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Navigation of *Lutzomyia longipalpis* (Diptera: Psychodidae) under dusk or starlight conditions

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Abstract

The responses of male and female *Lutzomyia longipalpis* (Lutz & Neiva) to different wavelengths of light was tested by presenting the sandflies with two light sources simultaneously, a series of test wavelengths between 350–670 nm and a 400 nm control. To test whether *L. longipalpis* could discriminate between the test and control, three sets of experiments were carried out in which the test wavelengths were presented at higher, equivalent or lower intensity than the control. In all three experiments, ultra-violet (350 nm) and blue-green-yellow (490–546 nm) light was more attractive to *L. longipalpis* than the control wavelength. However, at low intensity, UV was less attractive, than equivalent or higher intensity UV light. At intensities equivalent to or higher than the control wavelength, ultra-violet light was more attractive than blue-green. Furthermore, at low intensity, green-yellow (546 nm) light was more attractive to males whereas blue-green (490 nm) was more attractive to females. Blue-violet (400 nm) and orange-red (600–670 nm) light were least attractive in all three sets of experiments. Response function experiments indicated that the responses were dependent on both intensity and wavelength and that therefore more than one photoreceptor must be involved in the response. The results indicated that *L. longipalpis* can discriminate between different wavelengths at different intensities and thus have true colour vision. It also suggests that *L. longipalpis* may be able to navigate at dusk or under moonlight or starlight conditions using light in the blue-green-yellow part of the spectrum. The difference in response of males and females to light in this region is interesting and may indicate the different ecology of the sexes at night. Overall, these results may have important implications for sandfly trap design.

Introduction

Many haematophagous Diptera use visual cues to locate their host. Certain colours may be attractive over long distance whereas others may influence behaviour near the host. Diurnally active tsetse (Diptera: Glossinidae), for example, are particularly attracted to pthalogen blue from several metres (Green & Flint, 1986) while black induces a landing response (Green, 1986). Vision may also be used to determine relative velocity of the insect during host-odour mediated flight or to assess the size, shape and speed of movement of a potential host (Gibson & Torr, 1999). The eyes of nocturnal and crepuscular mosquitoes have nine times the light-gathering power of diurnal species (Land *et al*., 1997) and, although there is a concomitant loss of resolution, these species are able to orientate themselves in moonlight or even star-light conditions (Bidlingmayer, 1994). Night flying mosquitoes respond to the visual characteristics of the host but, although attractiveness of coloured targets is probably related to the mosquitos' spectral sensitivity, colour

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vision has not been demonstrated (Gibson & Torr, 1999).

The sandfly species complex, *Lutzomyia longipalpis* (Lutz & Neiva) (Diptera: Psychodidae) is the vector of *Leishmania chagasi* (Cunha & Chagas) (Kinetoplastida: Trypanosomatidae) the causative agent of visceral leishmaniasis in South and Central America (Lewis & Ward, 1987). Males and females are attracted to a wide range of warm-blooded animals (Deane, 1956; Quinnell *et al*., 1992; Morrison *et al*., 1993) where males form mating leks on or near the host (Quinnell & Dye, 1994; Kelly & Dye, 1997). Females are attracted to host animals by a combination of male sex pheromones and host odours (Morton & Ward, 1989; Hamilton, 1992; Kelly & Dye, 1997; Dougherty *et al*., 1999). Physical factors also play a role in the orientation of females to the blood meal host and these include temperature and humidity gradients and host size (Nigam & Ward, 1991; Quinnell *et al*., 1992). Males are also attracted by host odour (Hamilton & Ramsoondar, 1994) but other physical and non-physical factors may also be important. Both sexes require a sugar meal which they obtain from plant nectar and other sources (Chaniotis, 1974; Cameron *et al*., 1995; Hamilton & ElNaiem, 2000) and by feeding directly on plants (Schlein & Muller, 1995).

Little is known about the importance of vision in the ecology of *L. longipalpis*. It is a crepuscular and nocturnal insect and it has been suggested that flight activity is triggered by a reduction of light intensity, i.e. nightfall (Chaniotis *et al*., 1971). However, its eyes have a spectral sensitivity that is similar to the diurnally active *Glossina morsitans* Westwood (Diptera: Glossinidae) (Mellor *et al*., 1996). Kelly & Dye (1997) showed that sandflies returned 'preferentially to the site of their previous night's aggregation' and Dougherty *et al*. (1999) showed that adult female sandflies create a host-odour template that enables them to recognize a host. It is therefore possible that sandflies can learn a 'familiar area map' using visual and olfactory cues that enables them to locate blood and sugar meals, safe resting and suitable oviposition sites.

