



# Visual modelling can optimise the appearance and capture efficiency of sticky traps used to manage insect pests

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## Abstract

Sticky traps are one of the most important tools for monitoring and mass trapping of insect pests. Their effectiveness depends on attracting and capturing target pests efficiently. Trap colour strongly affects capture rates, but currently a principled approach to identifying optimal trap colour for a given pest and growing context is lacking. Here we propose that modelling pest colour vision enables identification of trap colours that optimise pest capture rates. We test this novel approach to trap design in field trials on Western flower thrips (WFT) *Frankliniella occidentalis*, an economically damaging pest of agriculture and horticulture worldwide. Prior studies have reported that WFT prefer blue and yellow sticky traps, aligning with recent evidence that WFT have trichromatic colour vision with peak sensitivities in the UV, blue and green portion of the visual spectrum and a blue-green colour opponent mechanism. Therefore, we hypothesised that a shade of blue that maximally stimulates the blue photoreceptor whilst minimally stimulating the green photoreceptor would improve sticky trap capture rates, while a shade of blue that decreased the opponent response would reduce capture rates. In three field experiments, we found strong support for this hypothesis: the optimised blue colour captured 1.3–2.6 times more WFT than current commercial trap colours. Our results also demonstrated that visual modelling can identify optimally contrasting colours for two-colour traps that further improve capture rates. This study provides a novel and principled approach to the design of visual traps that could be extended to other pest management contexts.

**Keywords** Visual modelling · Integrated pest management · *Frankliniella occidentalis* · Thrips · Sticky traps · Colour preference

## Key message

- We used visual modelling to identify shades of blue predicted to be optimised for trapping WFT
- Our predicted optimal blue colour captured 1.3–2.6 times more WFT than a commercial blue trap.
- Sticky trap capture was improved further by using strong internal contrast between blue and yellow.

- This study provides a novel and principled approach to the design of visual traps used to trap WFT
- The visual modelling approach could be extended to other important pests and management contexts

## Introduction

Control of insect pests in agricultural and horticultural settings is largely reliant on the use of chemical insecticides. Pressures to reduce pesticide input in agriculture have mounted due to the development of insecticidal resistance (Jensen et al. 2000), environmental risk (Tudi et al. 2021) and concerns over human health (Bandhari et al. 2021). For many pests, insecticide use can be limited by using sticky traps to monitor populations and ensure timely targeted intervention (Muvea et al. 2014; Sampson et al. 2004; van Tol et al. 2021). Sticky traps can also limit insecticide use when deployed at scale for mass trapping as an alternative or

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complementary control measure (Mouden et al. 2017; Reitz et al. 2020). Therefore, there is an urgent need to ensure sticky traps work as efficiently as possible for mass trapping and monitoring functions. This study develops and tests a novel method for optimising trap design based on modelling the colour vision of target pest species. We demonstrate our approach targeting Western flower thrips (WFT), *Frankliniella occidentalis* (Thysanoptera: Thripidae), a major insect pest of agriculture and horticulture worldwide (Kirk and Terry 2003; Mouden 2017). Considering the extensive host range (Reitz et al. 2020), transmission of plant pathogens (Scholthof et al. 2011), as well as feeding and oviposition damages (Reitz 2009), WFT form an economically important pest.

Previous research has demonstrated that the colour and pattern of sticky traps strongly influences trap performance (Kirk 1984; Vernon and Gillespie 1990; Ren et al. 2020). The best performing colour differs according to the target pest species. For example, many studies report yellow traps are effective for aphid species (e.g. *Myzus persicae*, *Aphis fabae*) over colours such as red, green and blue (Döring and Chittka 2007). For WFT, prior studies generally report blue as the most effective colour for sticky trap capture (Otieno et al. 2004; Cruz-Esteban et al. 2020). Yellow is generally the next most effective trap colour, with the benefit that it also attracts a broader pest range including aphids and leaf miners (Yudin et al. 1987; Cruz-Esteban 2021; van Tol et al. 2021). Accordingly, commercial sticky traps used for the monitoring and mass trapping of WFT are supplied in various shades of blue or yellow (Mateus and Mexia 1995; Sampson et al. 2004). The influence of colour on trap performance between species indicates that the colour vision of pests is an important consideration in optimising trap design (Yudin et al. 1987).

Insect colour vision involves comparison of the outputs of two or more classes of photoreceptor that differ in spectral sensitivity (van der Kooi et al. 2021). As photoreceptor classes typically have overlapping sensitivity ranges, most wavelengths of light excite more than one photoreceptor class but to different degrees. Stimulus colour is estimated via opponent responses that measure excitation ratios between combinations of two or more photoreceptor classes (Skorupski and Chittka 2011). Therefore, initial colour vision is dependent on the number of photoreceptor classes, their spectral sensitivity and opponent processing mechanisms exhibited by a given animal.

