32.5	33.5	33
63	12	12	12.5	11.5	63	40	38	36.5	37
100	14	14	13.5	13.5	100	42.5	44	44	45

Table A3.19: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 7, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	3.5	2	2.5	2
0.54	4.5	3.5	2.5	3	0.54	4	4	3.5	3.5
1	5.5	5.5	5.5	5	1	6.5	6.5	6	6.5
2.2	9	9	10	9	2.2	13.5	13.5	13.5	13
5	13.5	13.5	13	14.5	5	24	24	24.5	25.5
6.4	15	15	15.5	15	6.4	30	29.5	28.5	28
19.8	25.5	25.5	24.5	23.5	19.8	54.5	56	56.5	52.5
30.2	33.5	32.5	36.5	31.5	30.2	66	66.5	68.5	65.5
40.3	38	36.5	37.5	35	40.3	74	78	78	77
63	45	41.5	43.5	43	63	87.5	86.5	87	84.5
100	51.5	52	49	51	100	95	92.5	91	89
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4.5	3.5	2.5	3	0.54	0	0	0	0
1	5.5	5.5	5.5	5	1	0	0	0	0
2.2	9	9	10	9	2.2	1.5	1	1.5	1
5	13.5	13.5	13	14.5	5	2.5	2	2	2
6.4	15	15	15.5	15	6.4	2.5	2	2.5	2.5
19.8	25.5	25.5	24.5	23.5	19.8	5	6	6	6.5
30.2	33.5	32.5	36.5	31.5	30.2	8	9	8.5	8
40.3	38	36.5	37.5	35	40.3	10.5	10.5	11	10.5
63	45	41.5	43.5	43	63	14.5	16	15.5	16
100	51.5	52	49	51	100	20	19.5	18.5	19
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	3	3	3.5	3.5	2.2	0	0	0	0
5	5.5	5.5	5	5	5	0	0	0	0
6.4	8.5	6.5	7	6.5	6.4	0	0	0	0
19.8	11.5	12.5	10.5	12.5	19.8	1.5	2	1.5	1.5
30.2	14	14	13	14.5	30.2	2.5	2	2.5	2.5
40.3	18	18.5	17	17	40.3	3	3	3	3.5
63	20	19	19	18.5	63	4	4	4	4.5
100	24.5	24	22.5	22	100	5.5	5.5	5	5.5
590.1nm									
0.09	0	0	0	0					
0.54	0	0	0	0					
1	3	2.5	3	3					
2.2	3.5	4	5	3.5					
5	6.5	6	7	6					
6.4	7.5	8.5	7	6.5					
19.8	15.5	15.5	16	15.5					
30.2	22.5	23	22.5	23.5					
40.3	27.5	29	28.5	28					
63	33.5	34	34	34					
100	41.5	42.5	42	42.5					

Table A3.20: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 7, a male *Lucilia sericata,* using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3	4	4	4
1	0	0	0	0	1	4	4.5	4	4.5
2.2	0	0	0	0	2.2	4.5	4.5	4	4.5
5	0	0	0	0	5	6.5	6.5	7	7
6.4	0	0	0	0	6.4	8	6.5	7	5.5
19.8	0	0	0	0	19.8	12.5	13.5	13.5	13.5
30.2	0	0	0	0	30.2	12.5	12	14	15.5
40.3	2	3	2.5	2.5	40.3	17.5	12	13	14.5
63	3	4	2.5	2.5	63	20	21.5	20.5	21.5
100	6	6	6	6	100	26.5	26.5	21.5	21.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	4	2.5	2.5	2.5
0.54	0	0	0	0	0.54	3	4	3.5	3.5
1	3.5	3	2.5	2.5	1	4	3.5	4	4
2.2	4	4	3.5	4.5	2.2	7.5	5.5	5.5	5.5
5	4	4	5.5	6.5	5	8	9	9	9.5
6.4	5	5	5.5	5.5	6.4	7.5	8.5	9.5	8
19.8	9.5	10	11	8	19.8	15.5	15.5	17	16.5
30.2	10.5	11.5	10.5	12	30.2	19.5	19	16.5	16.5
40.3	13.5	13.5	10.5	9.5	40.3	19.5	18.5	20	20
63	11	14	14	15.5	63	22.5	22	23	25
100	20	18	14.5	15	100	30	27	29	28.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	2	1.5	1.5	1.5
0.54	1.5	3	2	2	0.54	5.5	4.5	3.5	5
1	5	4.5	5.5	4.5	1	6.5	6.5	7	6.5
2.2	6	5.5	6	4	2.2	8.5	8	9.5	8.5
5	9	9.5	9	9.5	5	14	11.5	11.5	12
6.4	9.5	11	10	11	6.4	14	14	14	13
19.8	11.5	13	10	9	19.8	21.5	20.5	20	19
30.2	18	18.5	18.5	17.5	30.2	26	26.5	25.5	24.5
40.3	23	23.5	23.5	21.5	40.3	27	27	27	28
63	16.5	17	18	21.5	63	29	32.5	32.5	28
100	23	21.5	26	26	100	32.5	35	36	37
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	4.5	4.5	4	4
1	2	3	2.5	2.5	1	3.5	5	5	5
2.2	3	3	4.5	4.5	2.2	8.5	9.5	9	8.5
5	5	4	4.5	4.5	5	11.5	12	12	14
6.4	5.5	6	5	5	6.4	14	13.5	13	13.5
19.8	7.5	8.5	8.5	8	19.8	21.5	21.5	22	22
30.2	12.5	10.5	8	8	30.2	27.5	27	27	27.5
40.3	11.5	11.5	12	10	40.3	31.5	28	25.5	27
63	13.5	13.5	16.5	14	63	33.5	35	33	30.5
100	19	19.5	17	18	100	37	40	38	38

Table A3.21: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 8, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4.5	4	4.5	4	0.54	3	3.5	3	3.5
1	5	5.5	5.5	5	1	6	5.5	6.5	6.5
2.2	8	10	9	7	2.2	9.5	10	10.5	12.5
5	8.5	10	9	7	5	14	16.5	18.5	19
6.4	11	9.5	13.5	13	6.4	18.5	23	21.5	21.5
19.8	21.5	22	23.5	23.5	19.8	27	30	33	33.5
30.2	20	23	24.5	25.5	30.2	41.5	42.5	44	44.5
40.3	30.5	29.5	31.5	32.5	40.3	36	35.5	37.5	43
63	30.5	28.5	27	29.5	63	42.5	42.5	47.5	49.5
100	38	39.5	40.5	38	100	51.5	52	53	50.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4.5	4	4.5	4	0.54	1.5	1.5	2	2.5
1	5	5.5	5.5	5	1	2.5	3.5	3.5	3
2.2	8	10	9	7	2.2	4.5	5.5	5.5	6
5	8.5	10	9	7	5	8.5	8	7.5	7.5
6.4	11	9.5	13.5	13	6.4	11	12	10	11.5
19.8	21.5	22	23.5	23.5	19.8	17.5	19.5	20.5	19.5
30.2	20	23	24.5	25.5	30.2	21	21.5	21.5	24.5
40.3	30.5	29.5	31.5	32.5	40.3	29.5	31	27	22
63	30.5	28.5	27	29.5	63	34	34	35.5	32.5
100	38	39.5	40.5	38	100	39	40	42	41
559.2nm					679.5nm				
0.09	3	3.5	3.5	3.5	0.09	0	0	0	0
0.54	6.5	7.5	5.5	6.5	0.54	0	0	0	0
1	7	8.5	8.5	8.5	1	0	0	0	0
2.2	12	12	13.5	13	2.2	0	0	0	0
5	19	20	20.5	20.5	5	3.5	2.5	2.5	2.5
6.4	20.5	21	22	24	6.4	3.5	4	4.5	3.5
19.8	30.5	33	33.5	35	19.8	6	6	6	6
30.2	41.5	39	36.5	39	30.2	8.5	9.5	9	9
40.3	45.5	44	39	38.5	40.3	9	10.5	9	9
63	51.5	52	52.5	47	63	13	13	14.5	14
100	54	55	55	55	100	16	14	16	17
590.1nm									
0.09	2	2	2.5	2.5					
0.54	4	4	4	4					
1	6.5	5	5.5	5.5					
2.2	8.5	11	9	8.5					
5	16	16	17	16.5					
6.4	20	19.5	20.5	16					
19.8	28	30.5	27.5	28					
30.2	35	31.5	32.5	33.5					
40.3	37.5	40.5	39	40					
63	45	44.5	46	38.5					
100	43	45.5	47	44					

Table A3.22: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 8, a male *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	2.5	2.5	1.5	1.5
1	0	0	0	0	1	3	2.5	2.5	4
2.2	0	0	0	0	2.2	5	5	5.5	6.5
5	0	0	0	0	5	12	11	10	10
6.4	1	1.5	1.5	1.5	6.4	11	11.5	12	12
19.8	2.5	2	2	2	19.8	20.5	20	20	20.5
30.2	2	2	2	2	30.2	26	29.5	28.5	27.5
40.3	2.5	2.5	2.5	2.5	40.3	31.5	30	31	31.5
63	2	3.5	3.5	3.5	63	39.5	38	39	38
100	8.5	9	8.5	8.5	100	46.5	47.5	48	45.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	1.5	2	2	2	0.54	2.5	2	2	2.5
1	2.5	2.5	2.5	3	1	5	4.5	5	4
2.2	6	5	5.5	5	2.2	9	8.5	7.5	8.5
5	8.5	9	8	9	5	14	14	14	14
6.4	9.5	9.5	10	9.5	6.4	16	17	17	18
19.8	16	16.5	17	18	19.8	27.5	26.5	27.5	27
30.2	20	21	21.5	20.5	30.2	36	35.5	34.5	35
40.3	24.5	22.5	22	23	40.3	40	37.5	40	38.5
63	30	28.5	28.5	28	63	46	49	48	45.5
100	38.5	37	35.5	40.5	100	54.5	53.5	55	54.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	4.5	4.5	5	5
1	4	3.5	4.5	5	1	9.5	8	8.5	9.5
2.2	8	9	8	7.5	2.2	14	14	13.5	15.5
5	18	15.5	14.5	16	5	23.5	23	22	25.5
6.4	16	18	18	17.5	6.4	26.5	27	25.5	27.5
19.8	29.5	30	28.5	27.5	19.8	44	44	42.5	42
30.2	32.5	36.5	39	35.5	30.2	53	50	53.5	52.5
40.3	39	41	40	39.5	40.3	60.5	61	58.5	57
63	48	50	48	47	63	65.5	67	65.5	67.5
100	53.5	53	54.5	58.5	100	72	71	70	75
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	1.5	1.5	3	2
0.54	3	2	2	2	0.54	4	4.5	6	5
1	4.5	4	3.5	4.5	1	6.5	7	8	7
2.2	6.5	6	6	4.5	2.2	11.5	10.5	11	12
5	9	10.5	9.5	11.5	5	18	17.5	17.5	18
6.4	12	12.5	12	13	6.4	20	21	22	21.5
19.8	21.5	20.5	19.5	21.5	19.8	33	32.5	33.5	35.5
30.2	30.5	28	26.5	29.5	30.2	42	43.5	43	40.5
40.3	34.5	33.5	35.5	33.5	40.3	46.5	45	44.5	46.5
63	43	39	40	40	63	55.5	55	54	55
100	47	47.5	45.5	44	100	61.5	62.5	60.5	62

Table A3.23: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 9, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	2.5	2	2	2.5	0.09	2	2	2	1.5
0.54	5.5	5	5.5	4	0.54	9.5	9	10.5	10
1	8.5	8.5	8	8.5	1	15.5	17.5	17.5	16.5
2.2	13	14	14.5	12	2.2	29.5	30.5	30.5	29
5	20	20	21	20	5	43.5	45	43.5	43
6.4	23.5	25	23.5	24.5	6.4	52	56.5	49.5	50
19.8	37.5	40	38.5	37	19.8	75.5	71	70	73
30.2	50	46	46.5	45	30.2	80.5	77	78	75
40.3	53	52	50	50	40.3	85.5	82	84.5	82.5
63	63	61	62.5	60.5	63	92	87	89.9	91
100	67.5	68	70.5	67.5	100	97	91.5	96	97
529.6nm					650.1nm				
0.09	2.5	2	2	2.5	0.09	0	0	0	0
0.54	5.5	5	5.5	4	0.54	4	5.5	5	5
1	8.5	8.5	8	8.5	1	9.5	9	8.5	8.5
2.2	13	14	14.5	12	2.2	18	16.5	17	14.5
5	20	20	21	20	5	29	29	28	28.5
6.4	23.5	25	23.5	24.5	6.4	35	36	34.5	34
19.8	37.5	40	38.5	37	19.8	56.5	59.5	63.5	57
30.2	50	46	46.5	45	30.2	68	69.5	73	68
40.3	53	52	50	50	40.3	73.5	78.5	74	75
63	63	61	62.5	60.5	63	89	86.5	83	85
100	67.5	68	70.5	67.5	100	89.5	91.5	96	90
559.2nm					679.5nm				
0.09	3	2	1.5	2	0.09	0	0	0	0
0.54	5	4.5	4.5	4	0.54	0	0	0	0
1	7.5	8	8.5	8	1	2	2	2.5	2
2.2	13	14.5	14.5	13.5	2.2	4.5	5	4	4.5
5	22	21	21.5	22	5	8	7.5	7.5	6.5
6.4	26	25	27	26.5	6.4	8.5	10	9.5	9
19.8	44	46	44.5	45	19.8	22	21	21	21
30.2	55.5	54	52.5	52.5	30.2	28	28.5	26	27
40.3	58	61.5	60	60	40.3	32.5	34	36	32.5
63	69	67	69.5	66.5	63	42	47.5	43.5	44.5
100	76	75	75.5	76	100	52	52.5	50.5	50
590.1nm					705.0nm				
0.09	2	1.5	2	1	0.09	0	0	0	0
0.54	4	3.5	2	2.5	0.54	4	4	3.5	3.5
1	5.5	6.5	6	6.5	1	7	7.5	6.5	6.5
2.2	13	11	11.5	11.5	2.2	14	14.5	14.5	14.5
5	19	20.5	18.5	19	5	24	24.5	25	23
6.4	26	24.5	26.5	24	6.4	29	30	29	28.5
19.8	43	42	41.5	40.5	19.8	54	55.5	55	55.5
30.2	57.5	52.5	50	49	30.2	67	64	63.5	64
40.3	58	55	55	55	40.3	73	71.5	72	72
63	67	65	62.5	63.5	63	80	81	80	76.5
100	72	70	68.5	71.5	100	87	86	87.5	88

Table A3.24: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 9, a female *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	0	0	0	0	2.2	9	11.5	10.5	11
5	0	0	0	0	5	15	15	14	12.5
6.4	0	0	0	0	6.4	18	15.5	15.5	15.5
19.8	0	0	0	0	19.8	25.5	25	22.5	23.5
30.2	0	0	0	0	30.2	25.5	30.5	26.5	26.5
40.3	5.5	5	5.5	5.5	40.3	30	31	30.5	28.5
63	7.5	7.5	7.5	7.5	63	31.5	30.5	33	34.5
100	13.5	18.5	15.5	15.5	100	42	40	37.5	38
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	7	6.5	7	6.5	1	6.5	8	6.5	6
2.2	11	11.5	8.5	8	2.2	13	12	12	12
5	12.5	12.5	16.5	14	5	16	18.5	17.5	16.5
6.4	16	17	16	16	6.4	17.5	18	18.5	17.5
19.8	23	22.5	23	23	19.8	27.5	28	27.5	29
30.2	26.5	26.5	26.5	28.5	30.2	32.5	31	32.5	32
40.3	26.5	30	28.5	31	40.3	36	34.5	34	35
63	34	32	35	32.5	63	42.5	42	40.5	37
100	42	35	36.5	38.5	100	47.5	46	45	47.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	7	6.5	9.5	8.5
2.2	12.5	13.5	12.5	13.5	2.2	14.5	12.5	14	11.5
5	18	18	19.5	22.5	5	18.5	17.5	19	19
6.4	20	21.5	19.5	23	6.4	18.5	22.5	21.5	21
19.8	30.5	29	26.5	29	19.8	30.5	31	31	30
30.2	33	33.5	34	32.5	30.2	38.5	38	37.5	37.5
40.3	36	35.5	35.5	36	40.3	40	43.5	41.5	39.5
63	41.5	42	40.5	42	63	47.5	47	47.5	47.5
100	45.5	46	46.5	47.5	100	54.5	54.5	50	53.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	6	5.5	6	5.5	1	7	7.5	8.5	8
2.2	6.5	7	7	7	2.2	14.5	13	14	15.5
5	11.5	11	11.5	10.5	5	17	17.5	18	17
6.4	12	13	13.5	13.5	6.4	18.5	17	19.5	20.5
19.8	18.5	21.5	22	21	19.8	29.5	25.5	29.5	30.5
30.2	20.5	22.5	20.5	21.5	30.2	35	32	30.5	37
40.3	25	23	23.5	23.5	40.3	31	35	36.5	34
63	31.5	31	30	29	63	43.54	44.5	43	39
100	37.5	37	38.5	35.5	100	40.5	46	47.5	54

Table A3.25: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 10, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	10	9.5	8.5	11	1	8.5	7	6.5	6.5
2.2	15	15	13.5	14.5	2.2	12	13.5	12	13
5	22	22	21	22.5	5	23	21	21	22.5
6.4	22	21	25	22.5	6.4	22.5	23.5	24	25.5
19.8	33.5	35	33	34	19.8	53.5	51.5	50	49.5
30.2	35	37.5	37.5	35.5	30.2	54.5	53.5	55.5	53
40.3	40	39	42	43.5	40.3	59	56.5	64	64
63	48	51.5	46	45.5	63	70.5	69.5	67.5	68.5
100	54	52	56	55	100	72	71	77.5	77
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	10	9.5	8.5	11	1	0	0	0	0
2.2	15	15	13.5	14.5	2.2	0	0	0	0
5	22	22	21	22.5	5	7.5	8	7.5	7
6.4	22	21	25	22.5	6.4	10	12	12.5	10.5
19.8	33.5	35	33	34	19.8	26.5	29.5	26.5	28.5
30.2	35	37.5	37.5	35.5	30.2	33.5	37	34.5	34
40.3	40	39	42	43.5	40.3	41.5	41	38.5	39.5
63	48	51.5	46	45.5	63	55	46	50.5	53.5
100	54	52	56	55	100	56	59	58	58
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	9.5	10.5	9.5	10	1	0	0	0	0
2.2	15.5	15	16.5	15	2.2	0	0	0	0
5	21	15.5	17.5	21	5	0	0	0	0
6.4	23.5	22.5	22.5	19	6.4	0	0	0	0
19.8	36.5	35.5	34	34	19.8	0	0	0	0
30.2	39.5	41	41	38.5	30.2	8	7.5	7.5	8.5
40.3	46.5	46	44.5	45	40.3	11	12	10.5	10.5
63	51	51.5	52	54	63	16.5	16	16.5	14.5
100	59	61	61.5	62	100	21.5	25.5	21	20
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	0	0	0	0	2.2	0	0	0	0
5	11	10	11	9	5	0	0	0	0
6.4	11	12	11	12.5	6.4	0	0	0	0
19.8	21.5	22.5	22.5	21	19.8	12	14	11	11
30.2	26	26.5	26.5	26.5	30.2	14.5	13.5	14	15
40.3	29.5	31	34	29	40.3	18.5	19	14.5	23
63	37.5	38	37	39	63	26.5	30.5	27	30.5
100	44.5	45	46	42.5	100	35.5	35.5	34.5	36