Previous studies have shown that both male and female adult sandflies are attracted to artificial light, e.g. Centres for Disease Control (CDC) light traps (Chaniotis, 1978; Molyneux & Ashford, 1983), behaviour that is considered to be an aberrant phenomenon for many nocturnal insects (Allan *et al*., 1987). These traps are commonly used to measure sandfly abundance (Sudia & Chamberlain, 1962; Quinell & Dye, 1994). However, their attractiveness is selective and some sandfly species are not attracted (Molyneux & Ashford, 1983; Chaniotis, 1978). CDC light traps emit light with wavelengths from ultraviolet (UV) to infrared (IR). It is not known which part(s) of the spectrum are most attractive to sandflies or whether intensity of the light emitted is an important factor in attraction. A previous electroretinogram study (Mellor *et al*., 1996) showed that both male and female *L. longipalpis* from Jacobina, Brazil, have a maximal electrophysiological response to light in the UV region with a secondary peak in the blue-green-yellow region (520 nm for females and 546 nm for males) and low sensitivity in the near-IR (670 nm). This spectral sensitivity was similar to that of the tsetse fly *G. morsitans* and the mosquito *Aedes aegypti* Linnaeus (Diptera: Culicidae) (Green & Cosens, 1983; Muir *et al*., 1992) in that the sensitivity maxima occur in the UV and blue-green-yellow regions of the spectrum.

The primary objectives of this study were to relate the electroretinogram (ERG) observations of our previous work (Mellor *et al*., 1996) to sandfly behaviour and determine which wavelengths of light were attractive to *L. longipalpis* and whether or not males and females were able to discriminate between different wavelengths of light (wavelength discrimination) independent of intensity. Tests were designed to determine whether the attractiveness of three wavelengths of light, (350, 490 and 520 nm) over a range of intensities (intensity response functions) was dependent on intensity and/or wavelength.

Materials and methods

Sandflies

Four-day-old adult male and female *L. longipalpis* were used in this investigation. They were from a colony established from individuals originally collected from Jacobina, Bahia State, Brazil, and reared at Keele School of Life Sciences according to the methods of Modi & Tesh (1983). Both males and females were maintained at 27°C (95% r.h. at 12:12 LD photoperiod). Female sandflies were not blood-fed but both males and females were allowed access to a saturated solution of sucrose. Sandflies were dark adapted under IR light (715 nm) for 30 min prior to being used in an experiment to increase eye sensitivity level to maximal levels (Mellor *et al*., 1996).

Light box

A light-box (16 cm × 20 cm × 30 cm), designed to produce light of known wavelength and intensity, was constructed from 6 mm plywood (fig. 1a). The interior surfaces of the lamp housing were painted matt black and lined with aluminium foil. The light source was a 75W xenon arc lamp (Osram XBO 75W/2 OFR, Ealing Electro Optics, Herts, UK) with two heat filters (Schott NG-1) which supplied a single beam of light that was split into two by a prism (beam splitter) and reflected onto optical flats. This produced two parallel beams of light of equal intensity. Each beam of light then passed through neutral density filters (Ealing Electro Optics) and 10 nm bandpass filters (Ealing Electro Optics) which allowed the intensity and wavelength of each beam to be regulated independently. The light then passed through the two 2-cm diameter holes (15 cm apart) drilled in the plywood end panel of the light box. Thus the light box produced two, parallel, 2 cm. diameter beams of monochromatic light. A 20 × cm × 20 cm sheet of Perspex (3 mm thickness) (Rubber Fast, Stoke on Trent, UK) was placed centrally over the end of the light box to allow it to fit contiguously with the choice chamber. The xenon arc lamp was switched on and allowed to stabilize 10 min before an experiment commenced.

Choice chamber

The light box was placed at the end (20 cm × 20 cm) of a 50 cm × 20 cm × 20 cm bioassay chamber made of 3 mm thick Perspex sheet. The Perspex was removed from one end of the chamber to allow the light box to be positioned. A black card with two 2-cm holes was placed between the light box and the bioassay chamber. The card was positioned so that one beam of light from the light box passed directly through each hole. Thus two 2-cm diameter sources of monochromatic light entered the choice chamber.