Electrophysiological studies of WFT vision confirmed the existence of two photoreceptor classes: one with peak sensitivity ( $\lambda_{\max}$ ) in the ultraviolet spectrum (365 nm), and another with  $\lambda_{\max}$  at 545 nm, perceived by humans as green (Matteson et al. 1992). Recently, a third photoreceptor class with peak sensitivity of approximately 467 nm, perceived by humans as blue, was strongly suggested by

choice experiments where WFT were presented with different coloured LEDs (Otani et al. 2014; Stukenberg et al. 2020). When investigating responses to blue and yellow LEDs, Stukenberg et al. [2020] demonstrated that attraction decreased significantly when blue and yellow light was combined, as compared to individual presentation. This suggests a blue-green colour opponent mechanism and that the attractiveness of blue to WFT is based on a strong opponent response. Therefore, we hypothesise that attractiveness will be optimised when blue colours maximally stimulate blue photoreceptors while minimally stimulating green photoreceptors, and that this will translate to improved trap capture of WFT. Identifying a shade of blue that optimises the opponent response can be achieved by modelling photoreceptor responses (Vorobyev and Osorio 1998; Troscianko and Stevens 2015) to different coloured stimuli.

Colour vision modelling, a basic tool of visual ecology, is increasingly being used to improve the design of products dependent on colour perception. For example, Paul and Stevens [2020] used a visual modelling approach to determine the visibility of horse racing jumps to horses. The study found that while the bright orange jump markers currently used are highly visible to trichromatic humans, they are much less conspicuous to dichromatic horses insensitive to differences in red and green hues. Visual modelling identified other colours such as blue that provide better visibility for horses. We extend the visual modelling approach to the new context of designing sticky traps and for the first time test the approach's effectiveness at improving product performance. In this paper, we propose that the most effective shade of blue and yellow for trap design can be identified by modelling trap appearance in terms of WFT colour vision.

Additionally, we evaluate whether two colour blue-yellow traps, with high internal colour contrast, can further improve WFT capture. Contrast is a key component of stimulus visibility and single colour traps rely on background contrast, which will differ between growing contexts and light environments. In other pest species such as fruit flies (*Drosophila suzukii* and *Zaprionus indianus*), Cruz-Esteban [2021] demonstrated that colour contrast plays a role in capture at close ranges. In line with previous research reporting that background colour influences attractiveness (Vernon and Gillespie 1995; Mainali and Lim 2010), we predict that high internal contrast between optimal shades of blue and yellow will further improve trap capture rates.

The effect of two semiochemical lures Lurem and ThripSCharm were tested in experiments 1 and 3. This was partly because we expected low population densities of WFT at the time of year these experiments took place. We also aimed to test for possible interactions between lure presence and trap colour. As chemical lures are frequently used by growers when monitoring WFT, it is important to establish whether they have a synergistic or antagonistic effect with any trap colours.

## Materials and methods

### Multispectral imaging calibration and analysis (MICA) toolbox

In this study, the cone catch quanta of WFT to different potential trap colours were estimated to select colours to identify hues that produced the strongest opponent response (Chittka 1996; Vorobyev and Osorio 1998). To model and compare the responses of WFT photoreceptors to different colours, ultraviolet (UV) and visible spectrum photographs of potential trap colours were measured using the MICA toolbox (Troscianko and Stevens 2015) within ImageJ version 1.53 (Schneider et al. 2012). The MICA toolbox facilitates image processing to: 1. Linearise images so pixel values correspond to object reflectance; 2. combine photographs imaging different parts of the spectrum (e.g. UV and human-visible wavelengths); 3. standardise images by measuring one or more reflectance standards situated within images to model lightness and colour constancy processes in different lighting conditions (Arnold and Chittka 2012), and 4. transform images from the camera's colour space to the colour space of the target species' (Stevens et al. 2007). The output is a matrix of estimated cone catch quanta enabling the measurement of receiver-dependent photoreceptor responses to a stimulus in a specified light environment.

### Colour swatch production

A swatch of potential trap colours was designed in Inkscape version 1.0.2 (Inkscape Project 2021). The swatch colours were blues and yellows that varied in hue, saturation, and lightness, spanning the range of likely target colours (Fig. 1). The swatch was printed onto A3 190 GSN Canon photo satin paper using a Canon 167IPF printer. Sticky insect glue (Sticky-trap Ltd, UK) was applied uniformly over the paper surface prior to colour measurement in line with the trap manufacturing protocol (2.5).

### Colour swatch photography

The swatches were photographed alongside commercial 100 × 240 mm blue and yellow sticky traps for WFT monitoring (Agrisense Ltd., UK). Photographs were taken outside in direct sunlight around midday in April (experiment 1), June (experiment 2), and October 2021 (experiment 3). Due to promising results in experiment 1, the optimal and suboptimal blue colours were retained and used in experiments 2 and 3. As perceived stimulus colour could have



**Fig. 1** Blue and yellow swatches measured for colour vision modelling of WFT

been affected by minor differences in the batch of glue, ink or paper, or a detail of the print process, to ensure we used the same blues between experiments we printed swatches and remeasured colour between experiments. Measurements were consistent across batches and experiments.

To accurately model WFT colour perception including ultraviolet (UV) photoreceptor responses, we combined ultraviolet and visible photographs. To take ultraviolet photographs we physically removed the built-in UV filter from a Samsung NX1000 camera. As the red sensor is also sensitive to UV wavelengths, using a BAADER U-Filter (Baader Planetarium GmbH, Germany), which only transmits UV light between 320 and 380 nm, enables UV reflectance to be recorded by the red sensor. A second image taken with a BAADER UV/IR-Cut/L lens filter, which transmits light between 400 and 680 nm, enables a standard 'visible' spectrum image to be taken with the same camera from the same position. 2.5% and 97.5% Spectralon reflection standards (Labsphere Inc, UK) were positioned within images to enable standardisation of images across different lighting conditions. The two images were manually aligned within MicaToolbox to generate a multispectral (.mspec) image.

