Lighting and behaviour in captivity: butterflies prefer light environments containing UV wavelengths

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Highlights

- Artificial light often lacks ultraviolet wavelengths that many animals use.

- This may impact animal welfare in captivity.

- Butterfly activity did not differ under UV-present and UV-absent lighting.

- However, butterflies were attracted to UV-present lighting when given a choice.

- These findings can inform the design of lighting for butterfly houses.

The behaviour and welfare of animals in captivity is of great importance to zoological collections, captive breeding programmes, food production and keepers of companion

animals. Artificial lighting is commonly deficient in UV wavelengths, and use of such lighting for indoor animal enclosures could have significant impacts on the behaviour and welfare of animals to which UV wavelengths are visible. This includes birds, reptiles and fish, but also insects. Here we investigated the effect of UV-present and UV-absent light environments on the behaviour of _Vanessa cardui_, a butterfly that possesses a trichromatic visual system typical of many insects. We conducted behavioural experiments using a free-flight arena divided in half, where each half could be subjected to UV+ or UV− illumination. When lighting conditions for the two arena halves were the same, we found no significant differences in activity between UV+ and UV− light environments. However when lighting conditions for the two arena halves were different, butterflies showed a significant preference for the UV+ over the UV− half. This remained the case even when the overall intensity of UV+ illumination was less than that of UV− illumination. Our results suggest that UV-deficient artificial lighting conditions do not themselves affect the activity of butterflies, but that given a choice, butterflies prefer lighting that contains UV. Based on these findings, captive light environments can be designed that use supplementary lighting or filters to improve the welfare of captive insects, and the visitor experience.
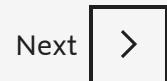
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Keywords

The welfare of captive animals is a widely recognized concern, whether those animals be raised commercially, kept as pets or public exhibits, or bred as part of conservation efforts. In assessing welfare, it is critical to ask not only whether an animal is healthy, but also whether it has what it wants (Dawkins, 2003). Environmental enrichments can address these needs and improve the 'biological functioning' of captive animals (Newberry, 1995). However, while sensory stimulation is a crucial aspect of environmental enrichment, creating enrichments that effectively provide for the sensory needs of captive animals can be challenging due to the frequent mismatch between the sensory experience of animals and that of their human caretakers.

The importance of lighting for the physiology and behaviour of humans is now apparent, with 'daylight spectrum' sources providing improvements in visual comfort, alertness, mood and sleep (Cajochen et al., 2019). However, human vision is not typical of most

animals kept in captivity, as humans are insensitive to UV wavelengths which form an important component of colour vision in many nonhuman species (Cronin & Bok, 2016). The spectral quality of illuminating light varies across habitats, weather conditions, times of day and seasons (Endler, 1993; Nilsson et al., 2022), and is proposed to contribute to the master control of behavioural states that modulates the probability pattern of behaviour (Nilsson et al., 2022). Furthermore, UV-reflecting structures commonly provide intra- and interspecific signals or cues that facilitate effective foraging, species or sex recognition, or resolution of aggressive conflicts in UV-sensitive taxa (Cronin & Bok, 2016). Consequently, lighting tailored to human specifications and lacking UV wavelengths might not promote natural behaviour or allow it to be performed effectively, impacting welfare. As such, lighting has been highlighted as a potential welfare concern for various types of animals, including mammals (Sørensen, 2014), birds (Maddocks et al., 2001, 2002; Sobotik et al., 2020) and reptiles (Baines et al., 2016).

In comparison to vertebrates, the welfare of insects has received much less attention, but the majority of species possess photoreceptors sensitive to UV wavelengths (Briscoe & Chittka, 2001; van der Kooi et al., 2021). Insects are now commonly held in captivity for education and entertainment (Boppré & Vane-Wright, 2012), captive breeding (Crone et al., 2007; Schultz et al., 2008), food production (Hawkey et al., 2021) and scientific research. Artificial lighting is well known to impact insect behaviour in their natural habitat (Owens et al., 2020), and lighting designed with an awareness of insect visual sensitivity has already yielded improvements in husbandry (Oonincx et al., 2016). As such, improved artificial lighting environments could benefit numerous captive insects.

One particularly important captive context is the butterfly house. Such exhibits are hugely popular, but take a wide diversity of different forms, and satisfy a wide diversity of different aims (Boppré & Vane-Wright, 2012). Butterflies rely on UV wavelengths in intra- and interspecific communication (for a review see Stella & Kleisner, 2022), and UV is a component of signalling between flowers and pollinators (Chittka et al., 1994; Koski & Ashman, 2013). However, while it is reported that butterflies of various species are attracted to artificial light, very little is known about the effects of lighting on butterfly behaviour (Seymoure, 2018), and the current ethical guidelines of the International Association of Butterfly Exhibitors and Suppliers specifically mention food, space, temperature, humidity and hygiene, but not light (IABES, 2022). Consequently, understanding butterflies' welfare needs with respect to lighting can lead to improvements in butterfly house husbandry, which might in turn improve sustainability by allowing more on-site breeding, and might improve the visitor experience by providing healthy and active specimens (Boppré & Vane-Wright, 2012). Improved husbandry practices might also

enhance the robustness of butterflies raised for release, since although the causes are not known, captive-reared monarch butterflies, _Danaus plexippus_, have morphological differences and behavioural deficiencies versus their wild-reared counterparts (Davis et al., 2020; Tenger-Trolander et al., 2019).