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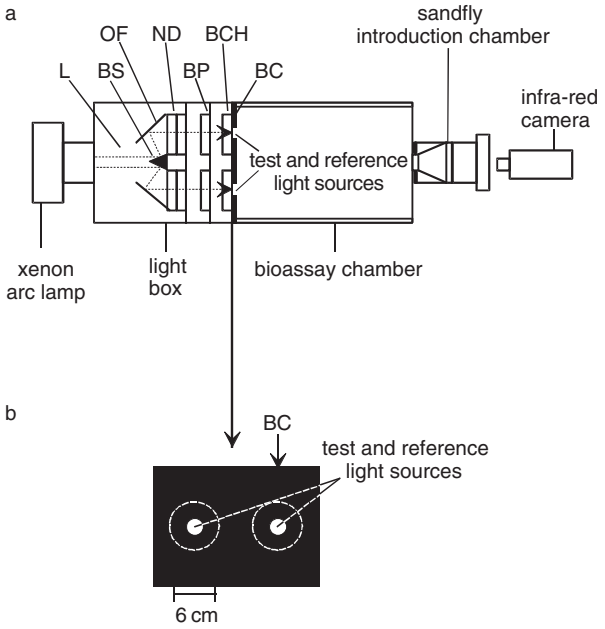

Fig. 1. Diagram of the apparatus used to measure; attraction to, and discrimination between test and control wavelengths and the response intensity functions. Figure 1a is the light box and bioassay chamber. BC, sheet of removable black card with holes at test and control light sources; BCH, slots for strips of removable black card; BP, slots for band pass filters; BS, beam splitter; L, beam of light; ND, neutral density filters; OF, optical flats; dashed line, light path from xenon arc lamp. Figure 1b is a plan view of the black card showing the two 2-cm holes and the 6-cm diameter circle around.

Sandflies were introduced into the bioassay chamber at the opposite end from the light source through a small introduction container that could be opened by a remotely operated mechanical gate which allowed the minimum disruption or interference of the sandflies. Light was prevented from entering the choice chamber until required by placing black cards in front of both light sources. Sandflies were unable to enter the light box because of the Perspex end plate of the light box.

Wavelength attraction and discrimination

Before the experiments began the apparatus was calibrated. The intensity of each beam of light (the test and control) was adjusted so that they were equivalent as they passed through the holes in the black cardboard. Measurements of intensity (T photons s^{-1} cm^{-2}) were made using a photodiode (Bellingham, 1994; Brown & Anderson, 1996) without neutral density or band pass filters, by placing the photodiode directly in front of the 2-cm diameter hole in the black card. The system was then calibrated at 350, 400, 490, 520, 546, 600 and 670 nm using neutral density filters to adjust the amount of light passed and a calibration curve drawn.

The choice chamber was used to compare the attractiveness of a series of seven test wavelengths, 350, 400, 490, 520, 546, 600 and 670 nm with a control wavelength of 400 nm (Mellor *et al.*, 1996). In our previous electroretinogram study, *L. longipalpis* eyes (Jacobina population) were shown to have minimal sensitivity to 400 nm over a range of intensities, thus 400 nm was chosen as the control wavelength. Three sets of experiments were carried out separately in which male and female sandflies were tested with wavelengths that were at either higher, equivalent or lower intensities than the 400 nm control wavelength. The combination of neutral density filters required to give the appropriate intensity were obtained from the calibration curve.

During the experiment the position of the control and test light sources were switched from left to right between replicates to eliminate any inherent or positional effects bias in the apparatus. For each replicate, the order in which the test wavelengths were tested was selected from a pre-randomized schedule and the neutral density filters required to give the appropriate intensity were obtained from the calibration curve. All experiments were carried out in the insectary at 27 ± 1°C 95% RH under infra-red (715 nm) light (Molynx, R.S., UK). Each experiment was replicated eight times for each wavelength of light, for each intensity of light tested and for male and female sandflies.

To begin each experiment, 25 dark-adapted sandflies were introduced into the bioassay chamber where they remained for 7 min. After 7 min black cards that had been covering the light sources were removed and the sandflies exposed to the test and control wavelength at the appropriate intensity for 7 min. To minimize interference and ensure the accuracy of observation, the number of landings made by sandflies in response to the lights was recorded on video tape by a Cohu (model 4722, Brian Reece Scientific Instruments Ltd, Newbury, UK) infra-red sensitive monochrome, solid state camera fitted with a Computar macro-zoom lens (18–108 mm/ f2.5), (CBC (Europe) Ltd, London, UK). Video signals were recorded with a JVC SuperVHS Nicam video recorder (model HR-S5000EK, JVC Professional, London, UK). After 7 min the video recorder was stopped and the black cards put back in place for a further 7 min then the next test wavelength at the appropriate intensity was tested and videoed and so on until all seven test wavelengths had been tested.