## Visual system modelling

The Samsung NX1000 spectral sensitivity provided by MicaToolbox was used as the camera colour space model. We specified a new WFT visual model within MicaToolbox to enable transformation from the camera colour space to WFT colour space. We used the estimated spectral sensitivity curves of WFT photoreceptors from Otani et al. [2014] which are based on electroretinogram (ERG) and behavioural responses to light-emitting diodes (LEDs). The peak sensitivities were 363 nm (UV), 476 nm (blue B) and at 535 nm (green G). Absorption sensitivity for each photoreceptor was normalised so that the area under each curve equalled 1. Data for each photoreceptor were interpolated to provide spectral absorption data per 1 nm bin for each photoreceptor as required by the MicaToolbox. For each photoreceptor, Weber fractions were specified as 0.1. ImageJ's area select tools were used to measure estimated relative quantal catches to every swatch colour and the Agrisense trap colour.

Luminance was calculated by taking the average of the quantal catch estimates for UV, blue and green photoreceptors. To isolate effects of colour on trap performance from potential lightness effects, we identified swatch colours that had the same perceptual lightness to WFT vision as the Agrisense trap. To do so, we estimated chromatic and achromatic just noticeable differences (JNDs) between the swatch colours and the Agrisense trap colours using the receptor noise limited model (Vorobyev and Osorio 1998). JNDs represent the smallest visual difference that can be perceived between stimuli under specified viewing conditions (Vorobyev and Osorio 1998). Quantal catch estimates from MicaToolbox were imported to the pavo package (Maia et al. 2019), within R version 4.1.2 (R Core team 2021). The intensity of chromatic ( $\Delta\text{chrom JND}$ ) and achromatic ( $\Delta\text{lum JND}$ ) were calculated using the 'coldist' function.

## Colour selection and trap production

Colours that were isoluminant ( $<2 \Delta\text{lum JND}$ ) to the corresponding blue or yellow Agrisense traps were considered for treatment selection. Of the isoluminant colours, treatments were selected based on the B/G opponent process excitation ratio (Chittka 1996) of swatch colours compared against the Agrisense trap.

Predictions to trap performance were based on the blue (B)/ green (G) ratio. The B/G ratio was calculated using the following formula:  $B/G = \frac{(B-G)}{(B+G)}$  where B = blue photoreceptor excitation and G = green photoreceptor excitation. The predicted 'optimal' hue maximised the B/G ratio (-0.018), which was greater than the Agrisense trap (-0.014) and predicted 'suboptimal' hue minimised the B/G ratio (-0.04).

For the yellow colours, the B/G ratio of all swatch colours was lower than that of the yellow Agrisense trap (0.54). Therefore, initial focus was on testing hypotheses using blue colours. The blue most similar to the Agrisense blue (minimum  $\Delta\text{chrom} + \Delta\text{lum}$ ) was also identified to test whether differences in printing between the prototype trap designs and the Agrisense trap could explain treatment performance in experiment 2. A further control of blank Agrisense traps applied with the same glue as prototype traps was tested in experiments 1 and 2 to examine whether differences in glue performance could explain treatment performance.

For experiment 3, which evaluates the effect of internal trap contrast on WFT capture, a yellow was identified that had strong chromatic contrast (JND 12.2) to the optimal blue. As floral shapes have been reported to be more attractive to WFT compared to other shapes (Ren et al. 2020), the contrast trap design consisted of two yellow eight petal floral shapes, designed to mimic chrysanthemum flower shapes, with the optimal blue used as the background shade. The floral shapes covered 42% of trap area. Stimuli were printed on A1 sheets similar to the production of swatches, with the same colour print settings. All printed traps were cut to the same size as the Agrisense medium blue sticky traps (100 × 245 mm). Printed traps were evenly coated with horsefly trap glue (Sticky-trap Ltd., UK) and covered with non-stick parchment paper prior to evaluation.

## Experiment 1

This experiment was conducted at Little Mockbeggar farm, Kent, England (51.421365, 0.489057). The study took place between 28/04/2021 and 30/04/2021 over two consecutive 24-h assessment blocks. Treatments evaluated were the

