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On the role of blue shadows in the visual behaviour of tsetse flies

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Tsetse flies (*Glossina* spp.), the vector for African trypanosomiasis, are highly attracted by blue and black surfaces. This phototactic behaviour has long been exploited to trap tsetse flies as one measure in the control of African trypanosomiasis. However, why blue and black are so attractive for tsetse flies is still unknown. We propose that the combination of blue and black is attractive for many *Glossina* species because when searching for a shady resting place to pass the day, the flies are probably guided by the blueness and darkness of daytime shadows. In contrast to people's experience that daytime shadows are colourless, actually on a sunny day all shadows are tinted bluish by the scattered blue skylight.

Keywords: *Glossina*; tsetse flies; blue shadows; colour attractants; visual behaviour

1. INTRODUCTION

Tsetse flies (*Glossina* spp.) are important as vectors for the transmission of sleeping sickness in humans and nagana disease in cattle in tropical Africa. Over 60 million people living in 36 sub-Saharan African countries are at risk of acquiring sleeping sickness and it is estimated that between 300 000 and 500 000 people have the disease (WHO 2001). In addition, 46 million cattle are threatened with nagana and the disease costs an estimated US$ 1.34 billion per year (Kristjanson *et al.* 1999). One important approach to the control of African trypanosomiasis is the control of tsetse flies by trapping (Green 1994; Jordan 1995; Lancien & Laveissière 1997; Leak 1999). Usually, the traps consist of a combination of black and blue surfaces (Green 1989, 1994; Jordan 1995; Lancien & Laveissière 1997; Leak 1999). However, the reason why blue and black are highly attractive for tsetse flies is still puzzling. Here, we propose the hypothesis that scattered blue light in shadow areas in association with behavioural patterns may explain the phototactic reaction of tsetse flies.

2. ATTRACTIVENESS OF COLOUR TO TSETSE FLIES

Early studies reported that tsetse flies were more often found on dark than on light surfaces (reviewed in Green 1994; Leak 1999). Behavioural experiments revealed that tsetse flies are attracted to near ultraviolet (UV) light followed by blue light (Green & Cosens 1983). However, while UV light attracts tsetse flies, UV-reflecting surfaces repel them (Green 1994). Challier *et al.* (1977) had found that the best trap material was royal blue cotton, which has a high blue reflectivity at 460 nm and little UV and green–yellow reflectivity (Green & Flint 1986). In addition, dark surfaces are also attractive and induce a strong landing response in tsetse flies (Green 1986).

3. SPECTRAL SENSITIVITY IN TSETSE FLIES

One simple explanation for the preference of *Glossina* for blue would be the presence of a single class of receptor cells with spectral sensitivity *ca*. 470 nm within the compound eye of tsetse flies. However, electrophysiological studies revealed that the spectral sensitivity in *Glossina* is similar to that of other Diptera (Green & Cosens 1983). Using electroretinogram measurements, maximum sensitivities of the eye of tsetse flies were recorded in the UV at 350 nm, in the blue and green between 450 and 550 nm, and in the red at 625 nm (Green & Cosens 1983). In addition, the anatomy of the eye of *Glossina* is similar to apposition eyes of many other insects (Turner & Invest 1973; Hardie *et al.* 1989). Hence, it can be excluded that the reason for the phototactic behaviour of tsetse flies is a consequence solely of the receptor types within the retina.

4. BLUE SHADOWS AND TSETSE FLY BEHAVIOUR

When sunlight passes through the atmosphere of the Earth, short-wavelength (blue) light is scattered in all directions by airborne molecules, whereas long-wavelength (red) light is scattered less. The process that gives rise to this is called Rayleigh scattering and it is this that makes the unobscured sky appear blue. On a clear sunny day, therefore, all shadows are tinted bluish by the blue skylight (Churma 1994). Recent work has shown that, in humans, the balance of the red–green opponent colour system is unchanged by shadows, whereas that of the older yellow–blue colour system responds strongly (Párraga *et al.* 2002). The effect of scattered skylight on shadow is shown in figure 1. Humans tend not to notice the blue coloration of shadows because they are also dark; however, the yellow–blue opponent system (which does not encode luminance) clearly marks them as being blue. Hence, shadows are both dark and blue and may be detected by this conjunction.

Tsetse flies spend most of the day at rest in shaded places in forested areas (Leak 1999). When tsetse flies are on the move, they are searching for hosts from which to take a blood meal or for resting places partly or wholly by sight (Lancien & Laveissière 1997).

Based on this information, we suggest that the preference of tsetse flies for the combination of blue and black is associated with their searching for shady resting places. To find a suitable resting place, tsetse flies are probably guided by the blueness and darkness of daytime shadows. In support of this idea, once attracted by the blue surfaces, the flies settle on the black (dark) surfaces of the trap (Lancien & Laveissière 1997). The settlement of the flies on the black surfaces of the trap may resemble their natural behaviour to hide in dark places like the underside of horizontal branches, between fissures of the bark on the boles of trees or in rot holes of tree trunks (Leak 1999). Considering the available evidence, it seems that tsetse flies are highly attracted by the combination black (dark)

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Figure 1. An image of a naturally illuminated scene obtained with a calibrated digital camera in Kibale Forest, Uganda. (*a*) The original photograph. (*b*) A representation of the same image as encoded by the 'yellow–blue' opponent system in primate vision. It can be clearly seen that the shadowed areas from the original image are more blue than the other regions, for each surface represented in the image.

and blue. In nature there are very few areas that are dark and blue at the same time, however, shadows have the combination and are common (Endler 1993; Churma 1994).

5. CONCLUSION

It is suggested that in the search for a suitable shady resting place to pass the day, tsetse flies are probably guided by the blueness and darkness of daytime shadows. This hypothesis would explain why blue and black surfaces in combination are highly attractive for tsetse flies.

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