The attractiveness of each test wavelength was compared to that of the control wavelength by calculating the percentage of sandflies landing within a 6-cm diameter circle around the centre of each light source. The landing response percentage was calculated as the number of landings per test or control divided by the total number of landings in both test and control multiplied by 100. Only three contacts per sandfly in either the test or control side were allowed, to eliminate the effect of highly active individuals hopping into and out of either circle of light. At the end of each experimental replicate the sandflies were removed and returned to the colony, the Perspex bioassay chamber was cleaned with detergent solution, hexane solvent and then dried thoroughly. Twenty five fresh dark adapted sandflies were used for each experimental replicate.

Intensity response functions

Using the same experimental protocol as above, responses were recorded to three test wavelengths 350, 490 and 520 nm, each over a range of intensities (response intensity functions). This allowed the attraction of the test wavelength compared to the 400 nm control to be gauged

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over a range of intensities. The response intensity function for each wavelength was the percentage landing response plotted against log relative intensity.

Statistical analysis

The Null hypothesis that both male and female sandflies would land on the test and control light source in equal numbers was tested by the Chi-square test. In the wavelength attraction and discrimination experiments Student-Newman-Keuls (SNK) tests were applied to determine similarities in response between the different test wavelengths.

Results

Wavelength attraction and discrimination

When the test wavelengths were set at lower intensities than the control wavelength, significantly more females of *L. longipalpis* were attracted to light in the blue-green region (490 nm, $P < 0.001$) than to the 400 nm control (fig. 2a). Significantly more males were attracted to light in the green-yellow region (546 nm, $P < 0.01$) than to the 400 nm control. For both males and females there was a secondary peak of attraction in the UV region where significantly more sandflies were attracted to near UV light (350 nm, male and female $P < 0.01$) than the control. There was no significant difference between male and female attraction to the UV or orange-red regions of the spectrum (SNK, $P < 0.01$).

When the test wavelengths were set at an equivalent intensity to the control wavelengths, there was maximum attraction in the UV region (350 nm) (fig. 2b). A significantly greater number of males and females were attracted to 350 nm compared to the 400 nm control ($P < 0.001$). There was also a broad secondary response in the blue-green-yellow region. Here a significantly greater number of males and females were attracted to 490 nm (male $P < 0.01$, female $P < 0.05$), 520 nm (male and female $P < 0.001$) and 546 nm (male $P < 0.001$, female $P < 0.02$) than to the 400 nm control. The attraction of both males and females to UV (350 nm) and green (520 nm) was significantly greater than attraction to UV (400 nm) and red (670 nm) (SNK, $P < 0.01$)

When the test wavelengths were set at higher intensities than the control wavelength, a significantly greater number of males and females were attracted to UV (350 nm, $P < 0.001$) than to the 400 nm control (fig. 2c). However, there was also significant attraction to light in the blue-green-yellow region of the spectrum. A significantly greater number of males and females were attracted to blue-green (490 nm, male and female $P < 0.001$), green (520 nm, male and female $P < 0.001$) and green-yellow (546 nm, male and female $P < 0.001$) compared to the 400 nm control. The blue-green-yellow peak may be differentiated into two distinct peaks with maxima at 490 nm and 546 nm in both sexes though it was more pronounced in the females. The response to UV was significantly greater than to any of the other colours (SNK, $P < 0.01$)

Intensity response functions

The landing response of male and female *L. longipalpis* to 350, 490 and 520 nm wavelengths over a range of intensities is shown in fig. 3 for all three wavelengths. The results show that as light intensity increased landing response increased. However, the intensity response function curve for 350 nm appeared to be a different shape to the other curves, which appeared to be parallel.