In this study we investigated the effects of UV-present and UV-absent light environments on the behaviour of painted lady butterflies, _Vanessa cardui_, aiming to address the central welfare question of what their lighting preferences are (Dawkins, 2003). These nymphalid butterflies possess UV-sensitive, trichromatic visual systems typical of many insects (Briscoe & Chittka, 2001; Briscoe et al., 2003; van der Kooi et al., 2021), and belong to the same family as many of the most popular species held in butterfly houses (Boppré & Vane-Wright, 2012). In separate experiments, we investigated the effects on behaviour of UV-present and UV-absent light environments, as well as light environments that offer a choice between the two conditions. By manipulating light intensity, we investigated whether the preference of butterflies is for UV light specifically, or brightness in general.

Methods

Animals and Husbandry

Vanessa cardui were purchased as caterpillars (Insect Lore, Cornwall, U.K.). Caterpillars were reared in individual plastic pots (3.5 cm diameter base, 5 cm diameter rim, 6 cm height), on a proprietary artificial diet mix ('Painted Lady (_V. cardui_) Cookie Dough Artificial Diet', Educational Science, TX, U.S.A.), at 24±1 °C and under 12:12 h light:dark using full-spectrum fluorescent tube lighting. Two days after pupation, pupae were transferred to a mesh cage (_ca._ 50×50 cm and 76 cm high) subject to the same lighting and temperature conditions. Pupae were monitored daily for emergence, and butterflies were used in experiments between 2 and 20 days postemergence. Adult butterflies were maintained on a 20% sucrose solution available ad libitum. Butterflies were sexed prior to experimentation and males and females were used in approximately equal numbers. Each individual was only used once in experiments to avoid pseudoreplication.

Experimental Arena and Lighting Environments

All experiments were conducted in a large Perspex chamber (87×56 cm and 88.5 cm high) with a ceiling-mounted lighting bank comprising two FSU18 Arcadia Natural Sunlight Lamps (Arcadia Reptile, West Sussex, U.K.) and three F18W/35 standard white, fluorescent

lamps (GE lighting, OH, U.S.A.), representative of commonly available lighting options (Fig. 1 a). Below the lighting bank was an optical filter, and this could either be of the same or different type for the two halves of the arena. The arena was shielded from extraneous light using blackout fabric across three sides. The average temperature of the arena during experiments was 25.4°C (range: 22.9–29.8°C).
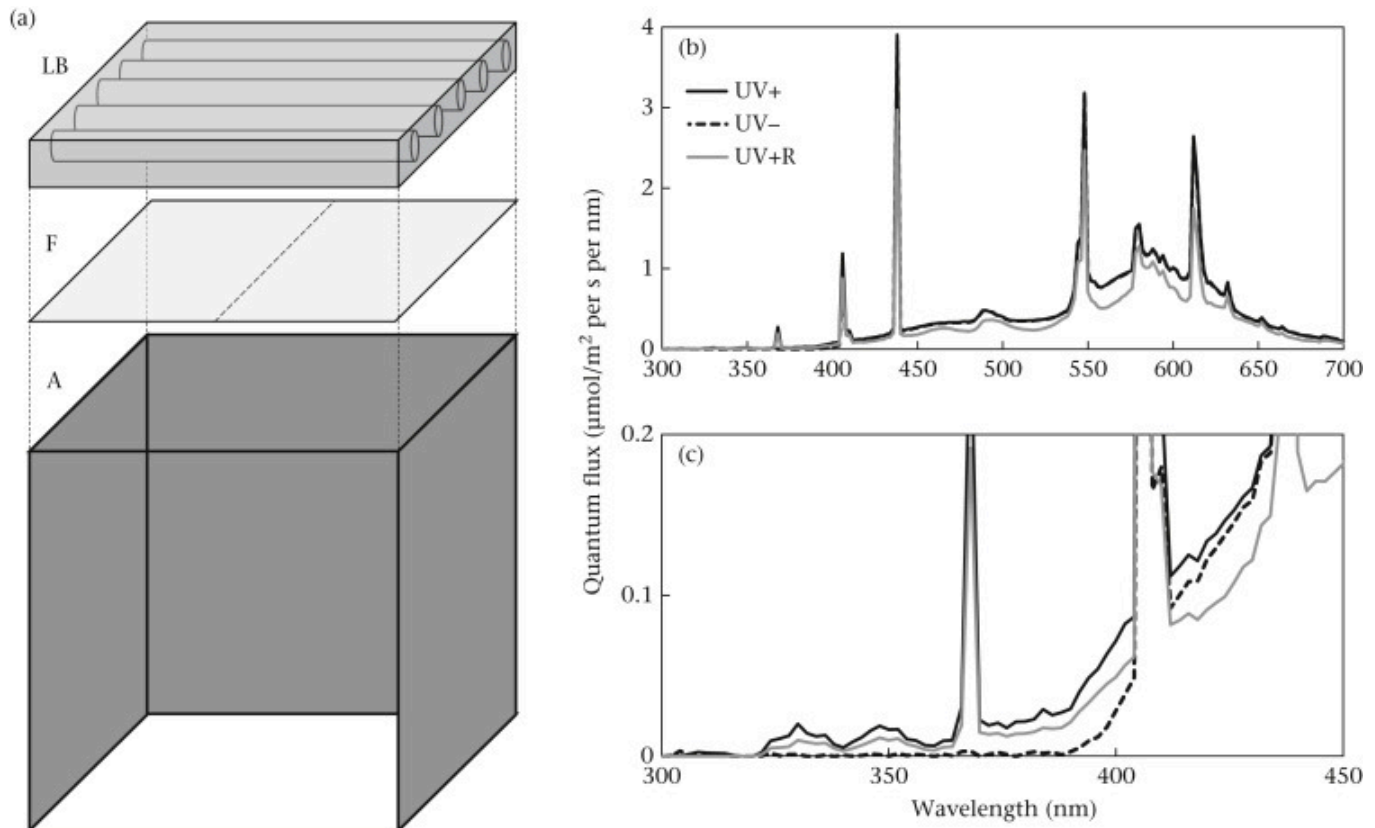
Figure 1. Experimental arena and lighting. (a) The experimental arena (A) was lit by a lighting bank of five commercially available fluorescent lamps (LB). Illumination from the lighting bank was modified using filters (F), which could be the same or different for the two sides of the arena. (b, c) Three different filter conditions were used, denoted UV+, UV− and UV+R. The corresponding irradiance spectra for these are shown across (b) the full spectrum visible to butterflies and (c) focused in on the UV region. UV− illumination had similar irradiance to UV+ above 450 nm where its plot is hidden by that for UV+ (b; black line). The spectra plotted have 2 nm resolution.