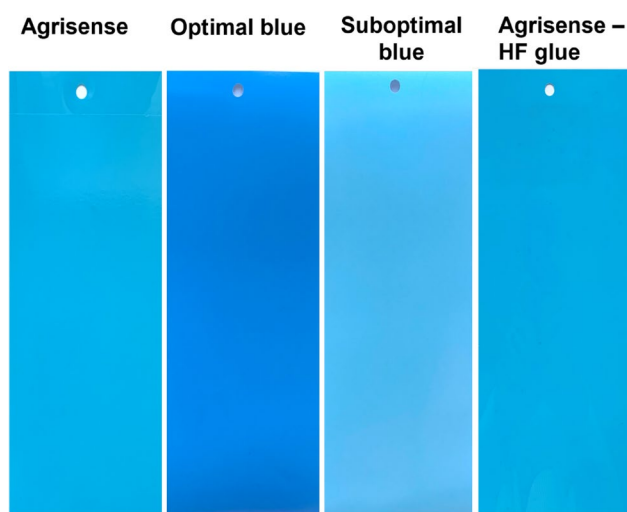


Fig. 2 Colour treatments evaluated during experiment 1, Kent, England

predicted optimal blue, predicted suboptimal blue, commercially available Agrisense trap and the uncoated blue Agrisense trap coated with the same horsefly glue application used in optimal and suboptimal treatments (Fig. 2). The first 24-h block measured trap capture rates without the presence of a chemical attractant. In the second 24-h block, traps were presented alongside LUREM-TR (Koppert Ltd., ND), a commercial WFT attractant. Three adjacent 8 × 155 m polytunnels used to grow strawberries (*Fragaria ananassa*; Var: Centenary) were used as experimental arenas. Each polytunnel contained five rows of table-top hydroponics systems elevated 1.2 m from the ground. Crops were 25 weeks old with a density of 6 plants per metre. Traps were suspended from bamboo canes and placed at 6 m. intervals across rows one and five starting 30 m from the tunnel entrance; each trap was positioned approximately 10 cm. above the crop canopy. The position of treatments within polytunnels was randomised at the start of each experimental block. Five replicates of each trap design were placed in each polytunnel each block, equating to 30 replicates across the experiment. The response measure was number of WFT captured on each trap. Insects were identified visually with the aid of a hand lens. Thrips species other than WFT were also recorded throughout the duration of the experiments.

## Experiment 2

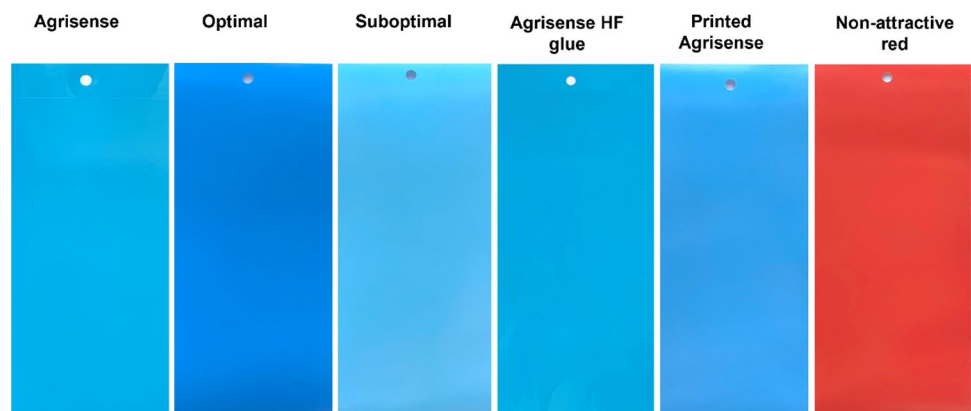
A larger field experiment was conducted at a different field site to further investigate how the hue of blue sticky traps affects WFT capture. The treatments evaluated were the same as in experiment 1 with two additional controls; the hue that matched the B/G ratio of the Agrisense trap to test for printing effects and a red hue that minimally stimulated WFT photoreceptors to assess capture rates using stimuli known to not be attractive (Fig. 3). The experiment took place at Homme Farm, Ross-on-Wye, England (51.8999255, -2.6119177), between 22/06/2021 and 25/06/2021. The treatments were evaluated over three

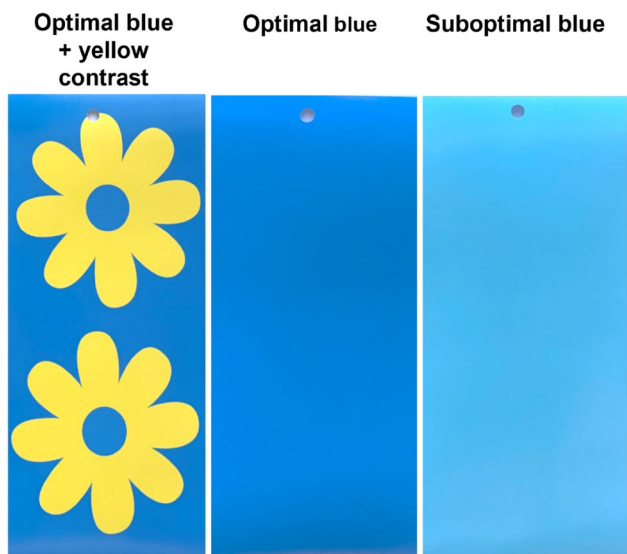
consecutive 24-h assessment blocks. Three adjacent 10 × 165 m polytunnels used to grow strawberries (Var: Arabella) were used as experimental arenas. Within polytunnels, six rows of tabletop hydroponics growth systems were 1.2 m from the ground. Crops were 24 weeks old with a density of 6 plants per metre per row. Traps were suspended, using bamboo canes, 10 cm above the crop canopy in rows one and five, each at 6 m intervals. Traps in each row were started 30 m. in from the polytunnel entrance to minimise edge effects. The order of treatments within polytunnels were randomised at the start of each block. There were 5 replicates of each treatment per polytunnel, equating to 15 ‘replicates’ per day and 45 across the entire study. The response measure (WFT trap capture) was the same as experiment 1. No chemical lures were used throughout this experiment.