Table A3.26: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 10, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	2.5	2.5	3.5	3.5
0.54	0	0	0	0	0.54	4	4	3.5	4
1	0	0	0	0	1	9	9	5.5	7
2.2	0	0	0	0	2.2	13.5	12	11	12
5	0	0	0	0	5	23	21	20	19
6.4	0	0	0	0	6.4	24	25	27	25.5
19.8	0	0	0	0	19.8	35.5	34.5	33	37.5
30.2	0	0	0	0	30.2	46	41	40	39
40.3	0	0	0	0	40.3	49	50	53	51
63	7	6	6	6	63	50	49	53.5	59
100	15.5	16	17	17	100	55.5	55.5	59.5	63
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	2	2	3	3
0.54	0	0	0	0	0.54	7	7.5	6	5.5
1	6.5	6.5	7.5	7.5	1	9.5	7.5	8.5	8
2.2	10.5	11	12.5	10	2.2	13.5	14.5	16	17.5
5	19.5	17	17.5	18.5	5	19	21	21.5	23.5
6.4	17	19	21.5	18	6.4	32	35.5	25.5	26.5
19.8	30.5	30.5	30.5	30	19.8	41	42	44	46
30.2	39	33.5	32.5	38.5	30.2	46	46	48.5	50.5
40.3	38.5	43	45.5	51.5	40.3	60	55.5	50	48
63	45.5	46.5	42	47.5	63	62	64	76	56
100	55.5	50.5	52.5	53.5	100	62.5	61	66	73
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	5.5	5	5	5
0.54	7	7	6.5	6.5	0.54	9	10	10.5	9.5
1	11	11.5	12	13	1	13.5	13	14.5	16
2.2	18	18.5	17.5	17	2.2	22	20.5	21	21
5	33	32	30	26	5	36	36.5	37	34
6.4	32	32	35	36.5	6.4	35	36	34	37.5
19.8	43.5	43.5	43.5	44.5	19.8	50.5	49	48.5	43.5
30.2	59.5	50	50.5	49	30.2	65	58.5	57	55
40.3	55	55.5	58	51.5	40.3	62.5	66.5	69.5	74.5
63	52.5	64.5	66.5	53	63	64.5	63	64.5	67
100	60.5	60	63.5	62.5	100	76.5	68	69	68
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	2.5	3	2.5	2.5	0.54	0	0	0	0
1	6.5	6	5	5	1	0	0	0	0
2.2	12.5	12	9.5	10	2.2	12.5	16	17	14.5
5	19.5	17.5	17	17	5	24.5	22.5	23	22.5
6.4	22	24	23.5	20	6.4	24	20.5	21	24
19.8	32	35	37	37.5	19.8	43	41	39	38
30.2	39	38	40.5	43.5	30.2	51	48	45	45
40.3	58	42.5	41.5	42.5	40.3	58	54	63.5	54
63	52.5	55	58	57.5	63	59	54	51	57.5
100	54	52.5	54.5	58	100	62.5	64	62	58.5

Table A3.27: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 11, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	4	4	3.5	3.5	0.09	0	0	0	0
0.54	8	8.5	7.5	7.5	0.54	15	14.5	14	15.5
1	14	13.5	13.5	14.5	1	26	24.5	23.5	23
2.2	19.5	21.5	22.5	24	2.2	37	36.5	37.5	37.5
5	31.5	30.5	29.5	30.5	5	54.5	53	54.5	55.5
6.4	42.5	34	36	33	6.4	69	68	60.5	57
19.8	57	54	48.5	46	19.8	88	81.5	74.5	77
30.2	58	65	65	58.5	30.2	82.5	88	93.5	83
40.3	58	59	61.5	66.5	40.3	84.5	84.5	90	96
63	67	67	65.5	65.5	63	109	93.5	90.5	86.5
100	80.5	73	70.5	66.5	100	95	102.5	107	107.5
529.6nm					650.1nm				
0.09	4	4	3.5	3.5	0.09	3.5	3.5	4	3
0.54	8	8.5	7.5	7.5	0.54	7	7.5	8	8
1	14	13.5	13.5	14.5	1	14	12.5	14.5	20
2.2	19.5	21.5	22.5	24	2.2	28	26	25.5	25.5
5	31.5	30.5	29.5	30.5	5	44.5	47	45	40
6.4	42.5	34	36	33	6.4	46	49.5	53.5	51
19.8	57	54	48.5	46	19.8	66	66	69	74.5
30.2	58	65	65	58.5	30.2	76	74.5	75	73.5
40.3	58	59	61.5	66.5	40.3	93.5	85	78	80.5
63	67	67	65.5	65.5	63	86	93	95.5	99.5
100	80.5	73	70.5	66.5	100	90.5	87.5	87	94
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	10.5	8	9	10	0.54	0	0	0	0
1	15	16	16	15	1	3	2.5	3	3
2.2	27.5	25.5	24	25.5	2.2	5	5	6	6
5	43.5	45.5	43	38.5	5	9	10	10.5	10.5
6.4	42	44.5	48.5	44	6.4	15	18	15	14
19.8	58.5	61	60.5	61	19.8	30.5	33	36	38
30.2	78	79.5	85	69.5	30.2	42	43	40	39
40.3	68	70	72	78.5	40.3	51	53	59.5	49
63	79	74	71.5	73	63	55	54	54	60.5
100	89	93.5	90.5	80.5	100	76	78.5	67	62.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	3.5	2.5	2.5	0.54	5.5	6.5	6.5	6.5
1	5	7.5	6.5	6	1	8.5	8.5	9	9
2.2	11.5	13	12	14.5	2.2	19	15.5	16.5	18
5	25	23	21.5	20	5	35.5	35	30.5	30.5
6.4	30.5	28.5	34	36	6.4	33	36.5	38.5	43
19.8	35.5	35	35	36.5	19.8	62.5	60.5	59.5	59.5
30.2	64.5	65.5	56.5	54	30.2	65.5	71.5	73.5	76
40.3	60	58.5	64	67	40.3	74	69.5	68.5	75.5
63	65	63.5	60.5	66.5	63	91	84	84	77
100	82	74.5	71	70	100	84	89	92	92.5

Table A3.28: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 11, a female *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3.5	3	3.5	3
1	0	0	0	0	1	4.5	5	3.5	3.5
2.2	0	0	0	0	2.2	6.5	6	6.5	6
5	0	0	0	0	5	12	11	12	12
6.4	0	0	0	0	6.4	13	14	13	13
19.8	0	0	0	0	19.8	22.5	23.5	23	23
30.2	3	3	3	3	30.2	29.5	30	28	29.5
40.3	4	3.5	4	4	40.3	32.5	32	32.5	32.5
63	4.5	3	4.5	4.5	63	38.5	36.5	39	39
100	11.5	10.5	11	11	100	44	44	44.5	43.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	4	4	3.5	3.5	1	3	3	2.5	2.5
2.2	6	5	4.5	5	2.2	5	5.5	4	5
5	10.5	10.5	11	11	5	8	8	8	8
6.4	11.5	12	12.5	12.5	6.4	9.5	9	10	9
19.8	20	21.5	21.5	21.5	19.8	15	17	17.5	17
30.2	23.5	25	25.5	24	30.2	23	22.5	20.5	22.5
40.3	29	28.5	27	28.5	40.3	25	25	25	25
63	35	32.5	34.5	33	63	30.5	31.5	31	30
100	42.5	41	41.5	41.5	100	35.5	35	34	37
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	3	2.5	2	3
0.54	3	3.5	3	3.5	0.54	5	4.5	3.5	3.5
1	5	5	4	5.5	1	6.5	4.5	4.5	5
2.2	9.5	8.5	9	8.5	2.2	7.5	8.5	8	9
5	17.5	17.5	16	16.5	5	13	10.5	13	13.5
6.4	17.5	18	17.5	18.5	6.4	15	15.5	15.5	16
19.8	28.5	31	29.5	28	19.8	26	24.5	24.5	24.5
30.2	33.5	33	34.5	33.5	30.2	30.5	31	37.5	31.5
40.3	37.5	38	37.5	37.5	40.3	34.5	35	35	43
63	41.5	43	43	41.5	63	42	43	43.5	41.5
100	50.5	48.5	49.5	51.5	100	47.5	45.5	46.5	47
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	4.5	4	4	4
1	4.5	3.5	3.5	4	1	4.5	6	6.5	6
2.2	5	5	4.5	4	2.2	10	10.5	11	10
5	7.5	8	6.5	7.5	5	15.5	17	17	17
6.4	9	9	8.5	8.5	6.4	18.5	21	19	19
19.8	17	17	16.5	17	19.8	30	29.5	30	30.5
30.2	20.5	20.5	21.5	21	30.2	36.5	36.5	35.5	37
40.3	21.5	21.5	22.5	21.5	40.3	39	40	40	38.5
63	29.5	27.5	26	27.5	63	49	44.5	46.5	48
100	34	32.5	33	33.5	100	53	52	51.5	52.5

Table A3.29: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 12, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	4	3	3	0.54	4.5	5	5	4.5
1	5	6	6	5.5	1	9.5	9.5	9	9
2.2	8.5	9.5	9	8.5	2.2	16.5	17	16.5	16.5
5	15	15.5	15	14	5	27	26	28	27.5
6.4	18.5	16.5	18	18.5	6.4	30.5	31	28.5	31
19.8	30	27.5	27	29	19.8	49	48.5	47.5	48
30.2	34.5	33.5	33.5	33	30.2	58	55.5	56.5	56
40.3	37.5	36.5	40	39	40.3	59.5	57.5	57.5	59.5
63	44.5	44.5	44.5	45	63	67.5	65	64.5	64
100	51	50	49	49.5	100	71.5	70.5	68	70.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	4	3	3	0.54	0	0	0	0
1	5	6	6	5.5	1	3	2.5	3	3
2.2	8.5	9.5	9	8.5	2.2	5.5	5.5	6.5	5
5	15	15.5	15	14	5	12	10.5	11	10.5
6.4	18.5	16.5	18	18.5	6.4	13.5	14	12	13.5
19.8	30	27.5	27	29	19.8	27.5	28.5	28	27
30.2	34.5	33.5	33.5	33	30.2	33	33	33.5	34
40.3	37.5	36.5	40	39	40.3	39	38	38	39.5
63	44.5	44.5	44.5	45	63	48	47	45	46
100	51	50	49	49.5	100	53.5	53	52	52.5
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	6	5	6.5	6.5	0.54	0	0	0	0
1	10	11	11	12	1	0	0	0	0
2.2	21.5	19.5	20	20	2.2	0	0	0	0
5	31	28.5	28	28	5	0	0	0	0
6.4	31	34.5	32.5	34.5	6.4	3	2.5	3	3.5
19.8	49	48	46.5	48.5	19.8	5.5	5.5	6.5	5.5
30.2	52.5	53	52.5	54	30.2	7.5	8.5	7.5	8
40.3	59	56.5	57.5	57.5	40.3	10	10.5	10.5	11
63	61	64.5	61.5	62.5	63	15	13.5	14	13.5
100	67	68.5	67.5	67.5	100	19	20	18.5	20
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	3	2	2	0.54	0	0	0	0
1	6.5	6.5	5.5	8.5	1	2.5	2	3	2.5
2.2	12	12.5	11.5	11.5	2.2	3.5	3.5	3.5	3
5	20	18	20	18	5	6.5	6.5	7	7
6.4	23.5	27	23.5	25	6.4	9	9.5	10	9
19.8	40.5	42.5	39.5	39	19.8	20	19	20	21.5
30.2	46	45.5	47	39	30.2	25.5	26.5	25	25.5
40.3	56.5	52	50	50.5	40.3	31	29.5	31	30.5
63	58.5	57	55	58	63	39	39	38	37.5
100	62.5	62	61.5	60.5	100	48.5	45	44	44.5

Table A3.30: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 12, a male *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	5	4	4	4.5
1	0	0	0	0	1	7.5	4.5	5	4
2.2	0	0	0	0	2.2	6	6.5	7	6.5
5	0	0	0	0	5	7.5	6.5	8	6
6.4	0	0	0	0	6.4	9	7.5	8	7
19.8	0	0	0	0	19.8	10.5	12	10.5	11
30.2	0	0	0	0	30.2	15.5	16.5	16.5	18
40.3	0	0	0	0	40.3	20	21	22.5	25.5
63	4.5	4	4	4	63	28.5	26	27	27
100	7.5	6	6.5	6.5	100	31	35	32	30.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	7.5	6.5	6.5	7.5	2.2	5	3.5	5	4.5
5	8	6.5	8.5	7	5	7	6.5	6	6
6.4	7	7.5	8.5	7.5	6.4	8	7	8.5	8
19.8	13.5	12	13	10	19.8	11	11.5	12	14
30.2	16.5	17	16.5	15.5	30.2	16	16.5	15.5	15.5
40.3	20	18.5	18	20	40.3	20	21	23	17
63	24.5	23.5	27	19	63	21.5	21	22	23
100	25	34	31	31	100	22.5	22	21.5	24
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	7.5	7	6	6
2.2	4	4	3.5	3.5	2.2	7.5	6.5	7.5	6.5
5	5	6	6.5	7.5	5	10.5	12	8.5	11.5
6.4	7	7.5	8.5	8	6.4	11.5	9	11.5	8
19.8	11.5	7	8	11	19.8	18.5	18.5	18	17
30.2	14.5	14	16.5	18.5	30.2	20.5	19.5	19	19.5
40.3	18	18	15.5	18	40.3	21	22.5	23	21
63	23.5	22.5	23.5	20	63	25.5	25.5	25	25.5
100	27	28.5	24.5	26.5	100	29.5	30	28	28
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	8	6.5	5.5	5.5	2.2	4.5	4.5	4.5	4
5	8.5	7.5	10	7.5	5	10	8.5	11.5	9
6.4	11	8.5	8.5	10.5	6.4	11.5	8	10.5	10.5
19.8	20	15.5	17	17	19.8	16	16.5	13.5	15.5
30.2	22	20	20.5	23	30.2	24	20.5	22.5	20
40.3	29.5	30.5	30	28	40.3	23.5	27	22.5	24
63	26.5	26.5	23	25.5	63	29	27.5	32	36.5
100	32	29.5	29	27	100	37	34.5	37	35

Table A3.31: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 13, a female *Lucilia sericata,* using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	5	5.5	6	5.5	1	7	6.5	8	7
2.2	7.5	6.5	7	6	2.2	12	10.5	11.5	8.5
5	9.5	9.5	10.5	8.5	5	17.5	17	19.5	20.5
6.4	8	10	12	11.5	6.4	23.5	19.5	16.5	17.5
19.8	14.5	14	15	14	19.8	27.5	28	26	26
30.2	22.5	19	20	19	30.2	33	33	24	33
40.3	21.5	24	22.5	25	40.3	39.5	35.5	36	36
63	28.5	25.5	27	27	63	44	43	44	43.5
100	31	34.5	32	30.5	100	51	48	46.5	64.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	5	5.5	6	5.5	1	0	0	0	0
2.2	7.5	6.5	7	6	2.2	12.5	12.5	14.5	13.5
5	9.5	9.5	10.5	8.5	5	17.5	16.5	18.5	18
6.4	8	10	12	11.5	6.4	25.5	26.5	25.5	26.5
19.8	14.5	14	15	14	19.8	48	43.5	46	40.5
30.2	22.5	19	20	19	30.2	56.5	54	54.5	58
40.3	21.5	24	22.5	25	40.3	59	59	69.5	58.5
63	28.5	25.5	27	27	63	83.5	76	76	79.5
100	31	34.5	32	30.5	100	87.5	84	77	91
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	8.5	7	8	7	1	0	0	0	0
2.2	15	14	14	13.5	2.2	0	0	0	0
5	22.5	22.5	26.5	25.5	5	0	0	0	0
6.4	28.5	27.5	25.5	26	6.4	6.5	4	4.5	4
19.8	41	42	40.5	38.5	19.8	12	11.5	11	10
30.2	51	49.5	50	51.5	30.2	15	15.5	17.5	15.5
40.3	57	57.5	56.5	57	40.3	21	19	19	19
63	63.5	64	64	63	63	22	21	24.5	22.5
100	65.5	67	66	64.5	100	29.5	28	30.5	36
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	8	7	8.5	6	1	0	0	0	0
2.2	11.5	13	15	14.5	2.2	5	4	6.5	5
5	17	19.5	18	19	5	8	8.5	9	8.5
6.4	20	21.5	21	23.5	6.4	10	7.5	11	7.5
19.8	30.5	34.5	31.5	33.5	19.8	17.5	17.5	17.5	20.5
30.2	41.5	42	39.5	43	30.2	24	25.5	22.5	24
40.3	49	47	48.5	47.5	40.3	30	30.5	29	28.5
63	56.5	58.5	55	57	63	41.5	37.5	42	33.5
100	56.5	56	53.5	54	100	46.5	40	32	40.5

Table A3.32: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 13, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	3	2.5	2.5	2.5
0.54	0	0	0	0	0.54	4	3.5	3	3.5
1	0	0	0	0	1	6	6	6	5.5
2.2	0	0	0	0	2.2	9	9	9	9.5
5	0	0	0	0	5	12	10	11.5	10
6.4	0	0	0	0	6.4	12	12	12	14
19.8	0	0	0	0	19.8	17.5	16	17.5	17
30.2	3	3	2.5	2.5	30.2	19.5	19.5	19	19
40.3	4	3.5	3.5	3.5	40.3	21	22	21.5	21
63	5	4	3.5	3.5	63	24	24	23.5	23
100	10	9	8.5	8.5	100	29	27.5	28.5	25.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	4.5	4	3	3
1	4.5	4.5	4	4	1	5.5	5	5	5.5
2.2	5.5	6	5.5	6	2.2	11	10	9	7.5
5	11.5	10.5	11.5	10	5	11	10.5	10.5	10.5
6.4	11.5	11	11.5	11.5	6.4	13.5	14	11	11.5
19.8	17.5	21	18.5	18.5	19.8	15.5	16.5	17	17.5
30.2	20.5	19	19.5	18.5	30.2	23	20	20.5	19.5
40.3	21.5	22	21	21.5	40.3	22.5	22.5	23	22
63	23	26.5	25	24.5	63	23	24	25	25
100	30.5	29	29.5	29.5	100	29	28	29	26.5
359.0nm					469.6nm				
0.09	1.5	1.5	1	1.5	0.09	3	2	1.5	2
0.54	3	3	2.5	3	0.54	6.5	5	6.5	6.5
1	3	3.5	3.5	3.5	1	8	8	7.5	7.5
2.2	5	5	5	5	2.2	9.5	10.5	10.5	10.5
5	7	7	6.5	6.5	5	15	13	13	13
6.4	7.5	7	7	7.5	6.4	15	15	14.5	14.5
19.8	12.5	9.5	10.5	10.5	19.8	19	18	18.5	18.5
30.2	13	12.5	14.5	13	30.2	25	21.5	21	21
40.3	13	12	13.5	14	40.3	23	23	23.5	24
63	16.5	16	17.5	15.5	63	26.5	25	25	25
100	18	18	18.5	20.5	100	30.5	28	28	28
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	3	2.5	3.5	3
0.54	2.5	2	2.5	3	0.54	5.5	5.5	5	6.5
1	4	3.5	3	3	1	8	8	7.5	7
2.2	5.5	6.5	5.5	5.5	2.2	12	12	12	11
5	9	9.5	9	9	5	15.5	14	15.5	15.5
6.4	11	12	10	10.5	6.4	19	19.5	17	17.5
19.8	14	14.5	15	16	19.8	23	22	22	23
30.2	17.5	17	17	17.5	30.2	29	27.5	30.5	26
40.3	20	20.5	20	18.5	40.3	29	29	30.5	29
63	23	22	22	21	63	33.5	32	32.5	33
100	25.5	25	25	23.5	100	37	37.5	35	39