Discussion

The results of this investigation show that ultra-violet and blue-green-yellow wavelengths of light are attractive to *L. longipalpis*. These wavelengths are more attractive than the

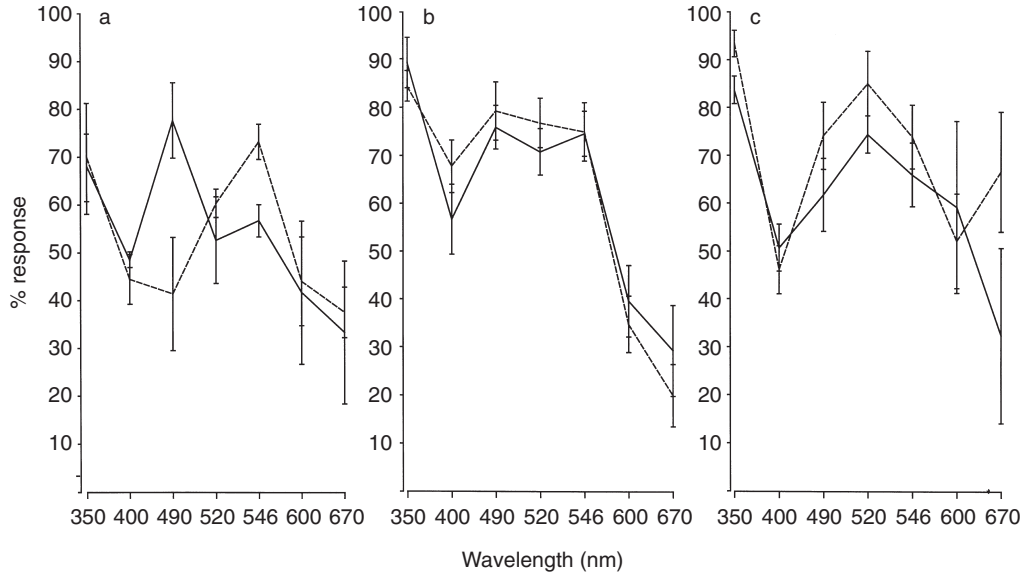

Fig. 2. The percentage response of male (dashed line) and female (solid line) *Lutzomyia longipalpis* to each test wavelength from 350 to 670 nm with (a) lower intensity, (b) equivalent or (c) higher intensity (T photons s^{-1} cm^{-2}) than the 400 nm control wavelength. Limits of bars indicate ± 1 standard error.

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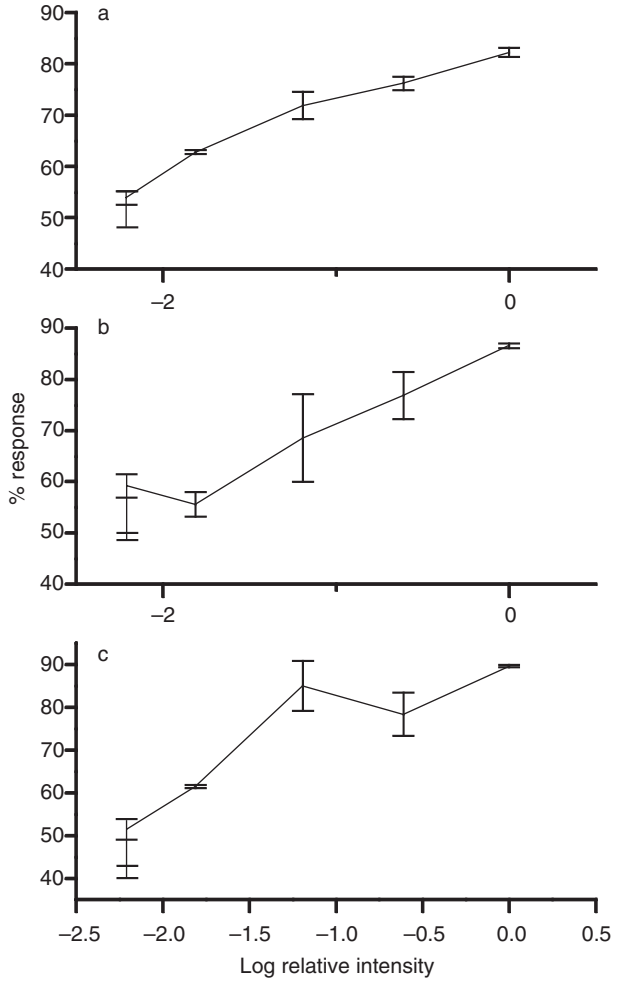

Fig. 3. Intensity response functions. The percentage landing response of female *Lutzomyia longipalpis* to three test wavelengths, (a) 520 nm, (b) 490 nm and (c) 350 nm, over a range of intensities. The percentage response is plotted against log relative intensity. The landing response of *L. longipalpis* in the 6-cm circle surrounding each light source was expressed as a percentage of the total number of *L. longipalpis* landing in both 6-cm circles. Log relative intensity = zero represents 15.089×10^{18} T photons s^{-1} cm^{-2}. Means and standard errors of eight replicates for each comparison. Limits of bars indicate ± 1 standard error.