## Experiment 3

This experiment aimed to investigate the effect of internal trap contrast and potential interactions between trap colour in the presence of a chemical lure. The experiment was conducted across two sites simultaneously; Little Mockbeggar Farm and Homme Farm, Ross-on-Wye (51.8999255, -2.6119177) during the late growing season (03/10/2021–07/10/2021) when WFT are less prevalent. At both sites, the experimental layout within polytunnels remained the same as those used in experiments 1 and 2. The only difference was the age of the crops, which were 38 weeks (Ross-on-Wye) and 44 weeks old (Kent) at this point. Response measures, WFT capture, were conducted in the same manner as in experiments 1 and 2. The contrast trap was evaluated alongside the optimal blue and suboptimal blue (Fig. 4). The three trap colours; contrast, optimal and suboptimal were evaluated both with and without lures. A new thrips lure, ‘Thrips Charm’ (RazBio Ltd., UK) was utilised.

**Fig. 3** Colour treatments evaluated in experiment 2, Homme Farm, Ross-on-Wye, England





**Fig. 4** Colour treatments evaluated in experiment 3. RNL modelling was used to select yellow hue with a strong chromatic contrast to the optimal blue (JND 12.2)

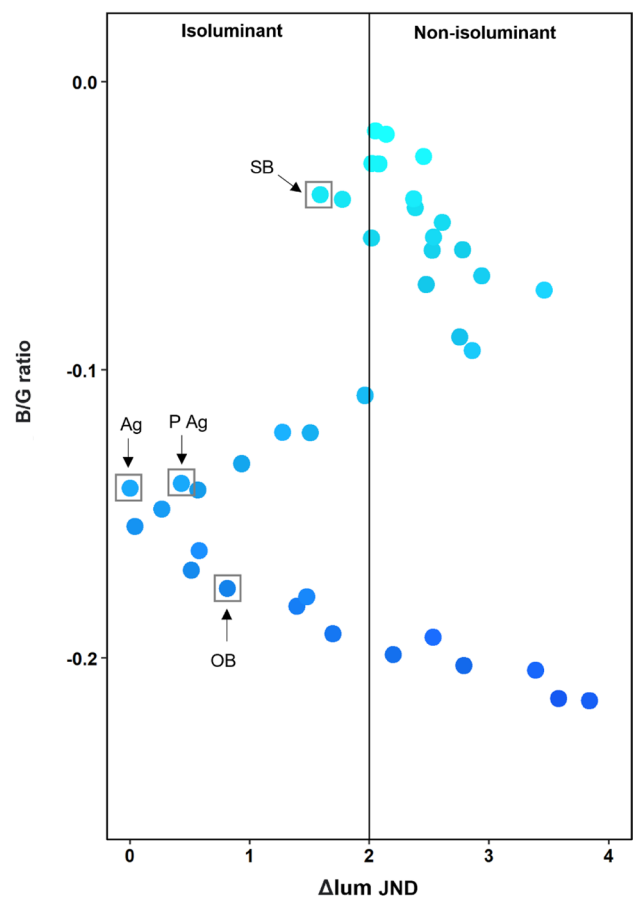
## Analysis

Data were analysed using R version 4.1.2 (R Core Team, 2021) using Poisson General linear mixed-effect models (GLMMs). To run models the ‘glmer’ function with the ‘mlmRev’ package was used (Bates et al. 2020). The Gauss-Hermite quadrature algorithm was used to calculate maximum likelihood within the models (Bolker et al. 2008). The number of iterations (nAGQ) per model was specified as 25. The response variable was trap WFT number. The fixed effects were treatment colour, and, in experiments 1 and 3, lure presence. Treatment colour was analysed as a categorical variable with the reference level set to the predicted optimal blue to facilitate comparisons between treatments. The random effects tested included site, polytunnel and polytunnel row. We used model AIC to evaluate support for models including different combinations of the random effects, and in experiments 1 and 3, the inclusion of either or both fixed effects and the interaction term. In all models reported, only the polytunnel row was retained as a random effect on the basis of AIC scores.

## Results

### Colour swatch modelling

The B/G ratios of the blue swatch colours varied between  $-0.012$  (low opponent response) and  $0.243$  (high opponent response). Of the colours measured, 15 were isoluminant to the Agrisense trap colour (Fig. 5). The Agrisense trap had

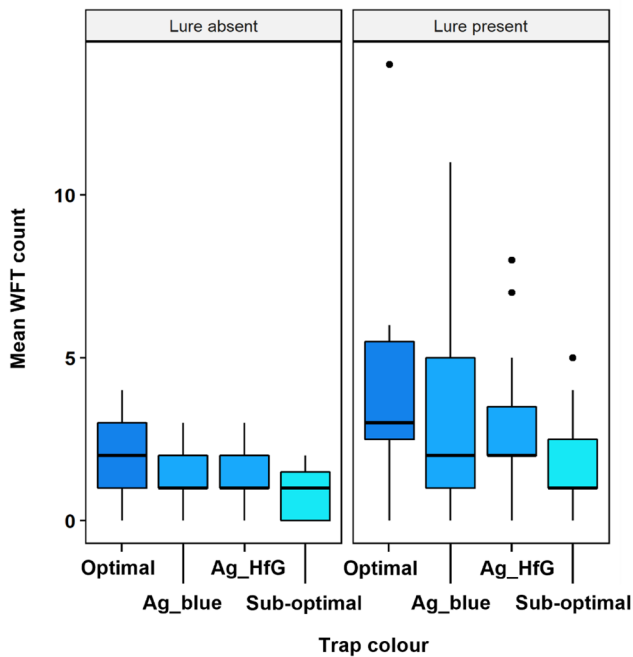


**Fig. 5** Estimated B/G excitation ratios of blue swatch colours and the Agrisense trap. Hues that were isoluminant to the Agrisense trap (left window) were considered for study. SB=suboptimal blue, Ag=Agrisense trap, P Ag=printed Agrisense control, OB=Optimal blue

a B/G ratio of  $-0.14$ . The colours chosen to test the initial hypothesis were: 1) optimal blue ( $B/G = -0.178$ ) and 2) suboptimal blue ( $B/G = -0.03$ ). For experiment 2, an isoluminant blue with a similar B/G ratio ( $-0.142$ ) to the Agrisense trap was selected as an additional control.