Table A3.33: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 14, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	3.5	3	3	3	0.09	2	2.5	3	2.5
0.54	7	6.5	6.5	6	0.54	9.5	9.5	9	9.5
1	10	10	10	9.5	1	13.5	13.5	13.5	14
2.2	14.5	14	14.5	13.5	2.2	22	20.5	21.5	19
5	18	18	18.5	18.5	5	30.5	30	30	31.5
6.4	22	23	21	21	6.4	34	34	32.5	32
19.8	28.5	26.5	26	27	19.8	43	42.5	45	45
30.2	33.5	31	30.5	30	30.2	54.5	53	49	49.5
40.3	32	33.5	33	35.5	40.3	52	50.5	51	54
63	36.5	36.5	35	35	63	57	56	54	54.5
100	40	39.5	38	38	100	62.5	60	61	58.5
529.6nm					650.1nm				
0.09	3.5	3	3	3	0.09	0	0	0	0
0.54	7	6.5	6.5	6	0.54	3	3	3	2.5
1	10	10	10	9.5	1	6.5	5	5.5	6
2.2	14.5	14	14.5	13.5	2.2	13	12.5	12.5	11.5
5	18	18	18.5	18.5	5	13.5	14	19	18
6.4	22	23	21	21	6.4	22	21.5	21.5	21
19.8	28.5	26.5	26	27	19.8	34.5	31	33	33.5
30.2	33.5	31	30.5	30	30.2	43.5	41	39	39
40.3	32	33.5	33	35.5	40.3	42.5	42.5	44	44
63	36.5	36.5	35	35	63	48	46	45.5	46.5
100	40	39.5	38	38	100	54	50	50	50.5
559.2nm					679.5nm				
0.09	4	4	4.5	4.5	0.09	0	0	0	0
0.54	10	9.5	9.5	8.5	0.54	0	0	0	0
1	15	12.5	12.5	12.5	1	0	0	0	0
2.2	17.5	16	17	17	2.2	2.5	3.5	2.5	2.5
5	22.5	21.5	21	20.5	5	5	6.5	5.5	6
6.4	24	23	24	23	6.4	9.5	7	6.5	7
19.8	31.5	28.5	29.5	32	19.8	14	14	15.5	16
30.2	39	35.5	33	31.5	30.2	19	18	17.5	17.5
40.3	38	37.5	38	39.5	40.3	20	20	21	20.5
63	42	40	39	41	63	29.5	24	24.5	23.5
100	46.5	46.5	48.5	43	100	29	28	29.5	31
590.1nm					705.0nm				
0.09	2	2.5	2.5	2.5	0.09	0	0	0	0
0.54	9	8	8	8	0.54	2.5	1.5	2	2
1	12	12	12.5	12	1	3.5	4	4	3.5
2.2	18.5	17.5	18	17.5	2.2	6.5	6	6.5	6.5
5	25	23.5	26	25	5	12.5	13	12	12
6.4	26.5	26.5	25.5	25.5	6.4	13.5	14.5	15	14
19.8	39.5	38	36.5	33.5	19.8	26.5	26	25.5	25
30.2	41	41	40.5	40	30.2	30.5	28.5	28.5	30.5
40.3	46	43	42.5	45.5	40.3	35.5	36	34	31.5
63	53	49	47	47.5	63	37.5	37.5	37.5	37.5
100	52	49.5	48.5	51.5	100	44	46.5	45	45

Table A3.34: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 14, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	4	4	3.5	3.5
2.2	0	0	0	0	2.2	6	6.5	6	7.5
5	0	0	0	0	5	13	11.5	11.5	12.5
6.4	0	0	0	0	6.4	14	12	11.5	13.5
19.8	0	0	0	0	19.8	25	27	23.5	21.5
30.2	0	0	0	0	30.2	32.5	27.5	32	30.5
40.3	0	0	0	0	40.3	34	35.5	31	29
63	3.5	3	2.5	2.5	63	38.5	36.5	35.5	40.5
100	14.5	14.5	14	14	100	44	38.5	39.5	40.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3	2.5	4	3
1	3	4.5	4	3	1	4.5	4.5	4	4
2.2	6.5	6.5	6	6	2.2	9	8.5	9.5	9
5	14.5	14	14.5	13.5	5	10	14	14	15.5
6.4	17.5	16	15.5	15.5	6.4	16.5	16.5	18	18
19.8	30	28.5	28.5	28	19.8	28	26	27.5	32
30.2	35.5	36	32	30.5	30.2	34.5	32.5	36	33
40.3	41.5	40	37.5	34.5	40.3	37.5	35.5	36	36
63	44.5	42.5	44	46.5	63	45.5	41.5	41	48
100	57	55	51.5	54	100	47.5	45.5	45.5	43.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	10.5	10	8.5	10.5
2.2	4	4	6	4.5	2.2	16.5	16.5	16.5	15.5
5	9.5	10	10.5	11	5	23	26	25	25
6.4	11	11	12.5	11	6.4	30	29	28.5	28.5
19.8	20.5	19.5	18.5	20.5	19.8	47	45.5	42	43.5
30.2	28	25.5	25.5	27.5	30.2	58.5	57.5	60	62.5
40.3	31	30.5	29.5	31.5	40.3	62	62.5	66	58.5
63	34	34	34	37	63	70	64.5	69.5	69.5
100	36	38.5	42.5	38	100	88	83	76.5	75.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	2.5	2	3	2.5
0.54	0	0	0	0	0.54	5	5	6	4.5
1	6	5.5	5.5	5.5	1	10	9	8.5	9
2.2	11.5	9	11	11	2.2	13	13.5	13	14
5	16.5	17	16	16	5	21.5	21.5	20	21
6.4	18.5	18	19	19	6.4	25	24	24	23
19.8	30.5	30.5	28.5	28.5	19.8	38	36.5	36	36
30.2	39.5	35	36.5	36.5	30.2	46	43.5	45	44
40.3	46	39	40	39.5	40.3	54.5	49.5	49	46
63	47	43	42.5	43	63	57	55.5	57	57
100	57.5	50.5	49.5	47.5	100	63.5	62	65.5	63

Table A3.35: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 15, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	3	3	3	2.5	0.09	2.5	2	2.5	2
0.54	4.5	5.5	5.5	7	0.54	13.5	11.5	11.5	12.5
1	8	8	8	8.5	1	20	23.5	19	19
2.2	16	14	13.5	16.5	2.2	34.5	33	37.5	38.5
5	23.5	21.5	21.5	21.5	5	52	50	50	49.5
6.4	26	24	26.5	26	6.4	54	51.5	50.5	48
19.8	44.5	42	39	37	19.8	72.5	66.5	59.5	59.5
30.2	48.5	50	49	48	30.2	85	90	79.5	80
40.3	59.5	52	52.5	51	40.3	88	83	83.5	88
63	61.5	59.5	57	58.5	63	93	88	86	88
100	74	67.5	66.5	65	100	120	125	93.5	100.5
529.6nm					650.1nm				
0.09	3	3	3	2.5	0.09	0	0	0	0
0.54	4.5	5.5	5.5	7	0.54	7.5	6.5	7.5	6.5
1	8	8	8	8.5	1	13.5	14	13	12
2.2	16	14	13.5	16.5	2.2	28	28	26.5	26
5	23.5	21.5	21.5	21.5	5	43	43.5	42.5	43
6.4	26	24	26.5	26	6.4	53.5	54.5	59.5	48.5
19.8	44.5	42	39	37	19.8	84	68.5	69.5	70.5
30.2	48.5	50	49	48	30.2	87	81.5	81	79.5
40.3	59.5	52	52.5	51	40.3	90	91	87	85.5
63	61.5	59.5	57	58.5	63	92.5	90.5	94.5	94.5
100	74	67.5	66.5	65	100	101	95.5	95.5	93.5
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	6	8	7	7.5	0.54	0	0	0	0
1	11	9.5	12	11	1	2.5	2	2.5	2
2.2	17.5	17	18.5	19.5	2.2	5.5	4	5	6.5
5	28.5	28	30.5	27	5	12	11	12.5	11.5
6.4	33	32	37	33.5	6.4	15	15	15.5	16.5
19.8	53	55.5	57	50	19.8	37.5	37.5	36	37.5
30.2	59	57	60.5	57.5	30.2	48.5	48.5	46	47.5
40.3	66.5	61.5	62	61.5	40.3	63	56	54	53
63	74	70.5	69.5	71.5	63	64.5	63	61.5	61
100	84	78.5	76.5	77	100	79.5	70.5	68.5	68.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4.5	4	4.5	4	0.54	5	5.5	5	4.5
1	8	8	7.5	7.5	1	9.5	11	9	10
2.2	14	13.5	14	14.5	2.2	18	18	18.5	18.5
5	21	20	20.5	20.5	5	38.5	35.5	32.5	33.5
6.4	25.5	24	25	25	6.4	38	41.5	46	41
19.8	48.5	42	43	41	19.8	67.5	67	72.5	70
30.2	50.5	50.5	50.5	48	30.2	77.5	76	75.5	70
40.3	55.5	61	59.5	55.5	40.3	89	80.5	78.5	79
63	63.5	63.5	68	71.5	63	91	93.5	98	88
100	71.5	71	69	67.5	100	97.5	94.5	93.5	93.5

Table A3.36: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 15, a female *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	7	7.5	7.5	7.5
2.2	0	0	0	0	2.2	12	12.5	11.5	13.5
5	0	0	0	0	5	20	20	22	20
6.4	0	0	0	0	6.4	23	24.5	23	23
19.8	6	5.5	5.5	5.5	19.8	35.5	36	34.5	34.5
30.2	6	5.5	5.5	5.5	30.2	44.5	43	45	42.5
40.3	6	6.5	6.5	6.5	40.3	49	45	46.5	47
63	8.5	8.5	8.5	8.5	63	54.5	53.5	53.5	54.5
100	21.5	19.5	19.5	19.5	100	64	62	59.5	63
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	4	3.5	4	4
0.54	0	0	0	0	0.54	7.5	7.5	7.5	9
1	7	6.5	8	8	1	11.5	13	11.5	13.5
2.2	9	9	10	10	2.2	19.5	21	19.5	20
5	17	20	17.5	17	5	29	28	30	27.5
6.4	20	21	19.5	18.5	6.4	33	32	32.5	32
19.8	32	31	33	31	19.8	48	46.5	47.5	45.5
30.2	37	37.5	35.5	36	30.2	56	55	56	54.5
40.3	41.5	43	40.5	40	40.3	60	60.5	59	58
63	47.5	47	47.5	48	63	67.5	67.5	66.5	66
100	58	60.5	57	57.5	100	77	73.5	76	74
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	12.5	12.5	13.5	11.5
1	9.5	10	10	9	1	19	20	18	18.5
2.2	16.5	16	16.5	15.5	2.2	27	23	32	22
5	25.5	26.5	25.5	25	5	34.5	34	35.5	35.5
6.4	28	28.5	31	31	6.4	41	40.5	41	40.5
19.8	42.5	43	41	43.5	19.8	52	53	50.5	49
30.2	50	52	50	51.5	30.2	66	60.5	61	62
40.3	54	52.5	52.5	55	40.3	68	65	63.5	64
63	62.5	61	61	61	63	73	67	82	70.5
100	70	72.5	70.5	71.5	100	79	76	74.5	76
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	4.5	5.5	5	0.54	5	4.5	5	5
1	7	9	7.5	9.5	1	12	8.5	10	10
2.2	13	12.5	13	13.5	2.2	18	16.5	18	16.5
5	20.5	20	20	20	5	24	24	23	24.5
6.4	23	24	23.5	23	6.4	32.5	32.5	34	35.5
19.8	33.5	34.5	34	34.5	19.8	50	50	49.5	49
30.2	40	42.5	42	43	30.2	57.5	58	57	57.5
40.3	42.5	45.5	45	45.5	40.3	61	61.5	61.5	59
63	53	51	52.5	54.5	63	70.5	68	69	68.5
100	59	57.5	60	56	100	77	76	76	77

Table A3.37: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 16, a female *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	4.5	5	5.5	6	0.09	2.5	3.5	3.5	3.5
0.54	13.5	13.5	13	12.5	0.54	10	10	9.5	9.5
1	18.5	20.5	20.5	19	1	17.5	16.5	18	16.5
2.2	26.5	27.5	29.5	27.5	2.2	30	31	30	30
5	37	36	38	37.5	5	46.5	46	47.5	47
6.4	41	41.5	42	41.5	6.4	52.5	54	54.5	54.5
19.8	56.5	58.5	57	57	19.8	79	75.5	76	76
30.2	65.5	65	63.5	66.5	30.2	88	88	87.5	87
40.3	70.5	70.5	70	68	40.3	94	93	93.5	91.5
63	77	74	76.5	76	63	101	97.5	99	101.5
100	86.5	87	86	82	100	113	111	108.5	107.5
529.6nm					650.1nm				
0.09	4.5	5	5.5	6	0.09	0	0	0	0
0.54	13.5	13.5	13	12.5	0.54	3	5	3.5	3
1	18.5	20.5	20.5	19	1	6	7	6	7.5
2.2	26.5	27.5	29.5	27.5	2.2	12.5	14.5	13.5	13.5
5	37	36	38	37.5	5	24	24.5	25.5	26
6.4	41	41.5	42	41.5	6.4	31.5	31	30.5	30.5
19.8	56.5	58.5	57	57	19.8	51.5	52.5	52	52.5
30.2	65.5	65	63.5	66.5	30.2	59.5	62	62.5	64
40.3	70.5	70.5	70	68	40.3	69.5	67.5	69	68.5
63	77	74	76.5	76	63	77.5	78.5	81	79.5
100	86.5	87	86	82	100	90.5	89.5	86.5	87.5
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	7	7.5	7	9	0.54	0	0	0	0
1	14.5	16.5	14.5	14.5	1	0	0	0	0
2.2	24	27.5	21.5	23.5	2.2	3.5	3	3.5	3
5	32.5	33.5	34.5	32	5	5.5	5	6.5	5.5
6.4	35.5	36.5	36	38	6.4	7	7	6.5	8
19.8	54	55.5	55	55.5	19.8	19	17.5	18	18
30.2	65	63.5	67.5	65.5	30.2	24.5	26.5	25	24
40.3	71.5	69	68.5	68.5	40.3	31.5	31	30.5	30.5
63	78.5	78.5	77.5	77	63	39	40	39.5	40.5
100	90	86.5	85.5	87	100	50.5	49	49.5	50
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5.5	5.5	5.5	5	0.54	0	0	0	0
1	8.5	8	7.5	8.5	1	3	3	3	3.5
2.2	15	15.5	15	15	2.2	6.5	7.5	7	7
5	22.5	23	24	23	5	15.5	16.5	17	17
6.4	28.5	28	28	28	6.4	20	20	21	20.5
19.8	48	45.5	47	47	19.8	40	42	42.5	41
30.2	56	55	54	51.5	30.2	51.5	53.5	52.5	53
40.3	61.5	61.5	58.5	62	40.3	60	58	60	58.5
63	68	69	68	67	63	72.5	69.5	68	69.5
100	78.5	74	74	76.5	100	76.5	81	76.5	76.5

Table A3.38: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 16, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	8	9	8	8
1	0	0	0	0	1	12	12.5	13	11
2.2	0	0	0	0	2.2	16	16.5	17	17
5	0	0	0	0	5	24	25	25	24
6.4	0	0	0	0	6.4	28	25.5	27.5	25.5
19.8	3.5	2.5	3	3	19.8	36	35.5	36.5	34.5
30.2	3.5	4	4	4	30.2	45	46	46.5	44.5
40.3	4.5	4	4	4	40.3	49	47.5	46.5	48.5
63	5	4.5	4.5	4.5	63	60	61.5	55	55
100	8	7	6.5	6.5	100	64	61.5	62	64
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	6.5	7.5	6	7
1	5	5.5	5	6.5	1	13	11.5	11	12
2.2	8.5	10	10	9.5	2.2	16.5	17.5	15.5	16
5	15	17	17.5	17	5	23.5	24	22.5	23.5
6.4	20	17	18	18	6.4	26.5	26	24.5	24.5
19.8	26.5	25.5	26.5	27.5	19.8	38	37	39.5	37.5
30.2	31.5	32	32.5	33.5	30.2	46	45.5	47.5	47.5
40.3	39	34	35	36.5	40.3	52	50	51.5	51
63	44	40.5	43	42.5	63	58.5	59	60	58
100	46	55.5	61	53.5	100	63.5	70	70	63
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	4	3.5	3	5
0.54	5.5	6	5.5	6	0.54	5	7	6	6.5
1	8.5	9	9	9	1	11	10	11	10.5
2.2	14	15	15.5	14.5	2.2	15	15.5	14.5	14.5
5	19	19.5	21.5	21.5	5	21.5	20.5	19.5	21
6.4	22.5	23	22	22	6.4	24.5	25	24	23.5
19.8	31.5	34.5	34	32	19.8	34	34.5	35	35
30.2	38.5	41	41	41.5	30.2	44.5	44.5	42	44.5
40.3	42	43.5	41.5	40	40.3	47.5	47	47	45
63	51.5	51.5	47.5	51	63	58	57	55.5	55
100	59.5	57.5	55	53.5	100	61.5	63	63.5	65.5
379.7nm					489.0nm				
0.09	2.5	3	3	3	0.09	0	0	0	0
0.54	5.5	6	5.5	5.5	0.54	0	0	0	0
1	8.5	9.5	10.5	10	1	0	0	0	0
2.2	15	13.5	16	14.5	2.2	25	24.5	24	23.5
5	23	21.5	22	21.5	5	32.5	31	31	31
6.4	25.5	25	23	24	6.4	35	32	32	32.5
19.8	35.5	38	40	37	19.8	47	49.5	43	44
30.2	42.5	43.5	44	43.5	30.2	51.5	56	55.5	53
40.3	45.5	49	47	48	40.3	59	60	58	58
63	73	54.5	55	52	63	66	66.5	64	63
100	65	58.5	72.5	60	100	75	75.5	75	72.5

Table A3.39: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 17, a female *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	8.5	9.5	9.5	10	0.54	6.5	7.5	8	7
1	14.5	16	13	15	1	10.5	12	11.5	13
2.2	20	19	20.5	19	2.2	21	20.5	23.5	22
5	28.5	30	29	30.5	5	40	37.5	36.5	36
6.4	32	33	31.5	31	6.4	41	41	44.5	44
19.8	42	45.5	46.5	45.5	19.8	68	66	65	66.5
30.2	57	59.5	62	57	30.2	80	79	82.5	78.5
40.3	59	63.5	61.5	60.5	40.3	87	86	83.5	85
63	69.5	73	72.5	71.5	63	94	95.5	93	94
100	77	81	77	77.5	100	99	106	100	104.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	8.5	9.5	9.5	10	0.54	3	3.5	3	3.5
1	14.5	16	13	15	1	5	4.5	4.5	5
2.2	20	19	20.5	19	2.2	8.5	8	8.5	11
5	28.5	30	29	30.5	5	16.5	17.5	17.5	16
6.4	32	33	31.5	31	6.4	19	21	21.5	22
19.8	42	45.5	46.5	45.5	19.8	42.5	43.5	41.5	41.5
30.2	57	59.5	62	57	30.2	53	54	53	54
40.3	59	63.5	61.5	60.5	40.3	60.5	64	61.5	58
63	69.5	73	72.5	71.5	63	71	68	73.5	72.5
100	77	81	77	77.5	100	82.5	78.5	80	83.5
559.2nm					679.5nm				
0.09	5	4	5	4.5	0.09	0	0	0	0
0.54	10.5	10.5	10.5	11	0.54	0	0	0	0
1	18.5	19	19	19.5	1	0	0	0	0
2.2	27	27	25.5	25.5	2.2	0	0	0	0
5	38	38.5	40	37.5	5	2.5	3	2.5	3
6.4	48.5	46	46	46.5	6.4	5	4	4	4.5
19.8	66.5	66	65	65	19.8	10.5	10	10	9
30.2	78.5	77.5	81.5	77	30.2	15	16	13.5	14.5
40.3	83	86	86.5	83.5	40.3	18.5	19.5	20	19.5
63	90.5	87	88.5	92.5	63	24	25	26	25.5
100	105	103.5	102	97.5	100	33	32	33.5	33
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4.5	4.5	5	4.5	0.54	0	0	0	0
1	7	6.5	7.5	7.5	1	0	0	0	0
2.2	11.5	14	13	12	2.2	0	0	0	0
5	21	19	20	22	5	4	5	4.5	5
6.4	24	26	26	24.5	6.4	7	9	9.5	9
19.8	41.5	41	40.5	41.5	19.8	18.5	19	18.5	19.5
30.2	54	54	53.5	52.5	30.2	28.5	26.5	27.5	27
40.3	55.5	56.5	57.5	59	40.3	31	32	33	34.5
63	69.5	70	66.5	67.5	63	43.5	44.5	39.5	42.5
100	75	72.5	73	79	100	55.5	52.5	53	55

