Perspective

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Optimising the colour of traps requires an insect's eye view

Roger D Santer[a*] **and William L Allen**[b]

Abstract

Colour is a critical property of many traps used to control or monitor insect pests, and applied entomologists continue to devote time and effort to improving colour for greater trapping efficiency. This work has often been guided by human colour perceptions, which differ greatly from those of the pests being studied. As a result, trap development can be a laborious process that is heavily reliant on trial and error. However, the responses of an insect's photoreceptors to a given trap colour can be calculated using well-established procedures. Photoreceptor responses represent sensory inputs that drive insect behaviour, and if their relationship to insect attraction can be determined or hypothesised, they provide metrics that can guide the rational optimisation of trap colour. This approach has recently been used successfully in separate studies of tsetse flies and thrips, but could be applied to a wide diversity of pest insects. Here we describe this approach to facilitate its use by applied entomologists.
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1 INTRODUCTION

Insect pests damage the health of plants, animals and humans, so effective traps and lures are required to control or monitor these pests. Among the many features that attract insects to traps, colour is often critical and has been a major focus of applied entomological work.[1] This work has established 'standard' trap colours for many insect pests,[1] but efforts to improve colour and thus trap efficiency are ongoing. However, much of this trap development work considers colour from the perspective of humans rather than the target pest(s). We believe that this issue has been a significant impediment to trap improvement, but one that can be addressed by applying visual modelling approaches already widely established in sensory ecology. These approaches provide a powerful way to rationally improve insect traps.

2 THE MECHANISMS OF COLOUR VISION

Colours are psychophysical perceptions, partly resulting from the physical properties of the light environment and the object in question, and partly resulting from how visual information is detected and processed by the viewer's nervous system. Thus, colour only exists within the nervous system of the viewer, rather than being a simple property of the object being viewed.

Human colour vision relies on three classes of cone photoreceptor sensitive to short ('blue'), medium ('green') and long ('red') wavelengths of light. Each class is sensitive to different but overlapping regions of the electromagnetic spectrum, and produces a response proportional to the number of photons of light absorbed. Perceptions of colour derive from the subsequent neural processing of these photoreceptor signals, which is done in two ways. Chromatic mechanisms compare the responses of different photoreceptor types, corresponding to the qualities we call hue and saturation.[2] For example, a neural comparison of the 'green' and 'red' cone signals produces the green–redness of colour, and a comparison of the 'blue' cone signal to the other two types results in its blue–yellowness. Achromatic information, by contrast, is obtained from individual photoreceptor responses, or sums of those responses, and corresponds to the quality we call brightness.[2]

Insects possess very different photoreceptor complements from humans. Ancestral insects likely possessed three photoreceptor types sensitive to ultraviolet (UV), blue and green light respectively, which remains a common pattern across extant species.[3,4] However, there are numerous examples of the opsin proteins that form photopigments having been lost, duplicated or modified such that there is great variation across different insect species. For example, beetles lost the blue-sensitive opsin early in their evolution, but many lineages then regained a third or even fourth photopigment through duplication of the remaining opsins.[4] Possessing four or more opsins is common among flies, dragonflies and butterflies.[4] Furthermore, the spectral sensitivity of a photoreceptor is not solely determined by that of its photopigment, owing to a range of screening effects and the presence of sensitising pigments,[4] leading to even greater richness in photoreceptor types. The common bluebottle butterfly is an extreme example of this richness, with 15 different spectral types of photoreceptor based on five different opsins so far identified.[5]

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[*] *Correspondence to: RD Santer, Department of Life Sciences, Aberystwyth University, Aberystwyth SY23 3FG, UK. E-mail: rds5@aber.ac.uk*

[a] *Department of Life Sciences, Aberystwyth University, Aberystwyth, UK*

[b] *Department of Biosciences, Swansea University, Swansea, UK*

To further complicate matters, these different photoreceptor types may contribute to behaviour in different ways. It appears that in insects with a large number of different photoreceptor types, those photoreceptors may comprise subsets serving different behavioural tasks. For example, the Japanese swallowtail butterfly possesses eight spectral types of photoreceptor, but only four of them contribute to colour discrimination during foraging.[6]

To summarise, photoreceptors provide the inputs that nervous systems compare and sum to generate colour perceptions, and because insects possess different photoreceptor complements from humans, their colour perceptions must also be fundamentally different to ours.