We used three types of optical filter, comprising (1) a UV-opaque filter (LEE 226 UV, LEE Filters Worldwide, Andover, Hampshire, U.K.), hereafter 'UV−'; (2) a neutral density filter (LEE 130 clear), hereafter 'UV+'; and a neutral density filter with reduced transmission

(three layers of LEE 130 clear), hereafter 'UV+R'. We quantified the resulting UV−, UV+ and UV+R illumination using a USB4000 spectrometer sensitive to radiation of wavelengths 200 to 1100 nm, with a 400 μm optic fibre and a cosine corrector (Ocean Optics, Dunedin, FL, U.S.A.). To calibrate this equipment to irradiance units we used a LS1-CC3 calibration lamp (Ocean Optics, Dunedin, FL, U.S.A.) that was calibrated above 400 nm. We then ensured accuracy of the calibration below 400 nm based upon the relative sensitivity of the equipment within that region. To do this, we took an irradiance measurement for the light source and then switched the spectrometer to reflectance mode and recorded the reflectance of a calibrated Spectralon reflectance standard (SRT 99-020, calibrated from 240 to 2000 nm; Labsphere, North Sutton, NH, U.S.A.) illuminated by that same light source. Accounting for the known reflectance of the Spectralon standard, irradiance and reflectance measurements should be related by a fixed ratio. We calculated that ratio for wavelengths above 400 nm and used it to correct the irradiance calibration below 400 nm. We quantified illumination in the experimental arena with the same filter type above both arena halves and the cosine corrector pointed vertically upwards in the centre of the arena so that its surface was 55 cm below the light bank. For each filter type three measurements were taken and averaged. Measurements were converted from energy to photon units (see Endler, 1990 ; Fig. 1b, c). UV+ illumination had the highest irradiance across the spectrum (Fig. 1b, c; black line). UV− illumination had similar irradiance to UV+ above 450 nm but lacked UV wavelengths below 400 nm (Fig. 1c; dashed line). UV+R illumination was a reduced intensity version of UV+, with greater intensity than UV− below ca. 410 nm (Fig. 1b; grey line), and lesser intensity than UV− above ca. 410 nm (Fig. 1b, c; grey line).

To evaluate the appearance of illuminants to butterflies we computed quantum catches, Q, for each of *V. cardui*'s three types of photoreceptor. We obtained normalized absorbance spectra for each rhodopsin type from Briscoe et al. (2003). Data were extracted using DataThief software (Tummers, 2006), and used to construct sensitivity curves, R, with 2 nm wavelength resolution (Fig. 2a). Our measured illuminant spectra were subsampled to achieve the same resolution (Fig. 1b, c). We estimated Q for receptor type i and illuminant j as follows:

$$Q_i = 2 \sum I_j(\lambda) R_i(\lambda)$$
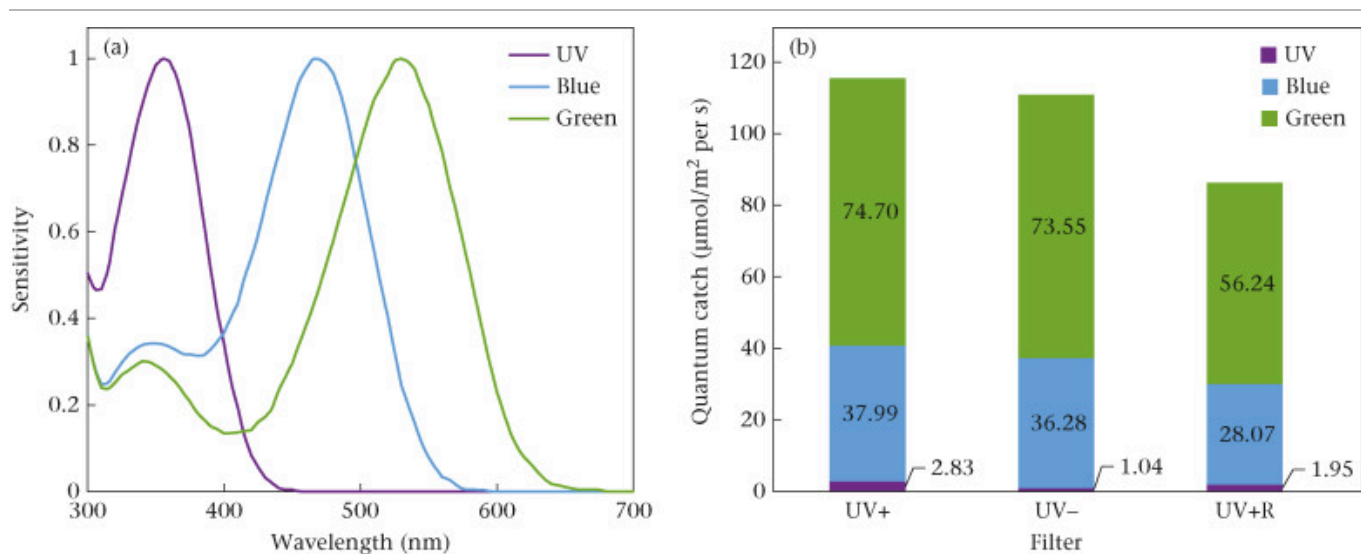
Figure 2. The calculated response of *V. cardui*'s photoreceptors to experimental illuminants. (a) Spectral sensitivity curves used for the three spectral types of photoreceptor cells (UV, blue, green) of *V. cardui*. Adapted with permission from Briscoe et al. (2003), copyright 2003 Wiley-Liss Inc. The CC license does not apply to this figure panel. (b) Calculated quantum catches for each spectral type of photoreceptor to each experimental light condition.

In our initial experiments we investigated behaviour under UV+ and UV− illumination, with the goal of understanding the effects of UV wavelengths on behaviour. Compared to UV− illumination, UV+ illumination elicited greater Q_{UV}, but it also elicited slightly greater Q_B and Q_G, and a slightly greater overall sum of quantum catches for all three photoreceptors (Fig. 2b). Thus, UV+ illumination included UV, but may also have been perceived by butterflies as slightly brighter across the spectrum. To determine whether butterfly behaviour was affected by the presence of UV or by brightness more generally, we subsequently compared behaviour under UV+R and UV− illumination. Compared to UV− illumination, UV+R illumination elicited greater Q_{UV}, but lesser Q_B, Q_G, and summed Q_i (Fig. 2 b). Thus, UV+R illumination was richer in UV specifically, but darker by all other photoreceptor metrics than UV− illumination. This meant that while a preference for UV+ over UV− might be due to UV specifically or perceived brightness more generally, a preference for UV+R over UV− would be indicative of a preference for UV wavelengths specifically because a preference for brightness would lead to UV− being preferred.

Behavioural Trials

We conducted three experiments in total, each using different combinations of the above illuminants in the two arena halves. In experiment 1, lighting was either UV+ or UV−, but lighting conditions were homogeneous with the same type of filter over both arena halves. In experiment 2 a lighting choice was provided, with UV+ in one arena half and UV− in the other. Experiment 3 also provided a lighting choice, but with UV+R in one arena half and UV− in the other. The rationale for this was that in experiment 2 UV+ illumination may have been preferred because it contained UV, or because it was perceived as brighter by other photoreceptor metrics (Fig. 2b). Thus, experiment 3 offered a choice of UV+R illumination which was richer in UV specifically, or UV− illumination that lacked UV but was brighter by the other photoreceptor metrics (Fig. 2b). Filters were randomly interchanged between arena sides between trials to prevent position effects.

We conducted 27 trials in experiment 1, with 12 butterflies experiencing UV− conditions and 15 experiencing UV+ conditions. We conducted 52 trials in experiment 2, and 24 trials in experiment 3, each on separate individual butterflies.

Each trial lasted for 600 s and began by placing the focal butterfly in the centre of the arena floor under a clear plastic pot (7 cm diameter base×7.5 cm height). Trials commenced when the pot was removed, and the butterfly was free to move within the arena. In each trial we recorded (1) the latency until a butterfly first moved, (2) the total time spent flying, (3) the total time spent alighted on the arena side or floor and actively moving (hereafter, 'active alighted'), and (4) the total time spent alighted on the arena side or floor and not moving (hereafter, 'inactive alighted'). For experiments 2 and 3 we also recorded (5) under which optical filter each behaviour was performed, and (6) the total time spent in any behaviour under each optical filter. Butterfly activity was recorded live by R.T.