400 nm control wavelength when at higher, equal and lower intensities indicating that male and female *L. longipalpis* are able to discriminate between wavelengths independently of intensity. This constitutes true colour vision according to the definition given in Menzel (1979).

Where the test wavelengths were of a lower intensity than the control wavelength, the responses of males and females in the blue-green region appeared to be different. In males, the peak response was at 546 nm and, in females, it was at 490 nm. Even though the apparent differences are not statistically significant, a similar observation was made in our earlier electroretinogram study (Mellor *et al*., 1996). In that study the peak response of males was at 546 nm and of females was at 520 nm. This discrepancy warrants further investigation as such sexual differences may be indicative of an important difference in male and female life history and could be of importance in the design of monitoring traps.

Many insects are more sensitive to UV than to green light (Menzel, 1979). Weiss *et al*. (1942) and Weiss (1943) tested many insect species and found that at low light intensities, most were strongly attracted by UV light. In competition experiments, where equal energy UV and green light were given as alternatives, all species choose the UV light. At higher intensities, UV light reduced positive phototactic responses so that visible light became relatively more attractive. In the present study, the reverse effect was observed. At higher and equivalent intensities, the percentage of both male and female *L. longipalpis* attracted to UV was greater than the percentage attracted to the blue-green-yellow wavelengths. At lower intensities, the responses to 546 nm light by males and 490 nm light by females (the blue-green-yellow wavelengths) were proportionately slightly higher than to UV. Other Diptera have been shown to respond in a similar way (Schümperli, 1973). Most Diptera possess three types of receptor, R1–6, R7 and R8 (White, 1985). Kirschfeld (1973) found that R1–6, which are dual UV blue-green receptors, have a higher sensitivity than R7, which is a UV receptor. This information has been used to explain why, at low light intensities, *Drosophila* is more sensitive to green light than UV light and, assuming *L. longipalpis* also possesses the three receptor types, the responses observed in the present study may also be explained.

Wehner (1981) suggested that sensitivity to both UV and blue-green wavelengths is related to wide-field motion detection, i.e. orientation and navigation by means of the contrast of the UV rich sky and the UV unreflective earth. Detection of objects contrasting against the sky even in low light conditions is maximized by the sensitivity to UV and the high relative abundance of UV at dawn and dusk (Gogala, 1978). Therefore the relatively high sensitivity and responsiveness of *L. longipalpis* eyes to blue-green and the decrease in UV sensitivity at low intensity may be related to their crepuscular/nocturnal activity. It is also worth considering that twilight (before dusk) is blue-shifted relative to daylight, but nightlight is not substantially different from daylight in spectral terms (Lythgoe, 1972; Endler, 1993). Therefore relative increased sensitivity of *L. longipalpis* to blue-green-yellow at low intensity levels would extend the visual capabilities of sandflies at twilight and dusk and perhaps accounts for their increased activity at this time of the day. It would be interesting in the future to determine if response to UV and blue-green light depended on the physiological state of the insect, e.g. whether the insect was blood-fed or not.

The response of *L. longipalpis* to three different wavelengths over a range of intensities, intensity response functions, may have demonstrated wavelength specific behaviour in *L. longipalpis*. Wavelength-specific behaviour is where one wavelength stimulates one type of behaviour and another wavelength stimulates a different behaviour. For example, Coombe (1981) suggested that short wavelengths stimulate flight and inhibit landing of the glasshouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) while longer wavelengths stimulate landing and inhibit flight. The intensity response functions in this study were determined for 350, 490 and 520 nm. Since the shapes of the curves were different for at least two of the

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wavelengths, univariance (Naka & Rushton, 1966; Menzel, 1979) could not be assumed for the landing response. The principle of univariance states that the response of a single photoreceptor is dependent on the intensity and not the wavelength of the light and so, if univariance holds for a given response (e.g. the landing response in this study), intensity response functions will be parallel. The intensity response functions for 490 and 520 nm were similar and may be considered as being parallel. The intensity response function for 350 nm appears to be a different shape and does not run parallel to the other two. It could be speculated that if univariance holds for single photoreceptors, then at least two photoreceptors could be involved in these behavioural responses. However, further studies should be undertaken to clarify this point. The phototactic responses observed in this study involved several different behaviours including flight and landing.