3 THE PROBLEM WITH CURRENT APPROACHES

A great number of applied entomological studies have been concerned with creating and improving visual traps for different pest species (for a review, see Ben-Yakir *et al.*[1]). Such studies have traditionally created traps in a large number of different colours, and then evaluated their pest capture rate in field or laboratory trials. Through trial and error over time, researchers have identified effective colours for different pests, and have tested variations on those colours in the hope of finding an improvement. Results from such studies have often been reported using human colour descriptions such as 'blue', 'green', 'yellow' or 'red' to describe the traps tested (Fig. 1(a)). Clearly there are significant issues with this approach because it is guided by human colour perception and does not adequately account for the very different colour perceptions of the insects being studied. Human viewers might not appreciate the colour qualities relevant to insect behaviour, such as UV reflectance perceptible to most insects but not to humans (Fig. 1(b)). Thus, confounding factors might affect experiments, and trap descriptions may be inadequate to allow them to be accurately reproduced. Most significantly in our view, human descriptions of trap colours cannot lead to a mechanistic understanding of the behaviour that causes insects to be caught in traps, meaning that they cannot provide a basis for the rational improvement of those traps, limiting the efficiency with which more effective trap designs can be developed.

Many studies use reflectance spectrometry to quantify the reflectance of traps across the complete range of wavelengths visible to humans and/or insects (typically 300–700 nm) (Fig. 1(b)). These spectra are excellent descriptions of the physical qualities of the stimulus that pertain to colour and are no longer human-specific. However, because colours are psychophysical perceptions, the physical component of colour is only part of the story, and reflectance spectra do not necessarily tell us how a stimulus is perceived by an insect. Depending on the visual system of the viewer, it is possible for objects with quite different reflectance spectra to appear similar, or for those with seemingly subtle differences in reflectance spectra to be perceived quite differently. As a result, it is not always straightforward to interpret the relationship between reflectance spectra and insect behaviour. For example, analyses of tsetse fly catches at coloured traps found that reflectance of red light was one of several reflectance features that significantly predicted catches,[10] yet it was subsequently found that tsetse lack a red-sensitive photoreceptor that would allow them to perceive that stimulus property.[11] Thus, relationships between reflectance features and behaviour might not always be a good indication of the sensory information driving insect behaviour.

4 A MODERN APPROACH TO COLOUR IN APPLIED ENTOMOLOGY

For many years, sensory ecologists have calculated values to represent the photoreceptor responses of their study organisms to objects of interest. Photon catches, P, are calculated by integrating spectra for the ambient light, I, object reflectance, R^o and photoreceptor sensitivity, S, and represent estimates of the photons of light absorbed by a photoreceptor as it views an object. Typically, these values are adjusted by an equivalent value calculated using the reflectance of the predominant background, R^b, to represent a photoreceptor's adaptation to the light environment:

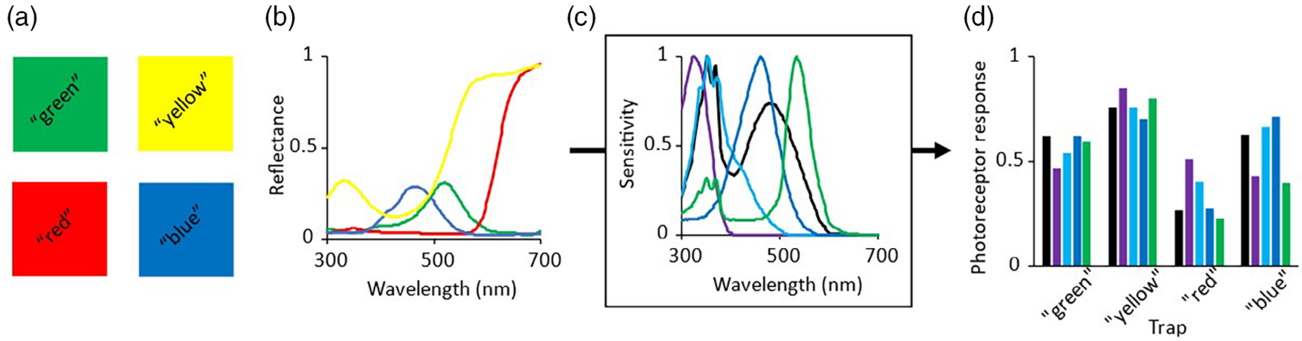

Figure 1. Insect eye view colour quantification for trap optimisation. (a) Entomological studies sometimes record catches at traps of different colours, but the human description of those colours is a poor approximation of the sensory experience driving insect behaviour. (b) Measurements of trap reflectance, using reflectance spectrometry or multi/hyperspectral imaging, characterise the physical properties of a trap pertaining to colour, and are much more informative. Here the yellow trap has significant reflectance in the UV (<400 nm), which can be perceived by insects but not by humans. (c) Light reflected from a trap excites an insect's photoreceptors according to their spectral sensitivity functions. Here shown are those of a fly, which has little sensitivity to longer wavelengths of light. Thus, the high reflectance of the red trap above 600 nm might not be perceived by a fly. (d) Values representing the responses of each class of photoreceptor in the target insect can be calculated using established procedures, and these represent the actual inputs to colour-guided behaviour. If the relationship of these values to trap catches is understood, trap selection or optimisation can be guided by these metrics. For tsetse flies, traps are most attractive when they maximise excitation of blue-sensitive photoreceptors relative to excitation of UV- and green-sensitive photoreceptors. Here the 'blue' trap should be most attractive, but if we could select or design a trap to enhance this pattern of photoreceptor signals, we would expect it to be a more effective trap. Data are replotted from the supplementary material of Santer.[7] Reflectance spectra data are originally from Lindh *et al.*[8] and photoreceptor sensitivity data are from Hardie.[9] Colours are indicative only, and do not relate to the true colours of the materials.

$$P=\frac{\int_{300}^{700} I(\lambda)\cdot \mathrm{R}^{\mathrm{o}}(\lambda)\cdot S(\lambda)d\lambda}{\int_{300}^{700} I(\lambda)\cdot \mathrm{R}^{\mathrm{b}}(\lambda)\cdot S(\lambda)d\lambda} \tag{1}$$

Because a photoreceptor's response scales nonlinearly with the number of photons absorbed, researchers often log-transform these values, or apply other established transforms.

The information needed to calculate these values is often readily available. In many cases it is adequate to assume a standard ambient light spectrum, although it is important to ensure that it is expressed in photon units.[12] Object and background reflectance can be measured using a reflectance spectrometer, or by multi- or hyperspectral imaging. Photoreceptor sensitivity data have been published for a wide diversity of different insect species, including many key pests (van der Kooi[4] and references therein). The calculations themselves are easily achieved in a standard spreadsheet program and accessible demonstrations of how to do so are available,[13] as are sophisticated packages to carry out the calculations in R.[14]

Photoreceptor responses can also be determined by digital photography. When the target species has three or fewer photoreceptor classes and their sensitivity overlaps with that of human photoreceptors, an appropriately calibrated, standard digital camera can be used to generate photoreceptor photon catches.[15] For visual systems with more photoreceptor classes and sensitivity outside the human range, cameras can be modified to have UV sensitivity, or else multi- or hyperspectral imaging can be used.[15,16] Software to support these applications in Image J is openly available.[16]

Because photoreceptor responses provide the actual inputs from which colour perceptions are generated by nervous systems, estimates of these values can be used to meaningfully describe coloured stimuli from an insect's point of view. Established approaches allow these values to be combined into species-specific colour spaces in which different colours can be assigned a locus,[17] and to assess the discriminability of any two colours to a given species,[18,19] based on the comparison of those signals that occurs in real nervous systems.