Table A3.40: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 17, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	6.5	7.5	7	7
2.2	0	0	0	0	2.2	7.5	8	6.5	7
5	0	0	0	0	5	13	10.5	11.5	11.5
6.4	0	0	0	0	6.4	15	15	15	15
19.8	0	0	0	0	19.8	23	23.5	22	21.5
30.2	0	0	0	0	30.2	30	33.5	30.5	31
40.3	2	2	2.5	2.5	40.3	31.5	31.5	29.5	30.5
63	9	6	6.5	6.5	63	35.5	35.5	35.5	32.5
100	23	19.5	19	19	100	45.5	46.5	43.5	43
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	2.5	2	3	2
1	0	0	0	0	1	3.5	3.5	3	4
2.2	5.5	6.5	6.5	6.5	2.2	5	5.5	4.5	4.5
5	12.5	13	12	10.5	5	9	8.5	10.5	10.5
6.4	12	13	12	12	6.4	10	9	10	10
19.8	20	19	19.5	19	19.8	17	17	17	16
30.2	26.5	24	24.5	22	30.2	23	24.5	24.5	22.5
40.3	24	24.5	23.5	25.5	40.3	24	23	24	24
63	29	27.5	27.5	27.5	63	29.5	28	27.5	29
100	35.5	38	37.5	38.5	100	32	32.5	34	34
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	2.5	2.5	2.5	2
1	6.5	7.5	6.5	6.5	1	6.5	6	6	6
2.2	13.5	13.5	10.5	11.5	2.2	10.5	11	10.5	10.5
5	17	19	17	19	5	15	13	14	14
6.4	19.5	17.5	18	18	6.4	16	16.5	16	16
19.8	25.5	25.5	26	24.5	19.8	24	24	24	22.5
30.2	29.5	32.5	33	31.5	30.2	31.5	29	29.5	29.5
40.3	37.5	36.5	34	33	40.3	37	37.5	38	38
63	38.5	38	39.5	38	63	41	36.5	38	40
100	43	42.5	45.5	43.5	100	41	40.5	42.5	42.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	2	2.5	2.5	3	0.54	0	0	0	0
1	5	5.5	4	4.5	1	9.5	9.5	7.5	7.5
2.2	6.5	5.5	5.5	6.5	2.2	12.5	13.5	11	12
5	11	13.5	12.5	10.5	5	16.5	18.5	18.5	18.5
6.4	12.5	10.5	13	11.5	6.4	24	24	23.5	23.5
19.8	20	19	19.5	20.5	19.8	34.5	33.5	35	35.5
30.2	25	24.5	25	26	30.2	39.5	41.5	41	40
40.3	33	33	30	27.5	40.3	48	45	45.5	48
63	34	32	32.5	32.5	63	56.5	57.5	53	52.5
100	38	37.5	36.5	38	100	57	53.5	57	63

Table A3.41: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 18, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	3	2.5	2	2
0.54	3.5	6	5	5	0.54	9.5	9.5	10	9
1	6.5	5	6.5	6.5	1	17.5	19.5	22	19.5
2.2	9.5	11.5	11.5	12	2.2	31	30.5	30.5	28
5	18.5	19	19.5	20	5	43	45	44	46.5
6.4	22	20.5	20.5	22	6.4	48	49	50	48.5
19.8	33.5	33	34	34	19.8	63.5	61	63	60.5
30.2	43	42.5	42	47.5	30.2	69	70.5	70.5	70
40.3	50.5	51.5	50	45	40.3	73	71	68	72
63	52.5	52.5	53	52.5	63	74	73	72.5	73.5
100	59.5	61.5	57.5	57.5	100	83	87	85.5	79.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	6	5	5	0.54	4.5	4	4	3.5
1	6.5	5	6.5	6.5	1	7.5	7	6.5	6.5
2.2	9.5	11.5	11.5	12	2.2	14.5	14	13.5	14.5
5	18.5	19	19.5	20	5	22.5	23	23	23.5
6.4	22	20.5	20.5	22	6.4	33	34	28.5	28
19.8	33.5	33	34	34	19.8	46.5	43.5	42	44
30.2	43	42.5	42	47.5	30.2	51	49.5	49	50
40.3	50.5	51.5	50	45	40.3	56	54.5	54	57
63	52.5	52.5	53	52.5	63	68	63.5	60	60
100	59.5	61.5	57.5	57.5	100	64.5	65	62.5	63.5
559.2nm					679.5nm				
0.09	2.5	2.5	2	2	0.09	0	0	0	0
0.54	7	9	9	9.5	0.54	0	0	0	0
1	15.5	14	15.5	15.5	1	0	0	0	0
2.2	23	22.5	24.5	24.5	2.2	0	0	0	0
5	35	33.5	36	34.5	5	7	8	8.5	9.5
6.4	41	35	37	35	6.4	10	12	13	10.5
19.8	50	49	47	47	19.8	25.5	23.5	23	22.5
30.2	60	59	58.5	59.5	30.2	31.5	32	34	31.5
40.3	61.5	60	59	60	40.3	39	40.5	35	33
63	65	62.5	62	63.5	63	42.5	39.5	42.5	40
100	80	69	69.5	65.5	100	52	52	55.5	51.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	6.5	6.5	6	6	0.54	0	0	0	0
1	10.5	11	10	9.5	1	0	0	0	0
2.2	16.5	13.5	15	15	2.2	8.5	13	10.5	11
5	27	26.5	26.5	25.5	5	21.5	23.5	17.5	18
6.4	26	28	28.5	25.5	6.4	22	25	22.5	21.5
19.8	42	43.5	40	42.5	19.8	44	43.5	43	41.5
30.2	53	56	54.5	57.5	30.2	57	57.5	57	55
40.3	56.5	56.5	53.5	56	40.3	56.5	55	56.5	53.5
63	61	59.5	59.5	57.5	63	66	64	65.5	66
100	64	67.5	65	66.5	100	69.5	65.5	65.5	70

Table A3.42: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 18, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	0	0	0	0	2.2	2.5	3	3	3
5	0	0	0	0	5	4	6.5	6	6
6.4	0	0	0	0	6.4	6	6.5	6.5	6.5
19.8	0	0	0	0	19.8	13	11	12.5	13.5
30.2	0	0	0	0	30.2	17.5	17.5	22	17.5
40.3	0	0	0	0	40.3	17	18	20.5	17.5
63	7	5.5	5	5	63	23.5	22	22	22.5
100	10.5	9	10	10	100	28.5	30.5	28	27.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	4.5	4	6.5	5	2.2	0	0	0	0
5	8	8.5	10	9.5	5	7.5	6.5	6.5	6.5
6.4	9.5	10	11.5	11	6.4	7	10	6.5	8.5
19.8	22	16	21.5	16.5	19.8	18	13	13.5	15
30.2	23.5	26	24.5	25.5	30.2	20.5	19.5	18	19.5
40.3	24.5	22	25.5	23	40.3	25.5	21	24	21.5
63	33.5	31.5	27.5	29.5	63	33.5	30	30	30
100	45.5	41.5	41.5	40	100	33.5	38	38.5	37
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	4.5	3.5	4	4.5	1	0	0	0	0
2.2	8	8	7	7	2.2	4	5.5	5.5	5.5
5	10.5	11	14	14	5	7.5	6.5	7.5	9
6.4	13.5	13	16.5	18	6.4	16	14	12.5	11.5
19.8	27.5	23.5	26.5	27.5	19.8	13.5	15	16.5	16
30.2	31.5	33.5	32	28	30.2	31	30	31	27.5
40.3	32.5	31	34	31.5	40.3	34	31.5	34	33
63	44.5	33	37.5	41	63	38	43.5	37.5	37
100	49	46	44.5	40	100	45.5	44.5	45.5	45
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	5.5	6	5.5	5.5
2.2	4.5	6	4.5	5	2.2	8.5	6	6.5	6
5	7	6.5	8	7.5	5	7.5	9.5	8.5	6.5
6.4	9	9.5	9	9	6.4	9.5	10.5	12	12.5
19.8	14.5	15.5	13.5	15.5	19.8	21.5	17	17	17.5
30.2	21.5	19	20	16.5	30.2	24	26	27	25.5
40.3	23	21.5	23	20.5	40.3	26.5	25.5	29	26
63	31.5	29	26.5	25.5	63	36	37.5	34.5	33.5
100	27	37	29.5	25	100	41	41	40.5	42

Table A3.43: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 19, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3	4.5	3	2.5
1	0	0	0	0	1	5.5	7.5	6	6
2.2	6.5	9	9.5	9	2.2	12	13	16	13
5	16.5	12.5	14.5	12	5	22	23.5	23	24.5
6.4	15	16	16.5	16	6.4	31	23	22	26.5
19.8	27	29	22.5	21	19.8	41.5	46	41	44
30.2	33	33.5	27	30.5	30.2	50	48	51	53
40.3	37.5	38	38	40	40.3	63	70.5	54	52
63	48	41	38.5	40.5	63	70	70.5	65	63
100	51.5	52.5	53	53.5	100	78	67	67	70
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	6.5	9	9.5	9	2.2	4.5	3.5	3	3
5	16.5	12.5	14.5	12	5	7	9	7.5	7.5
6.4	15	16	16.5	16	6.4	12	14	16.5	11.5
19.8	27	29	22.5	21	19.8	28	27	23	24
30.2	33	33.5	27	30.5	30.2	33	30.5	32	34
40.3	37.5	38	38	40	40.3	38.5	38.5	38	40
63	48	41	38.5	40.5	63	40.5	45.5	46	46
100	51.5	52.5	53	53.5	100	53	54.5	52	48.5
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	4	5	4	0.54	0	0	0	0
1	6	7.5	6	6	1	0	0	0	0
2.2	14	13.5	13.5	14	2.2	0	0	0	0
5	19	18	21.5	23.5	5	0	0	0	0
6.4	23	26.5	27.5	31	6.4	0	0	0	0
19.8	39.5	37	37.5	40.5	19.8	0	0	0	0
30.2	47	44	47.5	52	30.2	8	7.5	8.5	8
40.3	55	52	53.5	49	40.3	10.5	8.5	11.5	10.5
63	53	58.5	62.5	64	63	16	16	16.5	14
100	61	62.5	67	70	100	19.5	21	21	18.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	3	4.5	4	4	1	0	0	0	0
2.2	7.5	6	6.5	6	2.2	2	3.5	2.5	2
5	15.5	15.5	14.5	15	5	5	5.5	5.5	5.5
6.4	18.5	18.5	19	18.5	6.4	8	8	6	6.5
19.8	31.5	35	37.5	33	19.8	18	18.5	16	15
30.2	40	40.5	39.5	37	30.2	20	22	22	23.5
40.3	47.5	55	44	44	40.3	35.5	28.5	27.5	29
63	53	47.5	47	51.5	63	40.5	36.5	34	33.5
100	55.5	57.5	57	61.5	100	41	38.5	41	45

Table A3.44: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 19, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	0	0	0	0
2.2	0	0	0	0	2.2	0	0	0	0
5	0	0	0	0	5	11	11	8	8
6.4	0	0	0	0	6.4	11.5	12.5	13	13
19.8	0	0	0	0	19.8	18	18.5	19	21
30.2	3	3	2.5	2.5	30.2	27	23.5	21.5	20
40.3	3	4	4	4	40.3	23	23.5	23.5	26.5
63	8	8	7.5	7.5	63	27	28.5	25	24.5
100	21.5	20	20.5	20.5	100	26	28.5	31	35
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	9	8.5	6.5	5.5	1	4	4.5	6.5	6
2.2	10	10	11.5	10.5	2.2	8.5	8.5	7.5	6.5
5	19	17	15.5	17.5	5	13	16	14.5	14.5
6.4	16.5	20.5	22.5	22	6.4	13	14	12.5	14
19.8	23	25	29.5	31.5	19.8	21.5	23.5	18	19
30.2	38.5	37.5	28	26.5	30.2	31.5	32.5	24.5	24
40.3	28.5	30.5	30	30	40.3	26.5	25.5	27.5	30.5
63	32	38.5	32.5	32.5	63	27	29	29	29
100	39.5	36.5	37	40.5	100	41	32	30.5	31.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	4.5	6	5	5
2.2	10	11.5	12.5	10	2.2	8	10.5	9	11
5	13	11	17.5	17	5	16	18.5	21	22
6.4	20.5	16	19.5	18.5	6.4	17	18	15.5	17
19.8	21.5	24.5	21.5	25.5	19.8	22	30	21	25
30.2	27.5	26.5	29.5	26.5	30.2	31	29	28	29.5
40.3	29.5	29	29.5	30	40.3	31.5	31	32.5	33.5
63	35.5	39.5	40	43	63	36	36	39	36.5
100	33	33	33.5	36	100	44.5	42.5	35.5	37.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	4.5	8	5.5	5.5
2.2	0	0	0	0	2.2	6.5	6.5	7.5	6
5	11	13	13.5	11	5	14	13.5	12.5	15.5
6.4	13	16.5	12	14	6.4	19	16	15	15
19.8	18	19.5	14	21	19.8	22	26.5	26.5	27
30.2	24	27.5	29	28	30.2	35.5	37.5	43	28
40.3	28.5	29.5	23	22	40.3	32	30	32	32.5
63	29.5	32.5	28	26.5	63	36	36.5	38	34.5
100	29.5	31	29.5	30.5	100	44.5	49.5	38.5	38

Table A3.45: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 20, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	6	5.5	7.5	6
0.54	5.5	5.5	4	4.5	0.54	8	8.5	7.5	9.5
1	5	8	8	8	1	17.5	14.5	13.5	14.5
2.2	11.5	14.5	15.5	15	2.2	19	20	19	18.5
5	23.5	21	18.5	18.5	5	24	27.5	30	31
6.4	20	21.5	29.5	21	6.4	31.5	28.5	24	30.5
19.8	31	27.5	29	36	19.8	42.5	44	38	36.5
30.2	42	44.5	45	46	30.2	43	46	43	40
40.3	39	36	36	37	40.3	49	41	46.5	44
63	39.5	41	45	43.5	63	50.5	49.5	45.5	52.5
100	43.5	42.5	45.5	48.5	100	50	60.5	46	43.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5.5	5.5	4	4.5	0.54	3	6	3	4.5
1	5	8	8	8	1	6.5	9	5.5	5.5
2.2	11.5	14.5	15.5	15	2.2	13	10	9	11
5	23.5	21	18.5	18.5	5	17.5	19.5	18	20.5
6.4	20	21.5	29.5	21	6.4	21.5	18.5	18	18.5
19.8	31	27.5	29	36	19.8	33	34	35.5	36
30.2	42	44.5	45	46	30.2	37	40	41	39
40.3	39	36	36	37	40.3	40.5	38	39.5	41
63	39.5	41	45	43.5	63	56.5	56.5	56.5	49.5
100	43.5	42.5	45.5	48.5	100	49.5	50	47.5	49.5
559.2nm					679.5nm				
0.09	4	4	3.5	3.5	0.09	0	0	0	0
0.54	9	10.5	8.5	9	0.54	0	0	0	0
1	18	19.5	16.5	14	1	0	0	0	0
2.2	21	20	20	20.5	2.2	0	0	0	0
5	28	29	27	24	5	4.5	4	3.5	4
6.4	34.5	35	27	28.5	6.4	6.5	6.5	6	4.5
19.8	43	44.5	40	40	19.8	12	16	15.5	17.5
30.2	43	44.5	50	53	30.2	17	17	18.5	15.5
40.3	59.5	67.5	48	46.5	40.3	21.5	22	20	21
63	53.5	50	52	51	63	27.5	31	24	20.5
100	57	52	53	51	100	24.5	24	28.5	33
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	8.5	8.5	7.5	8	0.54	0	0	0	0
1	10	11.5	8	10.5	1	0	0	0	0
2.2	19	18	16	18.5	2.2	0	0	0	0
5	19	23	18	25.5	5	0	0	0	0
6.4	22	20	21.5	20.5	6.4	14.5	11.5	13.5	11.5
19.8	30	29.5	37.5	29.5	19.8	21	28	23.5	27.5
30.2	29.5	31	34	31	30.2	39.5	40	44	43.5
40.3	36.5	38.5	34.5	37.5	40.3	40.5	36.5	34	35.5
63	38	38.5	43	35.5	63	40.5	44.5	47	41.5
100	46	36	40.5	39.5	100	44.5	43	45.5	47

Table A3.46: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 20, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	7.5	8.5	8	8
1	0	0	0	0	1	18.5	16.5	12.5	10
2.2	0	0	0	0	2.2	20.5	20	20.5	23
5	0	0	0	0	5	29	30.5	28.5	28
6.4	0	0	0	0	6.4	35.5	34.5	30.5	35
19.8	7.5	8.5	8	8	19.8	48.5	46.5	51	45
30.2	9.5	9.5	8.5	8.5	30.2	55	60	58.5	57.5
40.3	9.5	9.5	9.5	9.5	40.3	64.5	61.5	60	58
63	14	14	11	11	63	65.5	65.5	64	66.5
100	38.5	39.5	39.5	39.5	100	71.5	76.5	75	73.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	10	10	9	9	0.54	6	5	6	5.5
1	14.5	13	10	12.5	1	12.5	11.5	10	10
2.2	20	19.5	22.5	21.5	2.2	14	16	16	17
5	37.5	34.5	32	37.5	5	23.5	25	23	21.5
6.4	36	39	36.5	39	6.4	32	31	36	36
19.8	57.5	53.5	53	49.5	19.8	40.5	40	37.5	35.5
30.2	60.5	64	59.5	59.5	30.2	51	51.5	49	50
40.3	63	69	65	63.5	40.3	63.5	58.5	57.5	58.5
63	73	69.5	67.5	74.5	63	69.5	70.5	69	69
100	84.5	82	79.5	82.5	100	74.5	76	97	75
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	6	7.5	6.5	6.5
0.54	13	11.5	10.5	12.5	0.54	17.5	15.5	14	14
1	18.5	22.5	20.5	20	1	25.5	23.5	23	23
2.2	30.5	28	29	29.5	2.2	32	32	32	31.5
5	43	43.5	41.5	42	5	40	42	41	40.5
6.4	45.5	44.5	48	45.5	6.4	46.5	46.5	46	44.5
19.8	67	62.5	63	59.5	19.8	59.5	59	62	61.5
30.2	69.5	65.5	71	68	30.2	70.5	70	67	63.5
40.3	79.5	76.5	72.5	71.5	40.3	72.5	69.5	76	71.5
63	80.5	77.5	82	81.5	63	75.5	82.5	78.5	77.5
100	82.5	82	86	87.5	100	87	84	81.5	88
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	10	5.5	8	8	0.54	12	14	12	12
1	14.5	13	15	17.5	1	21.5	19	18	16
2.2	19	18	19	19	2.2	29	30	30	30
5	27.5	26.5	29.5	28	5	40.5	41	38	38
6.4	32	30	26	30	6.4	45	42.5	40	44.5
19.8	42.5	40	40.5	44	19.8	57.5	56	60.5	57.5
30.2	50	47	50	50	30.2	65	67	55.5	64.5
40.3	55	55	56	54	40.3	70.5	70	71	64
63	58.5	57	62.5	59.5	63	79.5	75.5	73.5	82
100	66.5	63	68	68	100	83.5	83.5	90	82.5