### Experiment 1

In total, 259 WFT and 87 *Aeolothrips intermedius* were captured across all traps. The mean capture rate of the predicted optimal blue was higher than all other colours evaluated, both in the presence ( $\bar{x} = 4.1$ ) and absence ( $\bar{x} = 1.87$ ) of a lure (Fig. 5). A model including main effects of trap colour and lure presence ( $AIC = 139.3$ ) was better supported than a model adding the colour  $\times$  lure interaction ( $AIC = 145.2$ ) or removing either the colour ( $AIC = 158.8$ ) or lure effect ( $AIC = 178.4$ ). Overall, the predicted optimal blue ( $\bar{x} = 2.97$ ) caught significantly more WFT than the Agrisense trap ( $\bar{x} = 2.27$ ,  $\beta = 0.41$ ,  $p = 0.0134$ ), the Agrisense trap with

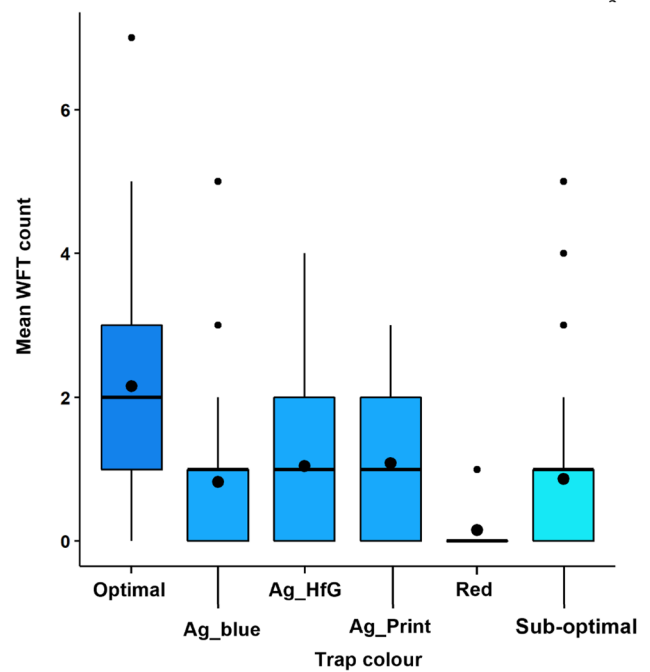


**Fig. 6** Mean WFT trap capture per 24 h for each colour evaluated in experiment 1, with lure absent (left) and lure present (right). Optimal=maximum B/G opponent response, suboptimal=minimal B/G opponent response, AG=Agrisense trap, AG\_HF=Agrisense trap with horsefly glue (same as printed traps)

horsefly glue ( $\bar{x}=2.1$ ,  $\beta=0.4$ ,  $p=0.015$ ) and predicted sub-optimal trap ( $\bar{x}=1.3$ ,  $\beta=0.94$ ,  $p<0.001$ ) (Fig. 6). Overall, suboptimal blue traps caught significantly less WFT than the Agrisense trap ( $\beta=0.53$ ,  $p<0.001$ ). No significant difference was found between traps using Agrisense glue and those using horsefly glue ( $\beta=0.01$ ,  $p=0.96$ ). The presence of a lure significantly increased WFT trap capture, independent of the colour ( $\beta=0.83$ ,  $p<0.001$ ).

## Experiment 2

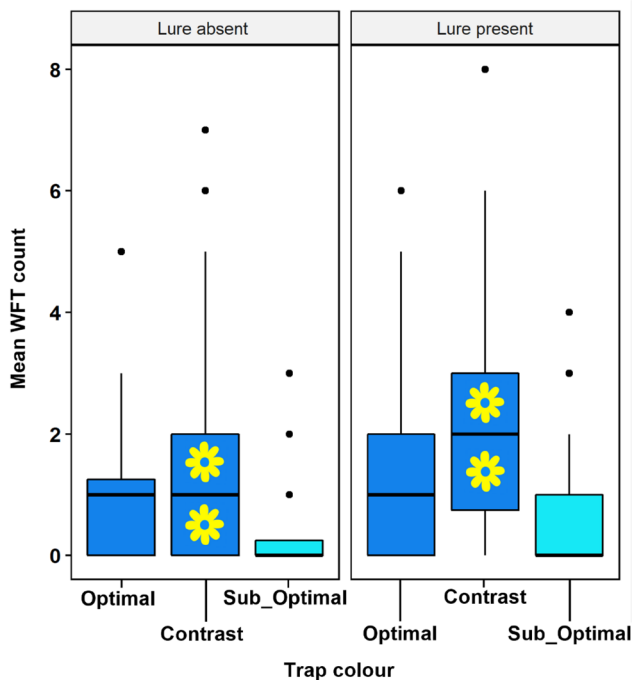
In total, 276 WFT and 5 *Aeolothrips intermedius* were captured across the experiment. On average, the optimal blue ( $\bar{x}=2.16$ ) caught significantly more WFT than the Agrisense trap ( $\bar{x}=0.82$ ,  $\beta=0.98$ ,  $p<0.001$ ) (Fig. 7) and all other treatments (all  $p<0.001$ ). The red trap was the worst performing trap, catching significantly less WFT than all other treatments (all  $p<0.001$ ). There was no significant difference in the number of thrips captured by the suboptimal blue and the Agrisense trap ( $\beta=0.07$ ,  $p=0.76$ ). There was no significant difference between the Agrisense trap and the Agrisense trap with horsefly glue ( $\beta=0.24$ ,  $p=0.18$ ).