Recently, studies on tsetse and thrips have demonstrated that calculated photoreceptor responses can provide a rational basis for insect trap optimisation (Fig. 1(c),(d)). Tsetse flies are biting flies that spread human and animal African trypanosomiases, and they are controlled using coloured fabric targets impregnated with insecticide. These targets are traditionally blue and/or black in colour, but optimising colour had the potential to improve the efficiency of tsetse control for the management of disease. Based on previous experimental studies that measured reflectance spectra of different coloured targets and the numbers of tsetse flies attracted to them, Santer[7,20] calculated fly photoreceptor responses and built statistical models that predicted tsetse catches based upon those signals (c.f. 'receptor-based models'[2]). These revealed that stronger responses in UV- and green-sensitive photoreceptors were associated with reduced catches, and stronger responses in blue-sensitive photoreceptors were associated with increased catches,[7,20] suggesting that a comparison of these photoreceptor signals within the fly's nervous system was responsible for attraction towards a target. Fabric colour engineering approaches were then used to predict the reflectance spectra that particular dye combinations would produce, and the attractiveness of those theoretical spectra was in turn predicted using the photoreceptor-based models of tsetse behaviour. Through iterations of this procedure, an improved 'violet' fabric was developed that better exploited the hypothesised mechanism of attraction by increasing blue-sensitive photoreceptor responses relative to UV- and green-sensitive photoreceptor responses.[21] Subsequent field tests proved the success of the approach. In experiments on savannah tsetse, the new violet fabric attracted significantly more flies than a standard black target, whereas blue fabrics – including one specifically manufactured for tsetse targets – did not.[21] In follow-up experiments on riverine tsetse, catches were more variable, but the greater attractiveness of the new violet fabric *versus* a typical blue fabric was still evident.[22]

Western flower thrips are major pests of agriculture and horticulture worldwide and are controlled using sticky traps that are typically blue or yellow in colour. Given the UV, blue, green trichromatic visual system of thrips, and previous work indicating attraction to blue stimuli in most instances, Dearden *et al.*[23] hypothesised that blue traps would be more attractive when they maximally stimulated the blue photoreceptor, and minimally stimulated the green one. This would create the strongest neural signal if photoreceptor responses were compared within the thrips nervous system. To test this idea, they produced a palette of blue colour swatches and evaluated them using multispectral imaging and thrips' photoreceptor response calculations. Based on those photoreceptor signals, they identified blues with better and worse blue/green photoreceptor response ratios than a standard commercial trap, and tested them in a polytunnel environment. As predicted, improved blue/green ratio traps performed better.[23] What is more, trap performance could be improved still further using internal colour contrast.[23]

This approach might easily be applied to other pest insect species. Catches of aphids[24–26] and pollen beetles[27] at differently coloured water traps have been explained by the green/blue photoreceptor response ratio, again representing the neural computation thought to underlie behaviour. Although these models have not yet been used to engineer more effective traps, they explain the attractiveness of the yellow traps currently preferred for aphids and pollen beetles, and provide a rational basis upon which new traps could be selected or developed.

5 CONCLUSIONS

Together, these studies demonstrate an improved way to consider colour in applied entomological experiments that can provide a rational basis for trap optimisation and improved insect control. Photoreceptor responses provide the inputs to colour-guided behaviour, so they provide the best way of describing the qualities of coloured stimuli relevant to insect behaviour. Furthermore, they allow the mechanistic relationship between those responses and behaviour to be hypothesised, which allows the rational selection or design of coloured traps to better exploit those mechanisms. This approach allows trap development *in silico*, with laborious fieldwork reserved for the testing of theory, or proving the effectiveness of the best designs, enhancing the efficiency of trap development.

A variety of sensory ecological techniques, tools and information are already available to the research community to facilitate this work in a wide variety of pest species.[2,4,13–19] The case studies described herein prove their utility in trap optimisation, but barely scratch the surface in terms of the potential that is available. Photoreceptor responses also provide inputs for processing other scene attributes (e.g. motion) in arthropod brains. Methods in sensory ecology for analysing spatial information in a way that incorporates the visual capabilities of pests could be applied to optimise trap pattern, or even shape and size. These approaches can be enhanced by computational techniques, such as the use of artificial intelligence to ascertain and model the relationships between arrays of photoreceptor signals and behaviour, and the use of optimisation algorithms to identify trap design parameters that would maximally exploit the hypothesised mechanisms. Widespread application of these methods across species and contexts has the potential to revolutionise the development of visual traps for the more efficient monitoring and control of insect pests.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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