Table A3.47: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 21, a male *Lucilia sericata,* using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	4.5	5.5	6.5	6	0.09	0	0	0	0
0.54	14	13.5	15	14	0.54	15.5	13	15.5	15
1	21.5	21.5	18	21.5	1	24.5	24.5	22	26.5
2.2	32	30.5	33.5	30	2.2	41.5	40.5	44.5	39.5
5	43	41	38.5	43.5	5	62	61.5	58	58.5
6.4	44.5	43.5	45.5	45.5	6.4	62	72	66.5	65.5
19.8	61.5	60.5	56.5	63	19.8	89.5	89.5	84.5	87.5
30.2	69	68	70.5	68.5	30.2	92.5	102.5	101	101
40.3	73	79	81	84	40.3	103	107	105.5	102
63	84	80.5	81	80	63	111	111.5	115	110
100	93	87.5	83	90	100	121.5	121	119	118
529.6nm					650.1nm				
0.09	4.5	5.5	6.5	6	0.09	0	0	0	0
0.54	14	13.5	15	14	0.54	6	6.5	6.5	6
1	21.5	21.5	18	21.5	1	9.5	10	9.5	6.5
2.2	32	30.5	33.5	30	2.2	17.5	15	21.5	18.5
5	43	41	38.5	43.5	5	30	34.5	32.5	32.5
6.4	44.5	43.5	45.5	45.5	6.4	40	40	36.5	40
19.8	61.5	60.5	56.5	63	19.8	68.5	69	68	64.5
30.2	69	68	70.5	68.5	30.2	79	77	80.5	78
40.3	73	79	81	84	40.3	84	82.5	85.5	88.5
63	84	80.5	81	80	63	89.5	93	89.5	92
100	93	87.5	83	90	100	105	99	97.5	100.5
559.2nm					679.5nm				
0.09	8	7.5	6	7	0.09	0	0	0	0
0.54	15.5	14.5	14.5	17	0.54	0	0	0	0
1	25.5	24.5	21	26.5	1	0	0	0	0
2.2	38.5	39.5	37.5	36	2.2	3	3.5	3.5	3.5
5	59.5	55.5	51.5	51.5	5	6	7.5	6.5	6.5
6.4	74.5	68	79.5	74	6.4	8.5	11	12	10.5
19.8	82.5	86	84.5	81.5	19.8	24.5	26	24	23.5
30.2	88	91.5	89	87	30.2	29.5	35.5	35	33
40.3	95	92	90	90	40.3	45	43	42.5	42
63	105	96.5	96	97.5	63	55.5	53	57	57
100	103.5	105	111.5	104	100	64	60.5	71.5	65.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	11.5	10	9.5	9	0.54	0	0	0	0
1	17.5	15	16.5	17	1	5.5	5.5	6	6.5
2.2	27	27.5	20.5	22	2.2	12	9.5	10	10
5	41.5	41	41.5	41.5	5	21	19	18	15
6.4	46	45	49	44.5	6.4	21.5	19	22.5	23.5
19.8	73	67	65	62	19.8	44.5	42.5	48.5	44.5
30.2	79	76.5	72.5	79	30.2	56	57	55.5	55
40.3	81.5	79	92	82	40.3	67.5	65	62	59
63	89.5	93	89.5	90.5	63	74.5	72.5	76	76
100	99.5	97	97	95.5	100	83.5	85	79	82

Table A3.48: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 21, a male *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	4	3.5	4	4.5
1	0	0	0	0	1	5.5	6	6.5	6
2.2	0	0	0	0	2.2	8	9.5	8.5	7
5	0	0	0	0	5	12.5	12.5	12	15
6.4	0	0	0	0	6.4	14	13.5	14.5	16
19.8	3.5	5	5	5	19.8	19.5	25	24	21
30.2	5	3.5	5	5	30.2	30	28	26	25
40.3	5	4.5	4.5	4.5	40.3	28.5	27	25	28
63	6.5	6.5	9	9	63	30.5	32.5	35	29
100	17	18.5	20.5	20.5	100	38.5	34.5	36	37
331.6nm					440.4nm				
0.09	3	2.5	3.5	3	0.09	5	4	4	5
0.54	7.5	7	7	9.5	0.54	7	7	7	7.5
1	14	13	11.5	13	1	13	13.5	12.5	12.5
2.2	19.5	19.5	20	19.5	2.2	20	21.5	21.5	21
5	31.5	29.5	30	30	5	34	31	30	29
6.4	31	30	31.5	31.5	6.4	34	31	32.5	30
19.8	47	43.5	40.5	40.5	19.8	51	52	50.1	47.5
30.2	48	47	47	48.5	30.2	57.5	57	56.5	55.5
40.3	49.5	47.5	56	51.5	40.3	64.5	61.5	59	58.5
63	54.5	51	56.5	62	63	74	70.5	66.5	69
100	62	57.5	61.5	66.5	100	76	74.5	79.5	73.5
359.0nm					469.6nm				
0.09	3	3.5	3	3	0.09	2.5	2	1.5	2
0.54	5.5	5.5	4.5	6	0.54	6	6	4.5	6.5
1	8	8.5	9	10	1	11.5	10	8.5	9.5
2.2	12.5	16	13.5	12	2.2	11.5	13	13.5	11
5	22.5	19	18.5	17.5	5	19	17.5	17.5	16.5
6.4	20.5	20.5	19.5	23	6.4	19.5	19	19.5	20.5
19.8	30.5	33.5	33	29	19.8	26	25.5	27.5	27.5
30.2	37	34	34	33.5	30.2	31	32.5	34	31.5
40.3	37.5	36	36.5	36.5	40.3	36.5	36	36	37.5
63	41	42	45.5	41	63	40.5	43	41	38.5
100	45	46	44	46.5	100	46.5	45.5	41	41.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	4	2.5	3	2.5
0.54	3.5	3.5	2.5	2.5	0.54	6	5.5	5.5	4
1	7	5.5	5.5	5	1	7	6.5	5.5	6
2.2	10	7.5	10.5	9	2.2	8.5	10.5	10.5	10
5	15.5	16.5	13	15	5	15	13.5	14.5	15.5
6.4	19	17	17	16	6.4	17.5	17	18.5	18.5
19.8	30	24.5	25	26.5	19.8	30.5	25.5	29	23
30.2	31	30.5	33.5	31.5	30.2	26.5	28	26	26
40.3	32	38	39	34.5	40.3	30	31.5	29	28.5
63	37	42	38.5	38.5	63	34	32	36	31
100	41.5	39	40.5	40	100	34	40.5	40.5	34

Table A3.49: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 22, a female *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	6	6	5.5	4	0.09	8	6.5	8	9
0.54	10	8.5	8	9.5	0.54	30.5	32.5	34	36.5
1	14	16	13.5	16.5	1	50	50.5	52	53.5
2.2	25	21	21.5	19.5	2.2	72.5	70.5	68.5	71.5
5	31.5	29	27.51	30.5	5	88.5	87.5	91	85.5
6.4	32.5	31	33.5	37.5	6.4	95.5	91	84.5	85
19.8	42	46.5	47.5	45	19.8	115.5	109	111	102.2
30.2	52	51.5	47.5	52	30.2	121	117	117	122.5
40.3	57.5	55	53	56	40.3	127	121.5	121	121
63	63	54	57.5	67.5	63	136	130.5	123.5	122
100	67.5	75.5	66.5	65.5	100	139.5	132.5	130.5	126.5
529.6nm					650.1nm				
0.09	6	6	5.5	4	0.09	0	0	0	0
0.54	10	8.5	8	9.5	0.54	13.5	15	14.5	13.5
1	14	16	13.5	16.5	1	25	22.5	22.5	23.5
2.2	25	21	21.5	19.5	2.2	37	36	36.5	40
5	31.5	29	27.51	30.5	5	54	47	55.5	54
6.4	32.5	31	33.5	37.5	6.4	56.5	62.5	61	61
19.8	42	46.5	47.5	45	19.8	87	82.5	77	81.5
30.2	52	51.5	47.5	52	30.2	91	89.5	86	82
40.3	57.5	55	53	56	40.3	92	89	92	92
63	63	54	57.5	67.5	63	109	100.5	106.5	98
100	67.5	75.5	66.5	65.5	100	113	106.5	103	104.5
559.2nm					679.5nm				
0.09	4	4.5	4	4.5	0.09	0	0	0	0
0.54	16.5	15.5	15.5	13.5	0.54	0	0	0	0
1	28	25.5	26	24.5	1	5	5	7	7
2.2	33.5	33.5	36.5	38	2.2	12.5	11.5	11	12
5	48	45.5	46.5	49.5	5	25	23.5	25	23
6.4	49.5	51	53	56.5	6.4	30	30	28.5	27.5
19.8	65	72	71	67.5	19.8	59.5	57.5	55.5	55
30.2	70	72.5	78	71.5	30.2	76	74	69.5	67.5
40.3	76.5	80	80	76.5	40.3	81.5	85.5	82.5	83.5
63	85	90.5	87	79.5	63	87.5	83.5	85.5	93.5
100	89.5	94	93.5	91.5	100	109	106	98.5	91.5
590.1nm					705.0nm				
0.09	2	2	2.5	2	0.09	0	0	0	0
0.54	4	4.5	7	4	0.54	7.5	8	8.5	7
1	10	9	10	9	1	13.5	13	12.5	13.5
2.2	16.5	19.5	18.5	18.5	2.2	24	24	29	26.5
5	23.5	23.5	25.5	26.5	5	39.5	41.5	45.5	47.5
6.4	33.5	35	33.5	32.5	6.4	46.5	45.5	45	44.5
19.8	38	37.5	37	36.5	19.8	79.5	82.5	85.5	83
30.2	48.5	47	44.5	41.5	30.2	81.5	77.5	78	85
40.3	46	49.5	50.5	49	40.3	88	83.5	90.5	95
63	57	58	52.5	48	63	92	93	101.5	98.5
100	61.5	58	62	60.5	100	102	102	106	100

Table A3.50: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 22, a female *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	3.5	4	4	4
2.2	0	0	0	0	2.2	6	5	7	5.5
5	0	0	0	0	5	9	10	11	10
6.4	0	0	0	0	6.4	13.5	12.5	11.5	11.5
19.8	0	0	0	0	19.8	20	18.5	17.5	18
30.2	0	0	0	0	30.2	28.5	25.5	25	23.5
40.3	0	0	0	0	40.3	27	26.5	27	28
63	3	3.5	3	3	63	34	34	33.5	32.5
100	9	8.5	10.5	10.5	100	40	37.5	38.5	38.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	4	3.5	4	4.5
1	3	4	2.5	3.5	1	7	7	8	8
2.2	6.5	5.5	5.5	7.5	2.2	13.5	11.5	12.5	11.5
5	12.5	11.5	10.5	12	5	18.5	20	19.5	18.5
6.4	13	12	14.5	13.5	6.4	21.5	21.5	20.5	20.5
19.8	21.5	21.5	22	20	19.8	35.5	32	34	32
30.2	28	29.5	28.5	26	30.2	41.5	40	40	37
40.3	29.5	28.5	29.5	28.5	40.3	45	44.5	43.5	43
63	37.5	35	36	35	63	51.5	49	49	47.5
100	46	44	44	45	100	60	57	57	56
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5	5	4.5	5	0.54	4.5	4.5	4	6
1	9	8.5	9	8.5	1	10	10	9.5	9
2.2	15	15	14.5	14	2.2	15.5	16	15	15.5
5	25.5	24	24	24	5	25	24	22	22.5
6.4	26.5	27.5	26.5	28	6.4	27	28	27	26.5
19.8	42	40	41	38	19.8	41.5	40	40.5	38.5
30.2	50.5	48	48.5	48	30.2	50.5	49.5	47.5	48
40.3	52	53	51	50.5	40.3	56	51.5	55	53.5
63	58.5	58.5	57	57.5	63	62	58	60	58
100	69	65	64	62.5	100	69	69	67	67.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3.5	3.5	4	3.5
1	4.5	4	7	4.5	1	8	8	8.5	9
2.2	6.5	8	9.5	8	2.2	15	15	13	14
5	13.5	13	14.5	14	5	21	21.5	21.5	22
6.4	16	15.5	15	15	6.4	25.5	25.5	24.5	26
19.8	25.5	27.5	27.5	26.5	19.8	42	39	40	39.5
30.2	33	33	32.5	32.5	30.2	51	50	48	47.5
40.3	38	37	34.5	36	40.3	54	52.5	53.5	50.5
63	42.5	45.5	43.5	42	63	57	57.5	56.5	56.5
100	50.5	51	51.5	52	100	67	64	66.5	66.5

Table A3.51: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 23, a female *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5.5	5	4.5	5.5	0.54	4.5	5.5	3	2.5
1	10	10.5	9.5	9.5	1	6.5	6.5	8	6.5
2.2	16	15.5	15	16.5	2.2	11.5	13	14	12
5	27	26	27	26	5	23.5	21.5	22.5	22.5
6.4	28.5	29	29	29	6.4	27	26	26	25.5
19.8	44.5	42.5	41.5	40.5	19.8	45.5	44.5	42	44
30.2	54	53.5	53	54	30.2	54.5	54	54	52
40.3	57	58.5	54	54	40.3	62	59	57	57.5
63	66.5	64	63	66	63	66	66.5	65.5	67.5
100	74.5	71.5	68.5	68.5	100	75.5	71.5	73.5	72
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	5.5	5	4.5	5.5	0.54	0	0	0	0
1	10	10.5	9.5	9.5	1	2	2.5	2	2.5
2.2	16	15.5	15	16.5	2.2	3.5	5	4.5	5
5	27	26	27	26	5	9.5	8.5	10	9.5
6.4	28.5	29	29	29	6.4	12	11	13	11.5
19.8	44.5	42.5	41.5	40.5	19.8	27.5	28	26.5	26.5
30.2	54	53.5	53	54	30.2	37.5	35.5	34.5	35.5
40.3	57	58.5	54	54	40.3	44	41.5	42	41.5
63	66.5	64	63	66	63	52.5	53	51	50.5
100	74.5	71.5	68.5	68.5	100	59.5	62	61	61.5
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	10.5	11	10.5	10.5	0.54	0	0	0	0
1	20	18	17.5	17.5	1	0	0	0	0
2.2	28.5	28	31	28	2.2	0	0	0	0
5	41	41.5	40	40.5	5	0	0	0	0
6.4	51.5	48.5	50	48.5	6.4	0	0	0	0
19.8	72	68.5	67	68	19.8	7.5	7	6	7.5
30.2	77	76.5	74	76	30.2	8.5	8	8.5	8.5
40.3	79.5	77.5	76	77.5	40.3	11.5	14.5	12.5	11.5
63	88.5	88.5	84.5	86	63	16	17.5	15.5	16
100	91.5	88.5	90.5	90	100	22	20	21	20
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	4	4	4.5	0.54	0	0	0	0
1	7.5	11	10	8.5	1	0	0	0	0
2.2	14.5	14.5	14	15.5	2.2	3.5	5.5	5	5.5
5	24	22.5	24.5	21.5	5	6	6.5	6	6
6.4	28.5	26	28	25.5	6.4	9	10	8	10
19.8	44.5	45.5	42	46	19.8	23	23	25.5	25
30.2	55.5	55.5	51.5	53	30.2	29.5	28.5	28	28.5
40.3	62.5	60.5	60	58.5	40.3	37	35.5	36.5	35
63	67.5	68.5	68	66.5	63	47.5	45	44	46
100	75	73.5	72	72.5	100	55.5	55	53.5	54.5

Table A3.52: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 23, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	1.5	2	1.5	1.5
1	0	0	0	0	1	2.5	3	3.5	3.5
2.2	0	0	0	0	2.2	7	7	6.5	6.5
5	0	0	0	0	5	11	11.5	11	10.5
6.4	0	0	0	0	6.4	13	13	13	13.5
19.8	0	0	0	0	19.8	20.5	20.5	19.5	20
30.2	0	0	0	0	30.2	27	25.5	25	26.5
40.3	3	3	2.5	2.5	40.3	31	31	28.5	31
63	4.5	4	4.5	4.5	63	35.5	32	35	34
100	9	7	6.5	6.5	100	38.5	39	39	36.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	4	6	4.5	4.5
2.2	5	4.5	4.5	4	2.2	5	6.5	6	6.5
5	8.5	8	8.5	8.5	5	8	10	9	10.5
6.4	9.5	10.5	9.5	10	6.4	11	11.5	10.5	13
19.8	14.5	16.5	15.5	15.5	19.8	17.5	16.5	18.5	19.5
30.2	20.5	18.5	21	19	30.2	22.5	22.5	23.5	23
40.3	21.5	22	20	21	40.3	26.5	24	25	25
63	26	27.5	28.5	25.5	63	29.5	29	30	30
100	34	33.5	35	33	100	35.5	36	32.5	33.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3	3	3.5	3.5
1	3.5	4.5	3.5	4.5	1	6.5	6.5	7.5	7.5
2.2	6	7	6	5.5	2.2	11	10.5	10.5	10.5
5	13	10.5	11	10	5	15.5	16	16	16.5
6.4	12.5	13	12.5	13	6.4	19	19	18	19
19.8	21	18.5	18	18.5	19.8	29	27	26	25.5
30.2	24.5	23.5	24	24	30.2	33.5	34	34	33
40.3	27.5	29.5	26	25.5	40.3	39.5	34	35	35.5
63	31	32.5	31	30	63	41.5	38.5	39.5	38.5
100	37	37	36	37	100	43	44.5	43.5	41.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3	3.5	3	3
1	0	0	0	0	1	6	6.5	5	6
2.2	3.5	3.5	4.5	4	2.2	11.5	12	12.5	11.5
5	9.5	8.5	9	7.5	5	17	18	17	18
6.4	9.5	9	8.5	8	6.4	21	22	20	20
19.8	15.5	17	16.5	16	19.8	30.5	30.5	29.5	31
30.2	20.5	23.5	20.5	21	30.2	37	36.5	36.5	35.5
40.3	26	22	23.5	23.5	40.3	41.5	39	39	40.5
63	28	27.5	27.5	28.5	63	45	44.5	43.5	46.5
100	33	31.5	33.5	31.5	100	49.5	46.5	47.5	48.5

Table A3.53: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 24, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	2.5	4	3.5	4	0.54	4.5	5	5	4.5
1	7.5	7.5	7	7.5	1	10	9.5	10.5	10
2.2	11.5	13	12	12.5	2.2	19.5	17.5	18	18
5	19	18.5	19.5	18.5	5	30.5	32	30.5	29.5
6.4	22.5	22	21.5	22.5	6.4	34.5	35	38	34
19.8	34.5	35	34.5	32.5	19.8	53.5	54.5	55	53.5
30.2	40	38.5	40	39	30.2	65.5	61.5	63	63
40.3	42.5	42	41	40.5	40.3	71	71	73	68
63	49	47.5	46	43	63	73.5	71	71.5	73.5
100	50.5	50	52.5	49.5	100	74	73.5	78.5	74.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	2.5	4	3.5	4	0.54	3.5	4.5	4	2.5
1	7.5	7.5	7	7.5	1	4.5	5.5	4	4
2.2	11.5	13	12	12.5	2.2	4	5	4	5
5	19	18.5	19.5	18.5	5	7.5	7	6.5	7.5
6.4	22.5	22	21.5	22.5	6.4	7.5	8	8.5	11
19.8	34.5	35	34.5	32.5	19.8	23	22	19.5	20.5
30.2	40	38.5	40	39	30.2	24	28	27	26
40.3	42.5	42	41	40.5	40.3	30	31.5	31.5	31
63	49	47.5	46	43	63	37	40.5	40	39.5
100	50.5	50	52.5	49.5	100	45	44.5	46.5	46
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4.5	5	6	5	0.54	0	0	0	0
1	12.5	12.5	11.5	12	1	0	0	0	0
2.2	20.5	20	19	20	2.2	0	0	0	0
5	28.5	27	26.5	26.5	5	0	0	0	0
6.4	33	33	33	33.5	6.4	2.5	2	3	3
19.8	46.5	49.5	45.5	45.5	19.8	8.5	8.5	9	8.5
30.2	57.5	58.5	55.5	53.5	30.2	15	13	13.5	11
40.3	60.5	57	59	58.5	40.3	15.5	17	17	16
63	64	65	63	66	63	22	22	22.5	22
100	67	67	67.5	68.5	100	29.5	27.5	28.5	27.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	7.5	7.5	7	6.5	1	0	0	0	0
2.2	14.5	10.5	12.5	14	2.2	2.5	2.5	2	2
5	21.5	21	23	22.5	5	6	6.5	7	6
6.4	26.5	26	24.5	26.5	6.4	8	8	10.5	8.5
19.8	43.5	41	40	41	19.8	20	21	20	20
30.2	49.5	49.5	46.5	47.5	30.2	26.5	26.5	24.5	25.5
40.3	56.5	50.5	54	51.5	40.3	32	34	32	30.5
63	63.5	60.5	58	60.5	63	36.5	40	38.5	36.5
100	67	68.5	71	72.5	100	44	45	45.5	47.5