Statistical Analyses

Statistical analyses were implemented using R version 4.3.1 (R Core Team, 2023). For most behavioural measurements we employed a hurdle-like approach to investigate (1) differences in the proportion of individuals that performed a behaviour under a particular circumstance (i.e. differences in the proportion of nonzero durations), followed by (2) differences in the duration of behaviour where it was performed (i.e. differences in the magnitude of nonzero durations). Our default approach was to employ generalized linear mixed models (GLMMs) implemented using glmmTMB (Brooks et al., 2017). In the case of (1), these models specified binomial distributions and logit link functions, and in the case of (2) they specified gamma distributions and log link functions since data were commonly positively skewed and zeroes had been removed following the first analysis step. The independent variable in all cases was 'lighting filter', and random intercepts for individual

were included for experiments 2 and 3 to account for paired data comprising measurements for the same individual in the two arena halves. We checked the fit of these models using DHARMa (Hartig, 2022). Fitting issues were sometimes identified for binomial-logit GLMMs where almost all individuals performed a behaviour, and in these cases we simply report the percentages involved (in no case did these models indicate a significant difference). Where fitting issues were identified for gamma-log GLMMs, we substituted a nonparametric approach. We used Mann–Whitney tests for the independent observations of experiment 1, and Wilcoxon signed-ranks tests for the paired observations of experiments 2 and 3. To analyse latencies we did not employ the hurdle-like approach since zero values had a different interpretation in that context. We compared latencies across the three experiments using Kruskal–Wallis tests. Where Kruskal–Wallis tests returned significant P values, Dunn's post hoc tests with Holm adjustment for multiple comparisons were performed using the FSA package (Ogle et al., 2023).

Ethical Note

Experiments were performed on a total of 103 adult *V. cardui*. Caterpillars were purchased from a supplier of classroom butterfly kits (Insect Lore, Cornwall, U.K.), and reared on a standard artificial diet used in that application. Each butterfly was subject to a single 600 s experimental trial. This work formed part of a Ph.D. project investigating multiple aspects of captive butterfly behaviour, so after experimental trials butterflies were not euthanized, but were transferred to mesh breeding cages (30–40 individuals per cage; cage dimensions: ca. 50×50 cm and 76 cm high), provided with a 20% sucrose solution ad libitum, and kept under the same lighting and temperature regime stated above. _Vanessa cardui_ is not protected under current U.K. legislation.

Results

Experiment 1: Butterfly Behaviour under UV+ and UV− Lighting

We first compared butterfly behaviour in homogeneous lighting environments that included or excluded UV wavelengths (see Fig. 3). There was no significant difference in latency to move between UV+ and UV− lighting environments (gamma-log GLMM: Wald χ^2_1 =0.014, P=0.907; Fig. 3a). Butterflies were equally likely to fly under each lighting environment: 87% (from a total of 15) butterflies flew under UV+ conditions and 83% (from a total of 12) flew under UV− conditions (binomial-logit GLMM: χ^2_1=0.059, P=0.809). Among those that did fly, there was no significant difference in the amount of time that they spent doing so between lighting conditions (gamma-log GLMM: Wald χ^2_1 =1.245, P=0.265; Fig. 3b).