In the evenings, male *L. longipalpis* start to locate host animals and set up leks before the females arrive (Jarvis & Rutledge, 1992). Although temperature, humidity and light intensity are believed to be important in stimulating flight activity in sandflies (Chaniotis *et al*., 1971) the trigger for the early onset of male activity in comparison to later female activity is unknown. In mosquitoes, entrained circadian rhythms and specific wavelengths of light have also been reported to stimulate flight and biting activity (Service, 1993; Clements, 1999) and these may be important in regulating sandfly flight activity. The results presented here suggest that changing light intensity and spectral quality may be important in promoting sex-specific flight activity in sandflies and could therefore provide a mechanism to at least partially explain the early flight activity of male sandflies. However much work remains to be done to fully understand wavelength specific behaviour in sandflies.

One of the most important findings from this study is that *L. longipalpis* is very sensitive to UV and the blue-green-yellow region of the visible spectrum. Modified CDC light traps which are commonly used for measuring sandfly abundance (Sudia & Chamberlain, 1962; Chaniotis & Anderson, 1968; Quinnell & Dye, 1994) utilize light bulbs with a tungsten filament as their light source which transmits an array of wavelengths across the whole spectrum. However, their spectral emissions include a small amount of UV and large amounts of yellow red and very large amounts (75%) of infra-red (Service, 1993). These light traps are very selective in their catches (Chaniotis, 1978; Molyneux & Ashford, 1983) and some sandfly species seem to be insensitive to this light and never, or rarely, enter these traps (Chaniotis, 1978). Similar observations have been made of the response of different species of mosquitoes to light traps (Service, 1993). The data from this study suggest that there may be scope for improvement of CDC light traps used for sandfly monitoring. In the future, trials could be carried out to compare catches of CDC light traps using bulbs transmitting white light with those transmitting UV and/or blue-green-yellow light. The intensity of the light from the bulbs should be controlled and equal in each case.

A significant amount is known about the chemical ecology of *L. longipalpis* species complex from laboratory experiments, e.g. the role and identity of sex pheromones, oviposition pheromones, oviposition stimulants and attractants and the role and identity of host odour attractants (Ward & Hamilton, 2002), yet little is known about the general ecology of *L. longipalpis*, other than events and behaviours relating to the acquisition of a blood meal. For example it is not clear how *L. longipalpis* locate their sugar meal or which plants they feed on, or how resting or oviposition sites are located. Other researchers have shown that vision is important in the location of a blood meal in some haematophagous insects, although the relative importance may depend on other factors, e.g. whether the insect is diurnal, crepuscular or nocturnal. There may be significant interaction or even synergistic effects between visual and chemical cues. In *Lucilia sericata* (Meigen) (Diptera: Calliphoridae), for example, a visual cue enhanced landing response when host odour cues were present (Wall & Fisher, 2001). Trap catches of *Glossina brevipalpis* Newstead (Diptera: Glossinidea) were enhanced when synthetic host odour and an attractive trap colour were presented simultaneously (Kappmeier & Nevill, 1999). However, visual attraction was found not to be an important component of attraction of *Glossina austeni* Newstead (Diptera: Glossinidae) to a synthetic host odour baited trap (Kappmeier and Nevill, 1999). It may be possible to exploit the attraction of *L. longipalpis* to specific colours as Burkett *et al*. (1998) have attempted to do with mosquitoes. They tested a range of different coloured super-bright light-emitting diodes in CDC light traps and found that some species of mosquitoes showed distinct preferences for different colours. Possibly a similar difference in preference could be found amongst different sandfly species. It may be possible to manipulate male and female preferences for different wavelengths as Katsoyannos & Kouloussis (2001) have with the olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae). They showed that yellow and orange spheres coated with an adhesive placed in an olive tree caught predominantly male *B. oleae*, whereas red and black spheres caught predominantly female individuals.

A great deal remains to be done to determine how the observations on visual ecology made in this and the previous study (Mellor *et al*., 1996) relate to the life history of *L. longipalpis* in the wild. Nevertheless the results obtained suggest that vision is an important aspect of *L. longipalpis* biology.

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