**Fig. 7** Mean WFT capture per 24 h for each colour evaluated in experiment 2. Optimal=maximum B/G opponent response. Ag\_blue=regular Agrisense trap. Ag\_HfG=Agrisense trap with horsefly glue (same as printed traps). Ag\_Print=Printed control matching Agrisense hue and B/G ratio. Red=Red(non-attractive). Sub-Optimal=minimal B/G opponent response

## Experiment 3

A total of 563 WFT were captured during the experiment. As in experiment 1, the model featuring main effects of colour and lure presence was best supported (AIC = 509.9, although the model including the interaction between colour and lure received similar support (AIC = 510.3). Dropping either colour (AIC = 594.2 or lure (AIC = 542.5) substantially reduced model fit. Overall, optimal blue ( $\bar{x}=1.15$ ) traps caught significantly more WFT than the suboptimal blue ( $\bar{x}=0.57$ ,  $\beta=0.72$ ,  $p<0.001$ ) (Fig. 8). Independent of lure, the contrast trap ( $\bar{x}=1.61$ ) caught significantly more WFT per trap than the optimal blue ( $\beta=0.33$ ,  $p<0.001$ ). Independent of colour, the presence of a lure significantly increased trap capture ( $\beta=0.51$ ,  $p<0.001$ ). Overall, the contrast trap caught 2.8  $\times$  more WFT than the suboptimal trap ( $\beta=1.05$ ,  $p<0.001$ ). Analysis of the interaction term suggested that it was mainly driven by a floor effect for the suboptimal blue where 63 traps caught zero WFT when the lure was absent, whereas only 43 traps caught zero WFT when the lure was present, a marginally non-significant difference ( $p=0.08$ ).



**Fig. 8** Mean WFT capture per 24 h for each colour evaluated in experiment 3, with lure absent (left) and lure present (right). Optimal=maximum B/G opponent response, Contrast=Optimal blue + Optimally contrasting yellow (flower). Sub\_Optimal=predicted sub optimal blue

## Discussion

Our results provide proof of concept for the use of visual modelling tools to optimise sticky trap design for the capture of insect pests. Across three experiments, trap colours selected to maximise the B/G opponent response performed better than existing products, while trap colours selected for reduced B/G response performed as poorly or worse, demonstrating that sticky trap design can be improved by modelling the visual response of the target pests. The optimised trap colour increased mean capture rates by a factor of 1.3 to 2.4. This increase in performance would enable more accurate monitoring of WFT populations, allowing precisely timed control strategies, such as targeted application of insecticide (Dara 2019). Moreover, optimised colour could make mass-trapping using large sticky rolls a much more effective and commercially viable control strategy. Thus, our study demonstrates a novel and principled approach to designing more effective visual traps.

As well as improved performance, the visual modelling pipeline allows for a dramatic reduction in the effort required to identify the most effective trap colours compared to previous trial-and-error-based approaches. The resources needed to evaluate trap colour using trial-and-error meant most previous studies only evaluated colours

occupying very different parts of the light spectrum, e.g. blue vs. green vs. red (Brodsgaard 1989; Broughton and Harrison 2012; Roth et al. 2016). Here we build on work using LEDs (Otieno et al. 2004) to show that substantial differences in trap performance can result from fine-scale differences in hue.

Trap performance was further improved using contrasting colours and floral shapes. This could be explained by increased conspicuousness of the trap as perceived by WFT. It may also be explained by the context in which traps were perceived in relation to WFT ecology. Insect visual systems can have innate sensory biases to key colours or patterns (Raine and Chittka 2007). For example, when assessing the colour preferences of western honeybees (*Apis mellifera*), individuals ignored learned colour preferences and chose colours that were not previously rewarded, suggesting innate preferences (Gumbert 2000; Nityananda 2016). A considerable body of evidence suggests that pollinator photoreceptor sensitivities and flower colours are matched (Chittka and Menzel 1992; Chittka 1996; van der Kooi et al. 2021). Other studies have shown that innate colour preferences or attractive responses can be mediated by the visual environment, such as background colouration and colour contrast (Kuenzinger et al. 2019). Therefore, it is possible that photoreceptors are tuned to encode the environment efficiently, rather than encode specific stimuli optimally. Future experiments should aim to determine whether attraction of pests to traps is based on visual conspicuousness or learned or innate preferences specifically. Here we show that modelled conspicuousness can rapidly identify effective colours and colour combinations.