Butterflies were equally likely to spend time active alighted under UV+ (87% of butterflies) and UV− conditions (83% of butterflies) (binomial-logit GLMM: Wald χ^2_1=0.059, P=0.809). Among those that spent time active alighted, the duration of this behaviour did not differ between lighting conditions (gamma-log GLMM: Wald χ^2_1=1.215, P=0.270; Fig. 3c). Butterflies were also equally likely to spend time inactive alighted under UV+ (87% of butterflies) and UV− conditions (67%) (binomial-logit GLMM: Wald χ^2_1=1.459, P=0.227). Among those that performed this behaviour, its duration was not significantly different between the two conditions (Mann–Whitney: W=42, P=0.500; Fig. 3d). Thus, we found no effects of homogeneous UV+ or UV− light environments on any aspect of butterfly movement behaviour.
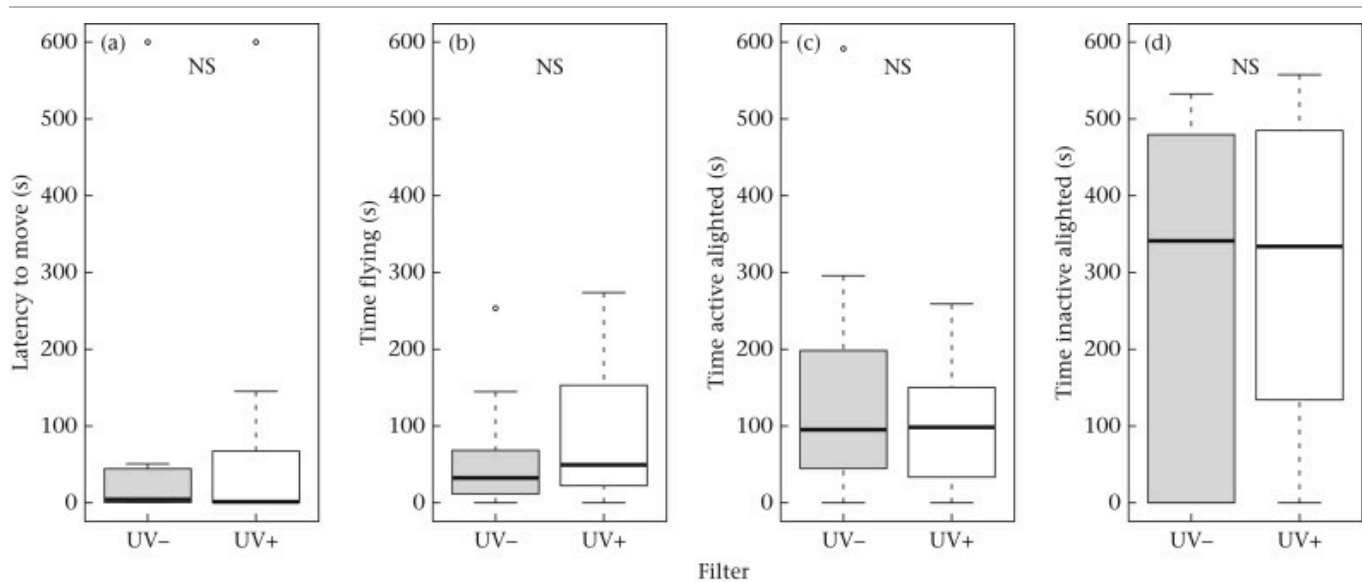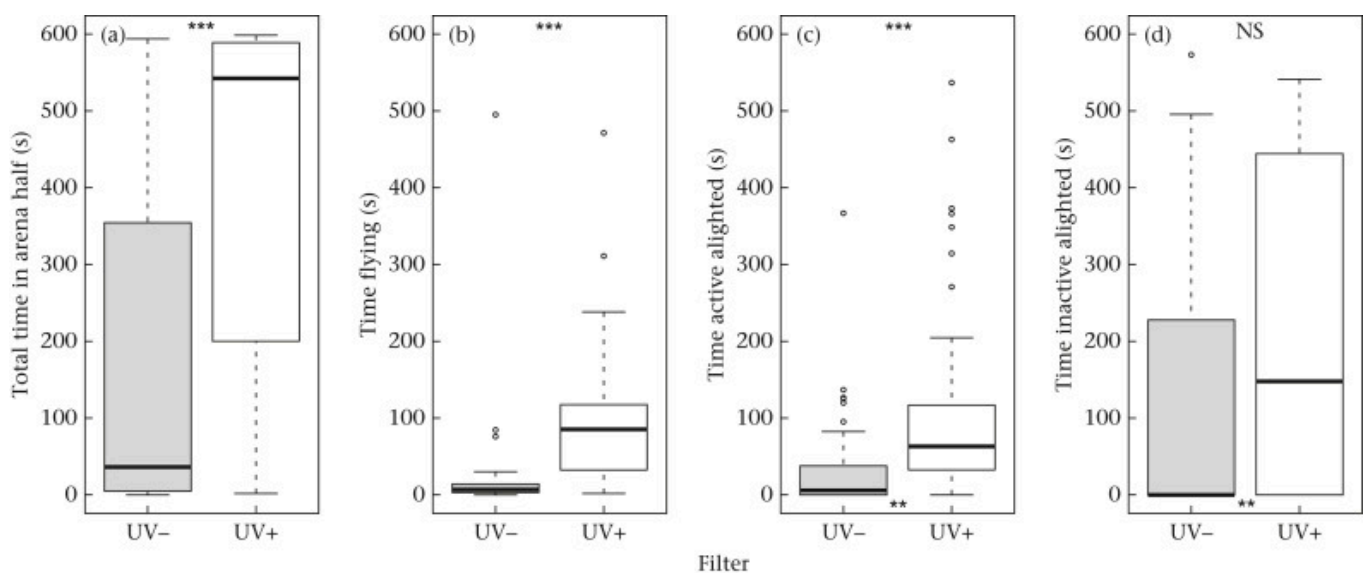

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Figure 3. Behaviour of *V. cardui* within homogeneous UV− and UV+ light environments. Box plots show (a) the latency to move, (b) the time spent flying, (c) the time spent active alighted and (d) the time spent inactive alighted during a 600s trial. Sample size is 12 individuals in the UV− group and 15 individuals in the UV+ group. Boxes indicate 25th, 50th and 75th percentiles, whiskers extend to the largest/smallest value within 1.5×IQR of the median, and more extreme observations are plotted as points. 'NS' refers to statistical analyses of both the proportion and magnitude of nonzero durations (see text for statistical tests).

Experiment 2: Do Butterflies Prefer UV+ or UV− Lighting?

We next investigated butterfly behaviour with a UV+ filter over one half of the arena and a UV− filter over the other (see Fig. 4). All 52 butterflies spent some time within the UV+ area, and 92% spent some time within the UV− area. Considering those butterflies that spent time within an arena area, a significantly greater amount of time was spent under UV+ than UV− (Wilcoxon signed-ranks test: $V=930$, $P<0.001$; Fig. 4a). All butterflies spent some time flying within the UV+ area, while 87% spent some time flying within the UV− area. Those that did fly within an arena area did so for a significantly greater duration within the UV+ area (gamma-log GLMM: Wald $\chi_1^2=106.210$, $P<0.001$; Fig. 4b). A significantly greater proportion of butterflies spent time active alighted within the UV+ (92%) compared to the UV− (63%) area (binomial-logit GLMM: Wald $\chi_1^2=10.560$, $P=0.001$), and those that performed this behaviour did so for significantly longer within the UV+ area (gamma-log GLMM: Wald χ_1^2 $=12.667$, $P<0.001$; Fig. 4c). Similarly, a significantly greater proportion of butterflies spent time inactive alighted within the UV+ (67% of butterflies) compared to the UV− (38%) area (binomial-logit GLMM: Wald $\chi_1^2=8.427$, $P=0.004$), but when this behaviour was performed its duration did not differ significantly between the two areas (Wilcoxon signed-ranks test: $V=26$, $P=0.922$; Fig. 4d). Therefore, butterflies tended to prefer the UV+ half of the arena and showed more activity in that area.