Table A3.54: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 24, a male *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	7	5.5	6	5
1	0	0	0	0	1	9	10	8.5	10.5
2.2	0	0	0	0	2.2	15.5	15.5	13	14
5	0	0	0	0	5	21.5	23	21	20
6.4	0	0	0	0	6.4	24.5	25	25	26
19.8	0	0	0	0	19.8	38.5	34	34.5	37
30.2	0	0	0	0	30.2	44.5	44	39.5	40
40.3	2.5	2	2	2	40.3	43	44	43.5	44
63	4.5	2.5	4	4	63	48.5	50	49.5	48.5
100	11.5	11.5	10	10	100	54.5	54.5	51.5	53.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	7	5.5	8	7
1	5	5	7	5.5	1	10.5	9	10	9
2.2	9.5	10.5	10.5	10	2.2	15	13	13.5	14
5	18.5	17.5	18.5	16.5	5	21	23.5	22	21.5
6.4	20	18	17.5	19	6.4	23.5	25.5	27	26
19.8	30	29	29	29	19.8	36.5	40.5	36	36
30.2	34	35	34.5	34	30.2	42	43.5	40.5	41.5
40.3	39.5	37.5	41.5	41	40.3	45.5	45	45.5	44.5
63	49	47.5	49	47.5	63	51.5	51	51.5	51.5
100	63.5	55	55	55	100	59.5	60	57	58.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	4	4	4	0.54	0	0	0	0
1	7.5	7.5	7	7.5	1	12.5	7	15.5	13
2.2	13	12.5	11.5	11.5	2.2	20	24	19	21
5	19.5	19	19	20.5	5	28	29.5	29.5	25
6.4	23	20	21	21.5	6.4	30.5	29	31	31.5
19.8	30	34.5	33.5	30.5	19.8	44.5	44	43.5	44
30.2	38.5	39	38.5	35.5	30.2	53	51.5	52.5	54.5
40.3	42.5	42	41	43.5	40.3	56.5	54	54	54.5
63	47	44	46.5	48	63	63	61.5	62	59.5
100	51	51	50	50	100	64.5	63	65.5	68.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	7	8	7	5
0.54	5	4	4.5	4.5	0.54	13	9.5	10.5	11.5
1	7.5	5.5	6.5	6	1	15	16	14.5	15.5
2.2	11.5	13	10.5	12	2.2	20	19	20	18.5
5	18	19	18.5	18	5	26.5	27.5	28	27
6.4	21	21	22	20	6.4	33	34	31.5	31
19.8	29	31	32.5	30	19.8	46	39.5	45	38.5
30.2	37.5	40	36.5	37.5	30.2	53	48.5	48.5	47.5
40.3	38.5	40	38.5	40	40.3	52.5	50	51.5	52
63	48	46.5	45	47	63	59	55.5	56	57
100	54.5	53.5	54	53	100	65	62	62	62

Table A3.55: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 25, a female *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	5.5	3	3	3	0.09	0	0	0	0
0.54	11.5	9.5	11	11	0.54	8.5	7.5	7.5	6.5
1	16.5	15.5	16	15.5	1	12.5	14	13.5	14
2.2	19.5	21	20.5	19	2.2	30	26	33.5	28
5	30	27	28.5	25.5	5	48.5	46.5	43.5	46
6.4	30	30	32.5	32	6.4	54	51	51	48
19.8	42	41.5	40	43	19.8	81	77	74	76.5
30.2	48.5	46	47	50	30.2	85.5	84	84.5	82.5
40.3	52.5	52	49	52.5	40.3	91.5	88.5	88.5	88
63	58.5	54.5	53.5	55.5	63	98.5	95	97.5	97
100	57	60.5	61.5	62	100	107.5	105	105.5	105.5
529.6nm					650.1nm				
0.09	5.5	3	3	3	0.09	0	0	0	0
0.54	11.5	9.5	11	11	0.54	0	0	0	0
1	16.5	15.5	16	15.5	1	4	4.5	4	4.5
2.2	19.5	21	20.5	19	2.2	11.5	9	10	7.5
5	30	27	28.5	25.5	5	21.5	19.5	18.5	21.5
6.4	30	30	32.5	32	6.4	25	25.5	23.5	25
19.8	42	41.5	40	43	19.8	50	50	48.5	48
30.2	48.5	46	47	50	30.2	60.5	60.5	62.5	60.5
40.3	52.5	52	49	52.5	40.3	68.5	65.5	69.5	66.5
63	58.5	54.5	53.5	55.5	63	80	77	78	79
100	57	60.5	61.5	62	100	86.5	88	85	87
559.2nm					679.5nm				
0.09	5.5	5.5	5	5.5	0.09	0	0	0	0
0.54	15	14.5	15.5	14.5	0.54	0	0	0	0
1	25	25.5	26	25.5	1	0	0	0	0
2.2	41.5	37	37.5	38.5	2.2	0	0	0	0
5	51	51	49.5	51.5	5	2.5	3	3.5	3
6.4	59.5	56	53	57	6.4	3.5	4	3.5	3.5
19.8	73.5	73	73	73	19.8	13	12.5	12	13.5
30.2	81	80	82	82.5	30.2	18	17	17	17.5
40.3	85.5	85	88	86.5	40.3	23	22.5	23	22.5
63	95	94.5	89	94	63	32.5	31.5	32	30.5
100	99.5	100	93	98.5	100	41	41.5	40.5	41.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	8.5	8	7	7.5	0.54	0	0	0	0
1	14.5	14	16.5	16	1	0	0	0	0
2.2	33	31	27.5	26	2.2	6	5	5.5	4.5
5	40	39	39	38.5	5	13	11.5	12.5	12
6.4	45	43.5	47.5	41.5	6.4	15.5	15.5	14	15.5
19.8	63	62.5	62.5	62.5	19.8	34.5	37	36.5	35
30.2	72	73	71	72.5	30.2	45	43.5	45	45.5
40.3	79.5	77.5	79.5	76.5	40.3	53.5	51.5	54	54
63	84	84	83	82.5	63	66	63	65.5	67
100	95	91.5	91	91	100	77	73.5	75	74

Table A3.56: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 25, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	1.5	2	2	2
0.54	0	0	0	0	0.54	5	6.5	6.5	6
1	0	0	0	0	1	12	12	11.5	13.5
2.2	0	0	0	0	2.2	18.5	18	16.5	17
5	0	0	0	0	5	23.5	27	23	22
6.4	0	0	0	0	6.4	26.5	26	27	27.5
19.8	3	4	3	3	19.8	35	36.5	33.5	34.5
30.2	4	3.5	3.5	3.5	30.2	40	40.5	42	41
40.3	7	7.5	7	7	40.3	46	47	43	41.5
63	9	10	9	9	63	47	47.5	49.5	47.5
100	26	28	23.5	23.5	100	54.5	55	51.5	55
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	3	2	2.5	2
0.54	6	4.5	4.5	4	0.54	6.5	7	8	5.5
1	8	9.5	6	7	1	15.5	12.5	14	12.5
2.2	12.5	13.5	16	13.5	2.2	17	25.5	18	21
5	24.5	24.5	20	25	5	30	24.5	29.5	25.5
6.4	25	30.5	24.5	20.5	6.4	29	27	28.5	31
19.8	30.5	30.5	32	31	19.8	36	41	35.5	37
30.2	41.5	36	38	35.5	30.2	42	44.5	44	42.5
40.3	39.5	47	39	46	40.3	48	52.5	45	47.5
63	45	44.5	47.5	41	63	50	53	51.5	50
100	47.5	54	55.5	49.5	100	55	59	55	53.5
359.0nm					469.6nm				
0.09	8	7.5	7	7	0.09	4	3.5	4	4
0.54	8	7	12.5	8.5	0.54	9	8.5	8	9
1	13	15.5	13	13	1	14	13.5	13	13.5
2.2	22.5	19.5	19	21.5	2.2	19.5	19.5	17	19
5	31	25.5	29	26.5	5	26	23.5	24	25
6.4	30.5	29	32	28.5	6.4	29.5	27	28	30.5
19.8	44	38	37.5	35.5	19.8	36.5	39	40	35
30.2	44	45.5	42	45	30.2	44.5	48	48	41.5
40.3	45.5	48	48.5	44	40.3	48	50.5	50.5	53.5
63	46.5	51	52	46.5	63	51	57	53	53.5
100	55	55	52	54.5	100	59	58.5	64.5	58
379.7nm					489.0nm				
0.09	5	3	4	3	0.09	3	4.5	4	3
0.54	6	6	7	7.5	0.54	10	12	12.5	11.5
1	12.5	11	11	11	1	15.5	17.5	16	16.5
2.2	14.5	15.5	12	13.5	2.2	23	23	23	27.5
5	15.5	20	20	20.5	5	30	32	32	29
6.4	21	23	20.5	20	6.4	38	34	32.5	34
19.8	30	30	30	29	19.8	50	45.5	44	48.5
30.2	40	37.5	40	36	30.2	50.5	50	48	54
40.3	39.5	38.5	40	38.5	40.3	51.5	52	53	54.5
63	46	43	50.5	48.5	63	57	60	56	54
100	47	48.5	47	49	100	61	60.5	65	59

Table A3.57: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 26, a male *Lucilia caesar*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	5	3.5	4	3.5	0.09	3.5	4	4	3.5
0.54	8.5	11	9.5	11	0.54	20.5	23.5	22	22
1	20.5	18	17	16.5	1	30.5	34.5	35	31.5
2.2	24	21.5	23	24	2.2	47	46	48	50.5
5	28.5	31.5	30	29	5	63.5	65.5	59.5	60.5
6.4	32	30.5	35	35.5	6.4	67.5	64	64	69
19.8	39.5	44	40	39.5	19.8	77.5	74	77.5	80
30.2	47.5	47	48	46.5	30.2	83	86	83.5	78.5
40.3	48.5	53	54	50.5	40.3	87	86	90.5	85
63	54	59.5	56.5	52.5	63	92	92.5	94	91.5
100	59.5	63	61.5	60.5	100	100	97.5	95.5	98
529.6nm					650.1nm				
0.09	5	3.5	4	3.5	0.09	4	7	4	4
0.54	8.5	11	9.5	11	0.54	6.5	7.5	7	7
1	20.5	18	17	16.5	1	15.5	14.5	14	17
2.2	24	21.5	23	24	2.2	27	26.5	26	29
5	28.5	31.5	30	29	5	46	44.5	43	46.5
6.4	32	30.5	35	35.5	6.4	49.5	48	49.5	49
19.8	39.5	44	40	39.5	19.8	69	68	66.5	67
30.2	47.5	47	48	46.5	30.2	75.5	79.5	77	74.5
40.3	48.5	53	54	50.5	40.3	81	78.5	81.5	78
63	54	59.5	56.5	52.5	63	84.5	90	82	84.5
100	59.5	63	61.5	60.5	100	92.5	90	88	89
559.2nm					679.5nm				
0.09	5	4	5.5	5.5	0.09	0	0	0	0
0.54	16	17	15.5	15.5	0.54	0	0	0	0
1	20.5	22	21.5	20.5	1	5.5	7.5	8.5	9
2.2	30.5	29.5	30	29.5	2.2	7.5	7	10.5	8
5	36	39	38.5	37.5	5	11	10.5	11	10.5
6.4	42	40	39	43.5	6.4	14	13	14	14.5
19.8	50	44	51	49.5	19.8	16	19.5	15	18
30.2	58.5	57	58.5	61.5	30.2	37.5	42.5	37	36
40.3	61	59	64	60.5	40.3	44	47	50.5	44
63	63.5	63.5	67	65.5	63	59	59.5	61.5	58
100	72	70	69.5	70	100	71	72	65.5	68
590.1nm					705.0nm				
0.09	7	7	7	6	0.09	0	0	0	0
0.54	15	10.5	12	12	0.54	6	7	7	6
1	14	16	14.5	14.5	1	11.5	13	11	11
2.2	26	30.5	23	23	2.2	25	25.5	24	25.5
5	35.5	31.5	31	31	5	43	38.5	40.5	39
6.4	35	39	38.5	33	6.4	46	45.5	45.5	46.5
19.8	45	46.5	53	44.5	19.8	73	67	67	67
30.2	46.5	55.5	59	51	30.2	75.5	77.5	75	79
40.3	76	58.5	57	56	40.3	81	79.5	78	77
63	62	62.5	62.5	64	63	90	84.5	91.5	88.5
100	62	66	66.5	68	100	94.5	88.5	94.5	88.5

Table A3.58: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 26, a male *Lucilia caesar*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	0	0	0	0	1	3	2	2.5	2.5
2.2	0	0	0	0	2.2	3.5	4.5	4	4
5	0	0	0	0	5	5	4.5	4	5.5
6.4	0	0	0	0	6.4	5.5	6	5.5	7.5
19.8	0	0	0	0	19.8	10.5	10.5	11.5	10
30.2	0	0	0	0	30.2	13.5	14	13.5	15.5
40.3	1.5	1.5	2	2	40.3	14.5	14.5	19.5	16
63	3	2.5	2	2	63	19.5	21	19.5	19.5
100	8	7.5	6.5	6.5	100	25	24.5	24	23.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3	2.5	1.5	1.5	0.54	0	0	0	0
1	5	4	2	3.5	1	4.5	3	4	3.5
2.2	5	5	4	5	2.2	5.5	5.5	4	5
5	4	6	5.5	5	5	9.5	7	6	6
6.4	7.5	8.5	9.5	9.5	6.4	7.5	6.5	7	6.5
19.8	14	11	12	11.5	19.8	11	12.5	12	13.5
30.2	12.5	13	12.5	12.5	30.2	15	15	17.5	16.5
40.3	16.5	15.5	16	18	40.3	17.5	19	18.5	19.5
63	21	22	23.5	21.5	63	24	22.5	19.5	23.5
100	24	25.5	22.5	25.5	100	26.5	27.5	26.5	26.5
359.0nm					469.6nm				
0.09	2.5	3	2.5	2.5	0.09	0	0	0	0
0.54	3	3.5	3	4	0.54	3	2	3	3
1	3.5	4.5	3.5	4	1	4	3.5	4	3.5
2.2	5	6	4.5	6	2.2	5	6.5	5	6.5
5	8.5	8.5	9	9	5	9.5	8	9	8
6.4	9	11	11	9.5	6.4	10.5	11	11	10.5
19.8	18	17	16	17.5	19.8	17	17	18.5	18.5
30.2	23	21.5	20.5	20	30.2	22.5	22.5	26	25
40.3	22.5	23	23.5	23.5	40.3	26	27.5	26	25.5
63	25	27.5	29	26	63	31	31	31	31.5
100	33.5	30.5	31	34.5	100	37.5	38	37	37.5
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	2	2.5	1.5	1.5	0.54	2.5	1.5	1.5	2.5
1	3	2.5	2.5	2.5	1	4	4	3.5	3.5
2.2	5.5	4.5	3	3	2.2	4	4	7	5.5
5	6	4.5	5.5	6	5	9	8	8.5	6.5
6.4	6	6	6	7.5	6.4	9.5	9	8.5	9
19.8	11.5	12	13	11	19.8	16	17.5	16	16.5
30.2	16	14	16	15	30.2	21.5	22.5	20	20.5
40.3	17	15.5	17	18.5	40.3	22	23.5	26	23.5
63	21.5	21.5	20.5	20	63	29	29.5	30	28.5
100	25	25.5	26	26	100	33.5	34	34	33.5

Table A3.59: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 27, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	3.5	3	2.5	0.54	0	0	0	0
1	5.5	5.5	4	4	1	3.5	4	3.5	4
2.2	6.5	7	7	5.5	2.2	7.5	9	7.5	6.5
5	12.5	12	9.5	9.5	5	14	13	12.5	13.5
6.4	11.5	11.5	13	12.5	6.4	15.5	17	16	15.5
19.8	21	20.5	21	20	19.8	31.5	30.5	32.5	32
30.2	27	28.5	27	25.5	30.2	40.5	40.5	40	39.5
40.3	30	31	30	29	40.3	47	44.5	44.5	43.5
63	35.5	37	35.5	38	63	55	54.5	52.5	53
100	43	46	45	42.5	100	59	59	57.5	55.5
529.6nm					650.1nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	3.5	3	2.5	0.54	0	0	0	0
1	5.5	5.5	4	4	1	0	0	0	0
2.2	6.5	7	7	5.5	2.2	3	2.5	3	3
5	12.5	12	9.5	9.5	5	4.5	6	5	5.5
6.4	11.5	11.5	13	12.5	6.4	6.5	6.5	7	7
19.8	21	20.5	21	20	19.8	16	16.5	15.5	17
30.2	27	28.5	27	25.5	30.2	22.5	21.5	23	23
40.3	30	31	30	29	40.3	27	25.5	25.5	27.5
63	35.5	37	35.5	38	63	32.5	34	35	35.5
100	43	46	45	42.5	100	43	40.5	39	40
559.2nm					679.5nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3	2.5	4	3	0.54	0	0	0	0
1	3	3	3	3	1	0	0	0	0
2.2	7.5	6	6	4	2.2	0	0	0	0
5	14	8.5	8.5	9.5	5	0	0	0	0
6.4	10.5	11.5	13	12.5	6.4	2.5	3	2	2
19.8	22	23	22	23.5	19.8	5.5	5.5	4.5	6
30.2	29.5	29	29	30.5	30.2	5	7	6.5	7.5
40.3	35.5	33.5	37	36	40.3	8	8.5	9.5	8.5
63	43	43	42.5	41.5	63	11.5	13.5	12	11.5
100	49	49.5	51	50	100	16	16	16	16.5
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	0	0	0	0
1	3.5	3.5	3.5	3	1	0	0	0	0
2.2	3.5	3	4	4	2.2	1.5	1.5	1.5	2
5	6	7	6.5	6.5	5	4	2.5	3	4
6.4	8.5	9	8.5	9.5	6.4	3.5	3.5	4.5	5
19.8	16	15.5	16.5	16	19.8	11.5	12.5	11.5	12
30.2	23	20	20.5	23.5	30.2	15.5	16	16	16
40.3	23.5	24.5	23.5	23.5	40.3	19.5	20.5	20.5	20
63	29	27.5	27.5	27.5	63	26.5	27.5	26	26.5
100	34	33.5	34	32	100	31.5	35.5	33	32

Table A3.60: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 27, a male *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	2	2	2	2.5
0.54	0	0	0	0	0.54	4	3.5	3	4
1	0	0	0	0	1	6.5	6.5	6.5	7.5
2.2	0	0	0	0	2.2	11.5	9.5	9	9.5
5	0	0	0	0	5	13.5	13.5	12.5	12.5
6.4	0	0	0	0	6.4	14.5	15	15	15
19.8	6	5	6	6	19.8	22	21.5	22.5	23
30.2	5.5	5	5	5	30.2	28	28	28.5	27.5
40.3	6	6	6.5	6.5	40.3	30.5	30.5	30.5	30.5
63	7.5	8	8	8	63	35	37	34.5	34.5
100	16	15	15	15	100	41	40.5	40.5	40
331.6nm					440.4nm				
0.09	3	2	1.5	2	0.09	4.5	3	3	3.5
0.54	4.5	4	4	4	0.54	7	5	5.5	6
1	6.5	5.5	5.5	6.5	1	8	8.5	8	7.5
2.2	10.5	10.5	10	9	2.2	11.5	11.5	10	11.5
5	15	13	13.5	14	5	14.5	13.5	14	14.5
6.4	16.5	15	15	15	6.4	16.5	16.5	17.5	17
19.8	22.5	23	24.5	23	19.8	24.5	24	24	24
30.2	28.5	26	27	27	30.2	30	29	28.5	30
40.3	30.5	30	31	31	40.3	32.5	32.5	33	31.5
63	35.5	36.5	35	34	63	36.5	37.5	38.5	38
100	44	52	63	60.5	100	43	44.5	43	43
359.0nm					469.6nm				
0.09	2.5	2	2	2	0.09	4.5	5	4.5	4.5
0.54	5	4	4.5	4.5	0.54	10	9	8.5	9.5
1	8	7.5	8.5	6.5	1	13.5	13	12.5	13.5
2.2	11	10.5	11	10.5	2.2	17.5	17.5	16	17
5	15	15	14	15.5	5	23.5	23	22.5	24.5
6.4	16.5	17	15.5	16	6.4	27	26	23.5	26.5
19.8	23	24.5	23.5	23.5	19.8	35.5	34.5	35	34.5
30.2	30	28.5	30	28	30.2	41.5	41	42	42.5
40.3	33.5	31	31	32	40.3	44	43.5	45	44
63	36	34.5	35.5	34.5	63	51.5	48.5	50.5	48.5
100	40.5	39.5	40	42.5	100	54	54.5	56.5	56.5
379.7nm					489.0nm				
0.09	3.5	2	2	2	0.09	4.5	5.5	5.5	5
0.54	5	4	5	4.5	0.54	10.5	8.5	9	9
1	7.5	6.5	6.5	7.5	1	12.5	11	10	12.5
2.2	10.5	10	11	10.5	2.2	15	14.5	13	14
5	14	14.5	15	14	5	19	17.5	18	18
6.4	15.5	16	15.5	15	6.4	21.5	21	20	20.5
19.8	23.5	24	22	24	19.8	27.5	27	26.5	26
30.2	28.5	26.5	28.5	29	30.2	31	30.5	30.5	29.5
40.3	31.5	31	31	31.5	40.3	33.5	34	33	33
63	37	37.5	37	38	63	37.5	38	35.5	37.5
100	43	43.5	42	44.5	100	41	40	41	39.5