Our novel approach could be straightforwardly extended to other pest management contexts, requiring only basic information on the visual system of the target pest or pests. In this study, estimated photoreceptor sensitivity data presented in Otani et al. [2014] were used to calibrate our visual system model, with the predictions regarding trap capture rates made using this data confirmed in field experiments. Visual system data is now available for at least 309 insect species (Van der Kooi et al. 2021), including some major crop pests such as *Myzus persicae* (greenfly), *Drosophila melanogaster* (common fruit fly) and *Brassicoglyphus aeneus* (rape pollen beetle). Visual modelling also has potential as a principled method for designing traps that effectively target a range of pests using either a single compromise colour, or a range of colours—each one optimised to different target species. For example, we found that traps containing contrasting yellow-blue floral shapes were most effective at capturing WFT. As yellow is also known to be effective against a wide range of pests including whitefly (Family: Aleyrodidae) (Riyaz and Kathiravan 2019; Lima et al. 2020), we might expect these designs to also capture other target pests. Visual modelling could also optimise the shade of



yellow used so that traps target a wider pest complex, further benefitting growers.

Similarly, visual modelling offers an approach to find colours or combinations of colours that target pests while minimising conspicuousness or attractiveness to beneficials. For example, the yellow floral shapes against a blue background that were most effective in experiment 3 are likely to be attractive to other flower seeking insects including beneficial species such as bees (Ômura and Honda 2005; Moreira et al. 2016; Bukovac et al. 2017), although very few bees or other beneficials were caught during this study. Modelling the different visual system responses of pests and beneficials could predict colour combinations that maximise conspicuousness to pests while minimising conspicuousness to beneficials.

The visual modelling approach could also be extended to consider other features of the visual ecology of interactions between pests and pest management products such as the ambient light of growing environments and appearance of the backgrounds traps are viewed against. Recently, Cruz-Esteban et al. [2020] reported that blue sticky traps were preferred by WFT within polytunnels, and yellow traps preferred in open fields. These results suggest that the wider visual environment influences the performance of coloured sticky traps. Visual modelling of trap appearance in these different growing contexts could be used to investigate the basis for this difference. JNDs between trap and background colour and lightness could provide useful insights and enable design of products tailored to different environments.

The addition of Lurem (experiment 1) and Thrips Charm (Razbio Ltd.), a newly developed commercial thrips attractant (experiment 3), substantially improved sticky trap capture. This study provides further evidence that p-Anisaldehyde and verbenone are highly effective thrips lures (Mainali and Lim 2010; Abdullah et al. 2015). There were no strong interactions between trap colour and lure, though the presence of a lure significantly increased trap capture regardless of the trap design—demonstrating the effectiveness of combining olfactory-visual stimulation. While this was not unexpected, both synergistic and agonistic interactive multimodal effects of lure presence on trap performance are possible and should continue to be investigated (Partan and Marler 2005). For example, where trap colours and patterns are based on floral appearance, traps may perform especially well with lures based on floral compounds. As lures degrade over time and habituation of WFT to lures can be expected (Egger et al. 2014), long-term studies assessing lure performance in conjunction with sticky traps are required.

Temporal shifts in the visual appearance of traps throughout the year could be an important consideration in trap design; however, colour constancy (i.e. the ability of a visual system to perceive object colour relatively consistently despite changes in the spectral makeup of the illuminant) is well documented in insect species, especially flower seeking

insects and pollinators (Chittka et al. 2014). Therefore, we assume the stimulus colour perceived by WFT would appear largely unchanged following temporal changes in ambient light conditions. The advantage of the optimised blue in all three experiments is consistent with this; however, it is possible for colour preferences of thrips or other target pests to change seasonally (Roth et al. 2016), for example between foliage, sky and flowers. Visual modelling could be used to find trap colours that match the colour of key stimuli as perceived by the target pest.

Trials were conducted in April, June and October, taking into account three distinct seasons and high variance in thrip abundance. October (experiment 3) trials were conducted under extremely low abundance, yet the optimised blue traps still caught significantly more thrips than sub optimal hues. Use of optimised traps with lures could be highly advantageous for early detection systems in spring and autumn, spring thrip abundance could be effectively monitored at low density and treatments applied early—before damage thresholds were met. Thrips are known to overwinter within commercial strawberry crops and the media (Sampson et al. 2004), high numbers of overwintering thrips will survive and lead to early outbreaks in spring. Optimised traps that work in low density thrips populations could be used to predict spring outbreak, and pesticides applied late in the year to prevent development of overwintering population before the problem occurs in spring (Mori et al. 2014).

Overall, our study provides a novel application of visual modelling that can be used to design superior monitoring products such as sticky traps. We demonstrated that by utilising a colour that maximised the B/G opponent response in WFT trap capture rates under field conditions was significantly increased. We propose that there is great potential for a visual modelling pipeline to be used to design products and tools that will significantly improve trap capture rates, leading to improved monitoring and precision pesticide application within the context of an improved IPM strategy.

## Author contributions

AD contributed conceptualisation, data curation, formal analysis, investigation, methodology, project administration, software, validation, visualisation, writing—original draft preparation, writing—review and editing. MW contributed investigation (experiment 3), methodology (experiment 3 only), resources, writing—review and editing. HF contributed investigation (experiments 2 and 3). TB contributed funding acquisition, methodology, resources, writing—review and editing, supervision. WA contributed conceptualisation, funding acquisition, resources, project administration, methodology, writing—review and editing, supervision.

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**Data availability** Not applicable.

## Declarations

**Conflict of interest** Not applicable.

**Ethical approval** Not applicable.

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