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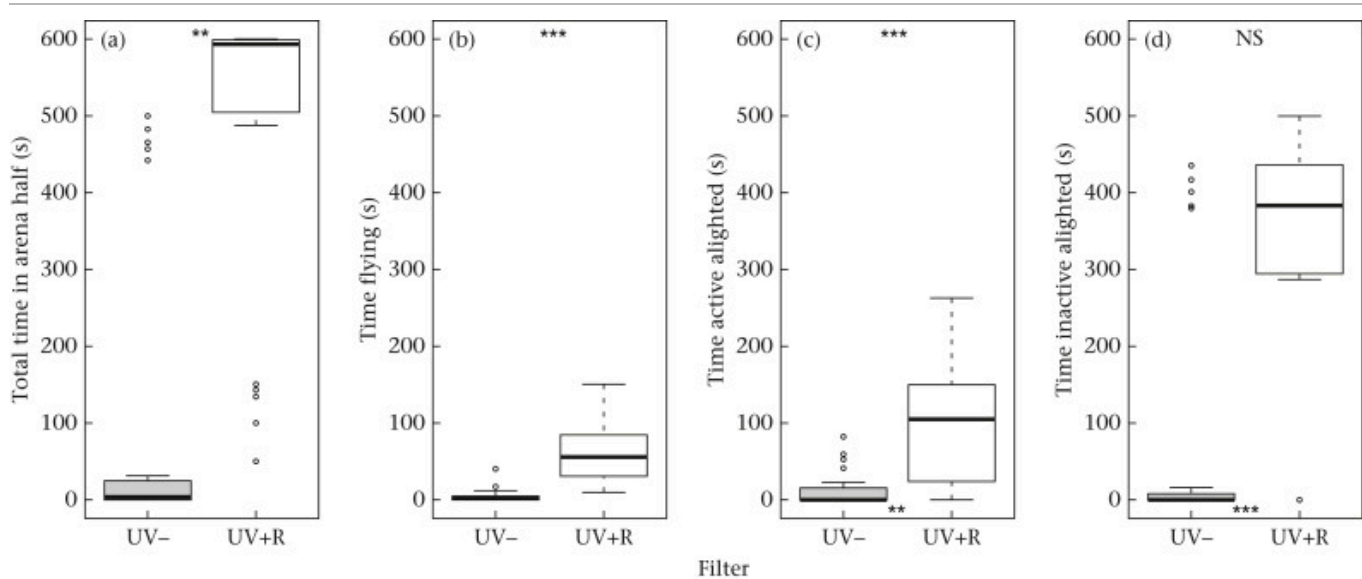Download: Download full-size image

Figure 4. Behaviour of *V. cardui* within a light environment comprising UV− and UV+ areas. Box plots show (a) the total time spent in each arena half, (b) the time spent flying, (c) the time spent active alighted and (d) the time spent inactive alighted during a 600s trial. Sample size is 52 individuals in total. Boxes indicate 25th, 50th and 75th percentiles, whiskers extend to the largest/smallest value within 1.5×IQR of the median, and more

extreme observations are plotted as points. Statistical analyses of the magnitude of nonzero durations are indicated above the box plots and the proportion of nonzero durations below them. $**P<0.01$; $***P<0.001$ (see text for statistical tests).

Experiment 3: Do Butterflies Prefer UV or Brightness Generally?

To identify whether butterflies were attracted to the UV content of UV+ illumination, or its brightness more generally, we observed behaviour with UV+R illumination (containing UV, but otherwise darker) in one arena half and UV− (lacking UV, but otherwise brighter) in the other (see Fig.2). All 24 butterflies spent some time within the UV+R area, and 71% spent some time within the UV− area. Among those that spent time within an arena area, significantly more time was spent within the UV+R area compared to the UV− area (Wilcoxon signed-ranks test: $V=138$, $P=0.002$; Fig.5a). All butterflies flew within the UV+R area, while 63% flew within the UV− area. Among those that did fly, the duration spent doing so was significantly greater within the UV+R than UV− area (gamma-log GLMM: Wald $\chi^2_1=76.034$, $P<0.001$; Fig.5b). Significantly more butterflies spent time active alighted within the UV+R area (88%) compared to the UV− area (46%) (binomial-logit GLMM: Wald $\chi^2_1=8.136$, $P=0.004$), and among those that performed this behaviour its duration was significantly greater under UV+R conditions (gamma-log GLMM: Wald $\chi^2_1=22.083$, $P<0.001$; Fig.5c). Similarly, significantly more butterflies spent time inactive alighted within the UV+R area (79%) compared to the UV− area (25%) (binomial-logit GLMM: Wald $\chi^2_1=12.472$, $P<0.001$), but when this behaviour was performed its duration was not significantly different between the two areas (Wilcoxon signed-ranks test: $V=1.000$, $P=1.000$; Fig.5d). Thus, butterflies showed a similar preference for UV+ areas as seen in experiment 2, even when the overall intensity of that illumination was less than that of the alternative UV− area.