Table A3.61: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 28, a female *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	5	4	4	4.5	0.09	5	3.5	3	4
0.54	9.5	8.5	8.5	7	0.54	11.5	11.5	12	11.5
1	11.5	10	10	10	1	16.5	16	16	15.5
2.2	15	13	12.5	13	2.2	23	23.5	24	25
5	18.5	18.5	20	19.5	5	34.5	35	34.5	34.5
6.4	21.5	22	22.5	21.5	6.4	39.5	37.5	37	40
19.8	31.5	31.5	31	32	19.8	56.5	54.5	53.5	53.5
30.2	39	38	38.5	37.5	30.2	65	63	60	63
40.3	42.5	42	43.5	42	40.3	67	63	65	65.5
63	50.5	50	49	48	63	72.5	72.5	70	69.5
100	53.5	54	53.5	55	100	78.5	78.5	80	76.5
529.6nm					650.1nm				
0.09	5	4	4	4.5	0.09	2	1.5	1	1.5
0.54	9.5	8.5	8.5	7	0.54	6	6.5	5.5	5
1	11.5	10	10	10	1	8.5	8	8.5	7.5
2.2	15	13	12.5	13	2.2	12	12.5	13.5	13
5	18.5	18.5	20	19.5	5	22	20	21	21.5
6.4	21.5	22	22.5	21.5	6.4	24.5	24	24	25.5
19.8	31.5	31.5	31	32	19.8	39.5	40	40	40
30.2	39	38	38.5	37.5	30.2	49.5	48.5	49	47.5
40.3	42.5	42	43.5	42	40.3	54.5	54.5	54.5	53.5
63	50.5	50	49	48	63	64.5	62.5	63	60.5
100	53.5	54	53.5	55	100	70	69.5	68	68
559.2nm					679.5nm				
0.09	5.5	4	4	3.5	0.09	0	0	0	0
0.54	10.5	10.5	10	9	0.54	0	0	0	0
1	15	16	16.5	16	1	2	2	3	2.5
2.2	23	21	21	22.5	2.2	4.5	4	5	4
5	30	31	32	29.5	5	7.5	7.5	8	8
6.4	34	33.5	34	34	6.4	9	9	8.5	7.5
19.8	56.5	46.5	45	46	19.8	16.5	17.5	17.5	17.5
30.2	55	54	54	53.5	30.2	21	23	21.5	22.5
40.3	59	57.5	60	57	40.3	25.5	27.5	26	26.5
63	65	63.5	63	62.5	63	32.5	33	32.5	33
100	70	69	69.5	68	100	40	41.5	41.5	41
590.1nm					705.0nm				
0.09	3	3	2	3.5	0.09	0	0	0	0
0.54	7	7.5	7.5	7.5	0.54	5	3	3.5	4.5
1	11.5	10.5	11	10.5	1	6.5	6.5	4.5	5.5
2.2	19	19.5	18.5	18	2.2	10.5	9.5	9.5	8.5
5	27	27	26.5	26	5	15.5	15.5	16.5	15
6.4	30.5	30.5	30.5	30.5	6.4	18.5	19	18.5	16.5
19.8	45.5	44.5	44.5	43	19.8	32	34.5	33	33
30.2	52.5	52.5	51.5	53	30.2	41.5	41	40	41
40.3	58.5	56	57.5	55.5	40.3	45.5	47.5	45.5	46
63	62.5	62	64	63	63	55	55	54.5	55
100	70.5	67	68.5	69.5	100	62.5	62	61.5	62

Table A3.62: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 28, a female *Lucilia sericata*, using light of various wavelengths (continued).

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
300nm					408.6nm				
0.09	0	0	0	0	0.09	3.5	2.5	2.5	2.5
0.54	0	0	0	0	0.54	4.5	3.5	2.5	3
1	0	0	0	0	1	4.5	5	4.5	5
2.2	0	0	0	0	2.2	7.5	6.5	8.5	7.5
5	0	0	0	0	5	10.5	10.5	10.5	10.5
6.4	0	0	0	0	6.4	12.5	12.5	12.5	11.5
19.8	0	0	0	0	19.8	18	17.5	17.5	17.5
30.2	0	0	0	0	30.2	22	21	22	22
40.3	3	3	3	3	40.3	26.5	23.5	23.5	23.5
63	4	4	4.5	4.5	63	26.5	27.5	27	27
100	7.5	8.5	8.5	8.5	100	28.5	29	28	28.5
331.6nm					440.4nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	0	0	0	0	0.54	3.5	3	4	4.5
1	3.5	4	3.5	3.5	1	6	6.5	6.5	6.5
2.2	8	7.5	7	8	2.2	10	9.5	9.5	10
5	8	8	8.5	8.5	5	14	14.5	14.5	14
6.4	8.5	13	13.5	13	6.4	16	17.5	16	16
19.8	16.5	17.5	17	16.5	19.8	21.5	22	22	22.5
30.2	18	18.5	17	18.5	30.2	27	27.5	27.5	28
40.3	22	21.5	22.5	23	40.3	29.5	29.5	27.5	29.5
63	25.5	24.5	23	24.5	63	33	33.5	33.5	34
100	30	29.5	29	29	100	39	37	37	38.5
359.0nm					469.6nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3	2.5	2.5	3	0.54	5	6	5	6
1	6	5.5	5.5	5.5	1	8.5	8	9.5	8.5
2.2	8.5	8.5	10	10	2.2	12.5	12.5	13	12.5
5	14	14.5	14	15.5	5	17.5	16.5	16.5	16
6.4	16.5	18.5	18.5	18	6.4	18.5	18	18.5	16.5
19.8	22.5	24	23.5	24	19.8	25.5	24.5	24.5	24
30.2	27.5	27	27.5	28	30.2	29	28	30	31
40.3	30	29.5	30	30	40.3	32	30.5	31	31.5
63	33.5	36	34	34	63	35.5	35	34	34
100	35.5	35.5	35	33	100	39	37	35.5	37
379.7nm					489.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	3.5	3.5	2.5	3.5	0.54	6.5	8.5	7	6.5
1	5.5	4.5	4	4.5	1	10.5	9.5	10.5	9.5
2.2	7.5	8	7	7.5	2.2	15	14.5	14.5	14
5	10.5	11.5	12.5	11	5	19	18.5	19	21
6.4	13.5	12	13	13	6.4	21.5	21.5	21.5	21.5
19.8	19	19.5	19.5	18.5	19.8	27.5	27	28	25.5
30.2	23.5	24	23	23.5	30.2	31.5	30.5	30	31.5
40.3	25.5	26	25.5	25.5	40.3	32.5	34.5	35.5	33.5
63	29.5	30	30.5	29	63	37.5	37	36	38
100	33.5	32.5	32.5	32.5	100	44	40.5	39	39.5

Table A3.63: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 29, a male *Lucilia sericata*, using light of various wavelengths.

Filters wavelength and % transmission	Light pulse 1	2	3	4	Filters wavelength and % transmission	Light pulse 1	2	3	4
500.3nm					620.5nm				
0.09	3.5	3	3	3	0.09	4	2.5	2.5	2.5
0.54	7.5	7.5	7	7.5	0.54	13.5	16	15	14.5
1	10.5	9.5	9	10	1	23	22.5	23	23
2.2	13	14.5	14.5	14	2.2	34	34.5	34.5	35
5	21	21	19	20.5	5	46.5	47	45.5	45.5
6.4	22	22.5	22	22	6.4	49.5	51	50	48.5
19.8	29.5	29.5	29	30	19.8	65	68.5	64	63
30.2	34.5	36.5	36.5	34.5	30.2	72	76	76	73.5
40.3	38	37	36.5	37.5	40.3	77	76.5	74	73.5
63	43	42	40.5	41	63	82.5	80.5	78	81
100	45.5	46.5	43	43	100	88	87.5	85	85
529.6nm					650.1nm				
0.09	3.5	3	3	3	0.09	0	0	0	0
0.54	7.5	7.5	7	7.5	0.54	3	4.5	3.5	2
1	10.5	9.5	9	10	1	6.5	6	6.5	7
2.2	13	14.5	14.5	14	2.2	12.5	13.5	13	14
5	21	21	19	20.5	5	25	25	24	23
6.4	22	22.5	22	22	6.4	28.5	29.5	29.5	29
19.8	29.5	29.5	29	30	19.8	45	46.5	45.5	43
30.2	34.5	36.5	36.5	34.5	30.2	56	55	53	52
40.3	38	37	36.5	37.5	40.3	58.5	58	59.5	63.5
63	43	42	40.5	41	63	66.5	67.5	65	65
100	45.5	46.5	43	43	100	78.5	78.5	77	72.5
559.2nm					679.5nm				
0.09	3	3	2.5	2.5	0.09	0	0	0	0
0.54	9	10.5	9.5	11	0.54	0	0	0	0
1	15	15.5	15	14.5	1	0	0	0	0
2.2	23	24	23.5	23	2.2	2.5	2	2.5	2
5	29.5	29.5	29	29.5	5	4.5	5.5	5	6
6.4	33	33.5	33.5	34	6.4	6.5	6.5	7.5	7.5
19.8	45	44	44.5	44	19.8	20	19.5	19	21
30.2	51	53	52.5	51.5	30.2	28.5	27.5	28	26.5
40.3	55.5	53	51.5	54.5	40.3	34.5	34	34.5	35
63	63.5	60.5	59.5	60	63	41	41.5	42	41
100	65	65	64.5	64.5	100	49	48.5	47	47
590.1nm					705.0nm				
0.09	0	0	0	0	0.09	0	0	0	0
0.54	4	3.5	3	5	0.54	0	0	0	0
1	8.5	8.5	8.5	7	1	5	6	4.5	5
2.2	14	14.5	15	14	2.2	10.5	10.5	11	12.5
5	23.5	22	22	21.5	5	21	22.5	22.5	22
6.4	25	24	24	25	6.4	27.5	27.5	28	26
19.8	35.5	37.5	34.5	34.5	19.8	48	48.5	48	47.5
30.2	40.5	40	40	39	30.2	58	56.5	58	56.5
40.3	42.5	44	43	42.5	40.3	64.5	62.5	63.5	62.5
63	47.5	46	46.5	47	63	75.5	75	74.5	72
100	49	49	49.5	51.5	100	80	81.5	81	81.5

Table A3.64: Measurements (mm) of electroantennograms (ERGs) produced by stimulation of the eye of Fly 29, a male *Lucilia sericata*, using light of various wavelengths (continued).

Fly	1	2	3	4	5	6	7	8
300.0 nm	15.50	10.36	9.45	7.52	14.91	7.06	6.44	6.50
331.6 nm	15.50	10.57	9.48	7.52	14.91	6.35	5.13	6.27
359.0 nm	15.50	10.92	9.66	8.42	14.91	7.24	7.32	6.38
379.7 nm	15.50	11.17	9.59	8.80	14.91	7.77	3.82	6.54
408.6 nm	15.50	10.42	9.56	8.67	14.92	6.17	6.01	6.42
440.4 nm	15.50	10.72	9.91	9.19	14.92	6.53	4.70	6.61
469.6 nm	15.50	10.62	9.73	8.55	14.92	5.46	7.75	6.84
489.0 nm	15.50	10.97	9.77	7.65	14.92	8.13	9.50	6.77
500.3 nm	15.50	10.47	9.84	7.52	14.91	5.99	8.63	6.34
529.6 nm	15.50	10.82	9.98	7.52	14.91	5.64	6.88	6.46
559.2 nm	15.50	10.52	9.95	7.52	14.92	5.81	5.57	6.92
590.1 nm	15.50	10.31	9.52	9.06	14.92	5.10	8.19	6.69
620.5 nm	15.50	10.87	9.70	8.16	14.92	5.28	9.06	6.31
650.1 nm	15.50	10.67	10.02	8.93	14.92	7.59	4.26	6.57
679.5 nm	15.50	10.77	9.63	8.29	14.91	6.70	3.39	6.65

Table 3.65: Maximum ERG response to white light recorded from flies 1-8 using a variety of bandpass filters.

Fly	9	10	11	12	13	14	15	16
300.0 nm	10.89	9.49	8.54	8.19	7.50	8.66	9.97	12.56
331.6 nm	10.88	9.32	8.54	8.19	8.44	8.43	9.86	12.38
359.0 nm	10.87	9.45	8.54	8.19	9.19	4.70	9.38	12.19
379.7 nm	10.88	9.03	8.54	8.19	6.93	7.73	9.27	12.31
408.6 nm	10.88	9.24	8.54	8.19	7.69	5.17	8.67	12.81
440.4 nm	10.88	9.57	8.54	8.19	6.56	7.50	8.80	12.44
469.6 nm	10.87	9.53	8.54	8.19	6.37	5.40	9.74	12.13
489.0 nm	10.89	9.11	8.54	8.19	8.82	7.26	10.56	12.94
500.3 nm	10.88	8.99	8.54	8.19	7.31	8.89	10.68	12.00
529.6 nm	10.87	9.20	8.54	8.19	7.13	6.56	8.92	12.06
559.2 nm	10.89	9.40	8.54	8.19	9.01	5.63	9.63	11.88
590.1 nm	10.90	9.65	8.54	8.19	8.06	8.19	10.32	11.94
620.5 nm	10.90	9.16	8.54	8.19	6.75	6.80	9.04	12.25
650.1 nm	10.89	9.28	8.54	8.19	9.57	7.96	9.51	12.69
679.5 nm	10.90	9.36	8.54	8.19	7.86	5.87	9.16	12.50
705.0 nm	10.89	8.91	8.54	8.19	8.63	6.33	10.21	12.62

Table 3.66: Maximum ERG response to white light recorded from flies 9-16 using a variety of bandpass filters.

Fly	17	18	19	20	21	22	23	24
300.0 nm	11.76	8.30	7.69	5.66	14.41	7.55	8.88	7.81
331.6 nm	12.22	7.32	7.67	5.62	14.47	12.44	10.12	7.88
359.0 nm	12.27	8.11	7.69	5.61	14.50	8.34	10.40	7.69
379.7 nm	12.12	7.32	7.67	5.60	14.64	6.97	10.21	8.01
408.6 nm	12.32	8.21	7.67	5.59	14.61	7.16	9.36	8.27
440.4 nm	12.06	7.32	7.68	5.65	14.24	12.44	9.93	7.43
469.6 nm	11.71	7.32	7.70	5.67	14.21	7.95	9.55	7.49
489.0 nm	12.37	8.25	7.66	5.66	14.55	6.77	9.64	7.75
500.3 nm	12.01	8.59	7.67	5.64	14.38	12.44	9.74	8.33
529.6 nm	12.17	8.49	7.69	5.63	14.58	7.36	9.07	7.62
559.2 nm	11.91	8.40	7.68	5.64	14.44	12.44	9.84	7.94
590.1 nm	11.66	8.45	7.68	5.62	14.35	7.75	9.26	8.07
620.5 nm	11.86	8.54	7.67	5.61	14.33	12.44	9.45	8.20
650.1 nm	11.96	7.32	7.68	5.65	14.30	12.44	10.02	7.36
679.5 nm	11.81	8.35	7.67	5.61	14.27	12.44	9.17	8.14
705.0 nm	11.56	8.64	7.68	5.63	14.66	12.44	10.31	7.56

Table 3.67: Maximum ERG response to white light recorded from flies 17-24 using a variety of bandpass filters.

Fly	25	26	27	28	29
300.0 nm	11.81	10.41	8.16	9.86	9.73
331.6 nm	11.89	9.74	8.60	9.87	9.73
359.0 nm	11.23	9.39	10.93	10.61	9.73
379.7 nm	11.09	9.10	8.17	10.57	9.73
408.6 nm	11.96	10.70	8.25	11.76	9.73
440.4 nm	11.81	10.68	8.54	10.01	9.73
469.6 nm	11.60	11.31	8.22	9.43	9.73
489.0 nm	10.65	10.34	8.32	8.35	9.73
500.3 nm	10.51	9.64	10.08	10.34	9.73
529.6 nm	11.53	10.65	9.87	9.96	9.73
559.2 nm	10.94	10.14	9.92	9.36	9.73
590.1 nm	10.80	9.35	8.47	10.25	9.73
620.5 nm	11.67	10.81	9.78	8.86	9.73
650.1 nm	11.74	10.36	10.07	10.05	9.73
679.5 nm	11.52	10.86	8.52	10.09	9.73
705.0 nm	11.38	10.41	8.22	9.61	9.73

Table 3.68: Maximum ERG response to white light recorded from flies 25-29 using a variety of bandpass filters.

Filter wavelength	Adjustment factor	Calibration factor	Equivalent multiplier
300.0 nm	18.353	1.852	71.233
331.6 nm	11.556	1.993	98.290
359.0 nm	6.638	0.974	9.424
379.7 nm	4.000	0.513	3.257
408.6 nm	2.213	0.038	1.092
440.4 nm	1.677	-0.019	0.957
469.6 nm	1.412	0.003	1.007
489.0 nm	1.328	0.024	1.057
500.3 nm	1.268	0.026	1.062
529.6 nm	1.139	0.022	1.052
559.2 nm	1.064	0.006	1.015
590.1 nm	1.000	0.000	1.000
620.5 nm	0.943	0.042	1.102
650.1 nm	0.894	0.039	1.093
679.5 nm	0.848	0.041	1.099
705.0 nm	0.813	0.042	1.102

Table A3.69: Adjustment and calibration factors for each bandpass filter used in ERG experiments. Adjustment factors were obtained from manufacturer's data sheet. All figures are relative to the 590.1nm filter. See text for further details of calculations.

Period	Position					
	1	2	3	4	5	6
1	F	D	C	B	A	E
2	B	F	E	D	C	A
3	A	E	D	C	B	F
4	E	C	B	A	F	D
5	C	A	F	E	D	B
6	D	B	A	F	E	C

Table A3.70: Latin square design for experiment 3.F.
Colours: A = White; B = Yellow; C = Red; D = Black; E = Green; F = Blue.

	Period		Colour											
No.	Start Date	Finish Date	White		Yellow		Red		Black		Green		Blue	
			F	M	F	M	F	M	F	M	F	M	F	M
1	5/8/96	7/8/96	17	2	51	6	16	3	3	0	5	1	41	6
2	7/8/96	12/8/96	14	3	19	5	2	0	5	1	5	2	25	7
3	12/8/96	14/8/96	78	9	55	5	3	1	10	3	24	3	16	4
4	19/8/96	20/8/96	39	11	13	5	22	5	12	3	6	2	29	8
5	20/8/96	21/8/96	22	1	11	0	8	0	1	0	11	0	7	0
6	21/8/96	23/8/96	71	14	72	15	141	39	4	2	5	2	35	7

Table A3.71: Catches of *Lucilia caesar* from experiment 3.F comparing horizontal adhesive targets of six different colours. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*.

Appendix 4

Test Chemicals	Replicate number					
	1	2	3	4	5	6
-	1.028	1.685	1.493	3.487	1.192	1.703
hexane	1.189	1.870	2.015	3.815	2.263	2.565
hexane repeat	1.156	1.568	1.843	3.585	1.989	2.295
-	1.274	0.639	1.061	0.836	1.421	1.343
paraffin oil	0.950	0.861	1.210	0.786	1.404	1.371
paraffin oil repeat	0.828	0.675	1.208	0.766	1.543	1.287
-	0.769	0.930	1.387	2.420	1.024	0.786
ethanol (80%)	0.730	0.803	1.465	1.880	1.175	0.811
ethanol (80%) repeat	0.720	0.737	1.460	2.052	0.963	0.652
-	0.976	0.990	1.119	1.027	2.131	0.974
water	0.878	1.001	1.325	1.019	2.137	1.086
water repeat	0.933	1.018	1.261	0.755	1.835	1.021

Table A4.1: Responses of *Lucilia sericata* females to stimulus by various potential solvents (mV).

Test Chemicals	Conc.	Replicate number					
		1	2	3	4	5	6
-	-	0.273	0.146	0.399	0.559	0.344	0.550
solvent	-	0.295	0.195	0.330	0.479	0.344	0.526
ethanoic acid	10^{-5}	0.289	0.216	0.410	0.412	0.356	0.470
ethanoic acid	10^{-3}	0.319	0.194	0.381	0.393	0.281	0.447
ethanoic acid	10^{-1}	0.448	0.191	0.350	0.317	0.315	0.537
solvent	-	0.347	0.161	0.332	0.462	0.233	0.361
solvent	-	0.257	0.225	0.180	0.216	0.245	0.205
2-methylpropan-1-ol	10^{-5}	0.287	0.205	0.186	0.259	0.259	0.188
2-methylpropan-1-ol	10^{-3}	0.404	0.219	0.195	0.305	0.243	0.180
2-methylpropan-1-ol	10^{-1}	0.446	0.324	0.277	0.587	0.350	0.252
solvent	-	0.258	0.212	0.203	0.316	0.216	0.157
solvent	-	0.258	0.212	0.203	0.316	0.216	0.157
butan-2-ol	10^{-5}	0.265	0.229	0.180	0.294	0.220	0.184
butan-2-ol	10^{-3}	0.265	0.202	0.181	0.316	0.261	0.207
butan-2-ol	10^{-1}	0.407	0.350	0.338	0.598	0.434	0.329
solvent	-	0.270	0.207	0.166	0.292	0.199	0.159
solvent	-	0.270	0.207	0.166	0.292	0.199	0.159
pentanoic acid	10^{-5}	0.283	0.203	0.191	0.331	0.196	0.177
pentanoic acid	10^{-3}	0.326	0.249	0.210	0.400	0.223	0.191
pentanoic acid	10^{-1}	0.358	0.261	0.228	0.351	0.233	0.199
solvent	-	0.260	0.202	0.159	0.281	0.183	0.161

Table A4.2: Responses of *Lucilia caesar* females to various olfactory stimuli (mV). The solvent was ethanol in each case.

Test Chemicals	Conc.	Replicate number					
		1	2	3	4	5	6
-	-	0.354	0.242	0.252	0.176	0.384	0.334
solvent	-	0.373	0.248	0.297	0.197	0.407	0.337
ethanoic acid	10^{-5}	0.300	0.197	0.336	0.197	0.549	0.381
ethanoic acid	10^{-3}	0.327	0.279	0.382	0.205	0.418	0.359
ethanoic acid	10^{-1}	0.407	0.285	0.262	0.162	0.473	0.377
solvent	-	0.329	0.221	0.271	0.159	0.403	0.309
solvent	-	0.950	0.861	1.210	0.786	1.404	1.371
2-methylpropan-1-ol	10^{-5}	0.953	0.761	1.288	0.752	1.224	1.297
2-methylpropan-1-ol	10^{-3}	0.942	1.117	1.296	0.848	1.812	1.375
2-methylpropan-1-ol	10^{-1}	1.164	1.246	1.316	0.879	1.723	1.409
solvent	-	0.828	0.675	1.208	0.766	1.543	1.287
solvent	-	0.828	0.675	1.208	0.766	1.543	1.287
butan-2-ol	10^{-5}	0.859	0.647	1.223	0.744	1.451	1.172
butan-2-ol	10^{-3}	0.845	0.690	1.209	0.767	1.443	1.161
butan-2-ol	10^{-1}	0.870	0.852	1.253	1.024	1.419	1.125
solvent	-	0.759	0.714	1.130	0.672	1.475	1.190
solvent	-	0.759	0.714	1.130	0.672	1.475	1.190
pentanoic acid	10^{-5}	0.743	0.669	1.226	0.766	1.398	1.287
pentanoic acid	10^{-3}	0.782	0.749	1.266	0.893	1.492	1.357
pentanoic acid	10^{-1}	0.791	0.739	1.308	0.807	1.487	1.394
solvent	-	0.588	0.583	0.974	0.716	1.258	1.161

Table A4.3: Responses of *Lucilia sericata* females to various olfactory stimuli (mV). The solvent was ethanol in each case.

Test Chemicals	Conc.	Replicate number					
		1	2	3	4	5	6
solvent	-	0.347	0.161	0.332	0.462	0.233	0.361
phenol	10^{-5}	0.346	0.182	0.348	0.512	0.298	0.430
phenol	10^{-3}	0.423	0.185	0.274	0.565	0.315	0.450
phenol	10^{-1}	0.511	0.213	0.318	0.666	0.376	0.494
solvent	-	0.316	0.137	0.259	0.491	0.265	0.356
solvent	-	0.316	0.137	0.259	0.491	0.265	0.356
2-mercaptoethanol	10^{-5}	0.252	0.168	0.310	0.530	0.286	0.410
2-mercaptoethanol	10^{-3}	0.261	0.162	0.393	0.473	0.326	0.383
2-mercaptoethanol	10^{-1}	0.368	0.188	0.476	0.418	0.406	0.411
solvent	-	0.250	0.131	0.399	0.335	0.282	0.428
solvent	-	0.250	0.131	0.399	0.335	0.282	0.428
butanoic acid	10^{-5}	0.314	0.193	0.465	0.408	0.277	0.429
butanoic acid	10^{-3}	0.484	0.222	0.476	0.489	0.303	0.454
butanoic acid	10^{-1}	0.401	0.235	0.439	0.470	0.336	0.453
solvent	-	0.345	0.125	0.364	0.413	0.307	0.389
solvent	-	0.345	0.125	0.364	0.413	0.307	0.389
swormlure-4	10^{-5}	0.325	0.153	0.420	0.477	0.365	0.470
swormlure-4	10^{-3}	0.644	0.258	0.857	0.711	0.457	0.444
swormlure-4	10^{-1}	0.859	0.560	1.665	1.472	1.070	1.090
solvent	-	0.356	0.146	0.484	0.422	0.260	0.273
solvent	-	0.356	0.146	0.484	0.422	0.260	0.273
dimethyldisulphide	10^{-5}	0.518	0.209	0.616	0.446	0.317	0.337
dimethyldisulphide	10^{-3}	0.547	0.285	0.995	0.789	0.317	0.380
dimethyldisulphide	10^{-1}	0.734	0.462	1.443	1.074	0.984	0.915
solvent	-	0.401	0.119	0.544	0.406	0.233	0.318

Table A4.4: Responses of *Lucilia caesar* females to various olfactory stimuli (mV). The solvent was ethanol in each case.

Test Chemicals	Conc.	Replicate number					
		1	2	3	4	5	6
solvent	-	0.730	0.803	1.465	1.880	1.175	0.811
phenol	10^{-5}	0.685	0.891	1.632	1.834	1.122	0.852
phenol	10^{-3}	0.647	0.915	1.711	2.023	1.060	0.772
phenol	10^{-1}	0.711	0.991	1.580	2.218	1.054	0.719
solvent	-	0.720	0.737	1.460	2.052	0.963	0.652
solvent	-	0.720	0.737	1.460	2.052	0.963	0.652
2-mercaptoethanol	10^{-5}	0.529	0.683	1.561	2.363	1.047	0.710
2-mercaptoethanol	10^{-3}	0.606	0.712	1.292	2.000	1.049	0.683
2-mercaptoethanol	10^{-1}	0.682	0.670	1.242	1.472	0.930	0.543
solvent	-	0.717	0.754	1.295	1.904	0.941	0.627
solvent	-	0.340	0.197	0.284	0.138	0.411	0.308
butanoic acid	10^{-5}	0.258	0.214	0.273	0.101	0.499	0.372
butanoic acid	10^{-3}	0.322	0.251	0.324	0.165	0.502	0.383
butanoic acid	10^{-1}	0.354	0.283	0.317	0.144	0.488	0.344
solvent	-	0.298	0.202	0.226	0.099	0.359	0.258
solvent	-	0.717	0.754	1.295	1.904	0.941	0.627
swormlure-4	10^{-5}	0.621	0.720	1.250	2.252	1.098	0.744
swormlure-4	10^{-3}	0.878	1.146	1.960	2.103	1.275	0.809
swormlure-4	10^{-1}	1.634	2.075	3.088	4.436	1.523	0.874
solvent	-	0.611	0.751	1.214	2.325	0.775	0.620
solvent	-	0.611	0.751	1.214	2.325	0.775	0.620
dimethyldisulphide	10^{-5}	0.716	0.996	1.329	3.246	0.862	0.605
dimethyldisulphide	10^{-3}	1.068	1.229	1.855	3.568	0.999	0.506
dimethyldisulphide	10^{-1}	1.479	1.874	2.093	4.868	1.211	1.000
solvent	-	0.677	0.969	1.118	3.015	0.777	0.443

Table A4.5: Responses of *Lucilia sericata* females to various olfactory stimuli (mV). The solvent was ethanol in each case.

solvent	-	0.299	0.555	0.328	0.645	0.504	1.082
dimethyldisulphide	10^{-5}	0.411	0.679	0.418	0.857	0.680	1.506
dimethyldisulphide	10^{-3}	0.666	0.986	0.590	1.019	0.897	2.068
dimethyldisulphide	10^{-1}	0.895	1.287	0.968	1.764	1.304	2.715
solvent	-	0.470	0.598	0.383	0.569	0.470	0.984

Table A4.6: Responses of *Lucilia sericata* females to dimethyldisulphide in paraffin oil (mV).

Test Chemicals	Conc.	Replicate number					
		1	2	3	4	5	6
-	-	0.343	0.385	0.245	0.112	0.143	0.472
solvent	-	0.364	0.409	0.231	0.116	0.134	0.373
Liver extract	10^{-5}	0.398	0.352	0.206	0.110	0.162	0.301
Liver extract	10^{-3}	0.394	0.357	0.338	0.164	0.197	0.266
Liver extract	10^{-1}	0.496	0.394	0.421	0.230	0.161	0.581
solvent	-	0.353	0.349	0.184	0.111	0.085	0.238
solvent	-	0.353	0.349	0.184	0.111	0.085	0.238
sodium sulphide	10^{-5}	0.321	0.381	0.265	0.103	0.085	0.231
sodium sulphide	10^{-3}	0.294	0.319	0.277	0.161	0.094	0.214
sodium sulphide	10^{-1}	0.301	0.327	0.338	0.213	0.122	0.294
solvent	-	0.284	0.279	0.184	0.089	0.096	0.184
solvent	-	0.284	0.279	0.184	0.089	0.096	0.184
ammonium sulphide	10^{-5}	0.325	0.225	0.220	0.101	0.110	0.179
ammonium sulphide	10^{-3}	0.366	0.318	1.024	0.310	0.180	0.231
ammonium sulphide	10^{-1}	0.473	0.381	1.297	1.188	0.277	0.516
solvent	-	0.350	0.250	0.240	0.118	0.103	0.190
solvent	-	0.350	0.250	0.240	0.118	0.103	0.190
L.e. + s.s.	10^{-5}	0.357	0.379	0.323	0.122	0.103	0.242
L.e. + s.s.	10^{-3}	0.422	0.315	0.326	0.122	0.122	0.249
L.e. + s.s.	10^{-1}	0.484	0.418	0.460	0.340	0.127	0.357
solvent	-	0.399	0.274	0.219	0.101	0.074	0.222
solvent	-	0.399	0.274	0.219	0.101	0.074	0.222
L.e. + a.s.	10^{-5}	0.476	0.302	0.288	0.099	0.111	0.343
L.e. + a.s.	10^{-3}	0.467	0.352	0.536	0.158	0.105	0.353
L.e. + a.s.	10^{-1}	0.587	0.445	1.271	0.549	0.254	1.034
solvent	-	0.382	0.244	0.181	0.116	0.059	0.221

Table A4.7: Responses of *Lucilia caesar* females to various olfactory stimuli (mV). The solvent was water in each case. L.e.= Liver extract; s.s. = sodium sulphide; a.s. = ammonium sulphide.

Test Chemicals	Conc.	Replicate number					
		1	2	3	4	5	6
-	-	0.976	0.990	1.119	1.027	2.131	0.974
solvent	-	0.878	1.001	1.325	1.019	2.137	1.086
Liver extract	10^{-5}	0.890	1.005	1.132	0.901	2.399	0.993
Liver extract	10^{-3}	0.870	1.075	1.164	0.909	2.408	1.139
Liver extract	10^{-1}	1.026	1.128	1.487	0.855	2.43	1.223
solvent	-	0.933	1.018	1.261	0.755	1.835	1.021
solvent	-	0.933	1.018	1.261	0.755	1.835	1.021
sodium sulphide	10^{-5}	0.959	0.851	1.235	0.710	1.685	0.966
sodium sulphide	10^{-3}	0.888	0.758	1.223	0.798	1.732	0.965
sodium sulphide	10^{-1}	0.944	0.798	1.319	0.894	2.172	0.989
solvent	-	0.829	0.617	0.962	0.679	1.802	0.929
solvent	-	0.829	0.617	0.962	0.679	1.802	0.929
ammonium sulphide	10^{-5}	0.849	0.666	1.085	0.719	1.935	0.895
ammonium sulphide	10^{-3}	1.049	0.660	1.174	0.701	2.067	0.863
ammonium sulphide	10^{-1}	1.748	1.013	1.680	1.033	3.104	1.074
solvent	-	0.918	0.550	1.037	0.664	1.631	0.800
solvent	-	0.918	0.550	1.037	0.664	1.631	0.800
L.e. + s.s.	10^{-5}	1.018	0.628	1.323	0.680	1.759	0.849
L.e. + s.s.	10^{-3}	1.056	0.530	1.231	0.700	1.814	0.850
L.e. + s.s.	10^{-1}	1.501	0.722	1.420	0.785	2.195	1.137
solvent	-	0.881	0.516	1.071	0.585	1.554	0.776
solvent	-	0.881	0.516	1.071	0.585	1.554	0.776
L.e. + a.s.	10^{-5}	0.867	0.524	1.264	0.634	1.805	0.799
L.e. + a.s.	10^{-3}	0.906	0.599	1.205	0.623	1.872	0.740
L.e. + a.s.	10^{-1}	1.341	0.924	1.578	0.858	2.501	0.865
solvent	-	0.756	0.543	0.956	0.525	1.539	0.656

Table A4.8: Responses of *Lucilia sericata* females to various olfactory stimuli (mV). The solvent was water in each case. L.e.= Liver extract; s.s. = sodium sulphide; a.s. = ammonium sulphide.

Period	Position					
	1	2	3	4	5	6
1	F	E	B	A	C	D
2	D	C	F	E	A	B
3	A	F	C	B	D	E
4	B	A	D	C	E	F
5	E	D	A	F	B	C
6	C	B	E	D	F	A

Table A4.9: Latin square design for experiment 5.4.
Traps: A, B, C = Horizontal adhesive targets; D, E, F = Fly City. Baits: A, D = Liver + sodium sulphide; B, E = Vegetable protein; C, F = Swormlure-4.

	Period		Trap and bait combination											
No.	Start Date	Finish Date	A		B		C		D		E		F	
			F	M	F	M	F	M	F	M	F	M	F	M
1	30/8/95	31/8/95	82	8	0	0	1	0	0	0	0	0	0	0
2	31/8/95	31/8/95	198	8	0	0	0	0	0	0	0	0	0	0
3	4/9/95	12/9/95	10	0	0	0	1	0	3	0	1	0	0	0
4	12/9/95	13/9/95	10	0	2	0	2	0	6	0	2	0	0	0
5	14/9/95	16/9/95	10	2	0	0	1	0	3	0	0	0	0	0
6	18/9/95	20/9/95	15	1	2	0	1	0	2	0	2	0	0	0

Table A4.10: Catches of *Lucilia caesar* from experiment 5.4 comparing horizontal adhesive targets of six different colours. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*. Traps: A, B, C = Horizontal adhesive targets; D, E, F = Fly City. Baits: A, D = Liver + sodium sulphide; B, E = Vegetable protein; C, F = Swormlure-4.

	Replicate	1	1	1	1	1	2	2	2	2	2
Period	Position	1	2	3	4	5	1	2	3	4	5
1		E	D	A	C	B	E	A	D	B	C
2		D	C	E	B	A	B	C	A	D	E
3		A	E	B	D	C	A	B	E	C	D
4		C	B	D	A	E	C	D	B	E	A
5		B	A	C	E	D	D	E	C	A	B

Table A4.11: Latin square design for two replicates of experiment 5.5.
Baits: A = Liver; B = Sodium sulphide; C = Ammonium sulphide; D = Liver + sodium sulphide; E = Liver + Ammonium sulphide.

	Period		Bait									
No.	Start Date	Finish Date	A		B		C		D		E	
			F	M	F	M	F	M	F	M	F	M
1	26/8/96	28/8/96	5	1	3	2	0	1	13	3	17	4
2	28/8/96	30/8/96	19	3	2	0	0	0	9	0	7	0
3	18/9/96	19/9/96	13	0	1	1	1	0	17	0	5	0
4	19/9/96	23/9/96	18	2	1	1	2	0	31	1	21	1
5	23/9/96	25/9/96	29	1	20	0	2	1	31	1	12	0
1	18/9/96	19/9/96	4	0	0	0	0	0	23	2	0	0
2	19/9/96	21/9/96	19	2	0	0	0	0	13	2	1	0
3	21/9/96	23/9/96	22	1	1	0	6	0	60	6	18	2
4	23/9/96	25/9/96	21	2	18	2	5	0	20	2	27	2
5	25/9/96	26/9/96	12	1	6	1	4	1	26	0	4	2

Table A4.12: Catches of *Lucilia caesar* from two replicates of experiment 5.5 comparing horizontal adhesive targets with five different bait combinations. In the case of female flies, data are for *L. caesar* group, and therefore include *L. illustris*. Baits: A = Liver; B = Sodium sulphide; C = Ammonium sulphide; D = Liver + sodium sulphide; E = Liver + Ammonium sulphide.

Appendix 5

Order	Family	Subgrouping	Total Trap 1	Total Trap 2	Total Trap 3
Diptera	Calliphoridae	*Calliphora*	82	92	35
		Lucilia	448	59	457
		Protophormia	1	0	0
		Other	47	7	11
	Muscidae		136	205	78
	Sarcophagidae		4	0	9
	Scatophagidae		0	4	0
	Syrphidae	Syrphinae	17	65	28
		Other	0	5	0
	Tabanidae		1	0	0
	Tipulidae		0	2	1
	Other		54	18	19
Coleoptera	Scarabaeidae		0	0	0
	Staphylinidae		1	0	0
Dermaptera	Forficulidae		0	0	0
Hemiptera	Cicadellidae		0	0	0
Hymenoptera	Apidae		2	1	2
	Ichneumonidae		0	0	0
	Sphecidae		2	1	0
	Vespulidae		3	0	1
Lepidoptera	Notodontidae		1	0	0
	Noctuidae		0	3	0
	Nymphalidae		1	0	2
Isopoda			0	1	0
Opiliones			0	2	0

Table A5.1: Catches of invertebrates on three adhesive targets during the first of two periods of 1996.

Order	Family	Subgrouping	Total Trap 1	Total Trap 2	Total Trap 3
Diptera	Calliphoridae	*Calliphora*	321	190	68
		Lucilia	78	48	32
		Protophormia	0	0	1
		Other	31	18	24
	Muscidae		262	77	219
	Sarcophagidae		1	1	1
	Scatophagidae		0	0	0
	Syrphidae	Syrphinae	0	9	9
		Other	0	5	0
	Tabanidae		0	0	0
	Tipulidae		0	0	1
	Other		44	36	30
Coleoptera	Scarabaeidae		1	0	1
	Staphylinidae		0	0	0
Dermaptera	Forficulidae		0	1	0
Hemiptera	Cicadellidae		1	0	0
Hymenoptera	Apidae		0	1	0
	Ichneumonidae		0	0	1
	Sphecidae		1	0	0
	Vespulidae		1	3	0
Lepidoptera	Notodontidae		0	0	0
	Noctuidae		0	0	0
	Nymphalidae		1	2	0
Isopoda			0	0	0
Opiliones			0	0	0

Table A5.2: Catches of invertebrates on three adhesive targets during the second of two periods of 1996.