Figure 5. Behaviour of *V. cardui* within a light environment comprising UV− and UV+R areas. Box plots show (a) the total time spent in each arena half, (b) the time spent flying, (c) the time spent active alighted and (d) the time spent inactive alighted during a 600 s trial. Sample size is 24 individuals in total. Boxes indicate 25th, 50th and 75th percentiles, whiskers extend to the largest/smallest value within 1.5×IQR of the median, and more extreme observations are plotted as points. Statistical analyses of the magnitude of nonzero durations are indicated above the box plots and the proportion of nonzero durations below them. $**P<0.01$; $***P<0.001$ (see text for statistical tests).

Comparison of Latency to Move across Experiments

Latency to move was occasionally zero in experiments 2 and 3 and, overall, latencies were significantly different across the three experiments (Kruskal–Wallis test: $\chi^2_2=10.946$, $P=0.004$). Latency to move in the two conditions of experiment 1 combined (median=4.08 s, interquartile range, IQR=48.75 s) was significantly greater than that in experiment 3 (median=0.00 s, IQR=2.14 s). The latency in experiment 2 (median=2.02 s, IQR=6.23 s) was not significantly different to that in experiments 1 or 3 (post hoc Dunn tests with Holm adjustment: $P<0.05$).

Discussion

In this study we investigated the behaviour of butterflies under UV− and UV+ light environments resembling those that might be found in captivity. The presence or absence of

UV in homogeneous lighting environments caused no effect on butterfly activity. However, when offered a choice between UV− and UV+ areas, butterflies showed a preference for the UV+ area, and were more active within that area. Because the preference for UV+ areas was evident even when the overall intensity of that light was less than in the UV− alternative, the preference was for UV wavelengths themselves and not for brightness in general. Since understanding what animals want is an issue central to providing for their welfare needs (Dawkins, 2003), our results provide new and valuable insight that can aid in the design of lighting environments for butterfly houses.

We found no effects of homogeneous UV− and UV+ lighting on time butterflies spent flying, alighted and active, or alighted and inactive. These findings are reminiscent of those for birds where evidence for the effects of homogeneous lighting regimes on behaviour has been variable. UV-deficient lighting conditions increased escape-like behaviour in starlings, _Sturnus vulgaris_, although this effect was masked by the initial stress of captivity (Maddocks et al., 2002), and domestic fowl, _Gallus gallus_ domesticus, reared under UV-augmented lighting showed significantly less fear-associated behaviour during handling (Sobotik et al., 2020). However, UV-deficient conditions caused only a nonsignificant reduction in exploratory behaviour in domestic fowl chicks (Maddocks et al., 2001), and had no effect on Japanese quail, _Coturnix japonica_, behaviour (Smith et al., 2005). In part, this variation might be attributable to context. In our study, the featureless arena provided no additional cues that might have motivated behaviour aside from lighting, so our observations were restricted to spontaneous activity. Since UV cues are used by Lepidoptera in intraspecific communication (Stella & Kleisner, 2022), and can be used by various taxa in foraging (Cronin & Bok, 2016), it is very likely that such behaviours that were beyond the remit of this study might be disrupted under UV-deficient lighting. The presence of such behavioural motivators might also expose differences in movement behaviour not seen in the current work.

When the light environment provided a UV+ and UV− area, butterflies spent more time overall in the UV+ area, and more time flying within that area. They were also more likely to alight in the UV+ area and spent more time in alighted activity within that area, although there was no difference in the duration of alighted inactivity between the two areas. In addition, butterflies' initial latency to move at the start of a trial was less under the lighting choice of experiment 3 than the homogeneous lighting of experiment 1. Thus, butterflies showed a clear preference for UV+ over UV− lighting. Again, these results are reminiscent of those for birds. When given a choice of UV-supplemented and UV-deficient lighting, bird species from high-light environments and circumpolar regions showed a preference for UV-supplemented lighting, and such lighting increased social behaviour in birds from patchy

light environments (Ross et al., 2013). However, where a similar preference was shown by European starlings, it was attributable to the overall brightness of the lighting regime rather than the presence of UV wavelengths themselves (Greenwood et al., 2002). In our study, butterflies showed a similar preference for UV+ and UV+R over UV− lighting. While UV+ was richer in UV and also brighter by other metrics than UV−, UV+R was richer in UV but darker by all other metrics than UV−. Therefore, butterflies showed a preference for UV and not overall light intensity.

One explanation for the behaviour of butterflies given a choice between UV− and UV+ lighting is that they displayed a simple phototactic response, since UV light is an important driver of such behaviour across insects including bees and flies (Yamaguchi & Heisenberg, 2011). During our experiments, butterflies often flew vigorously towards the lighting unit in the roof of the arena and sometimes zig-zagged back and forth beneath it, which would be consistent with such an explanation. Because sunlight is rich in UV wavelengths but most natural substrates reflect little UV, attraction towards UV light may relate to dispersal. Given that our experimental arena lacked food, shelter or conspecifics, the drive for butterflies to disperse may have been especially strong. However, butterflies were also significantly more likely to alight in the UV+ area, and showed more alighted activity in that area, which is consistent with a preference for the UV+ light environment itself. Since UV is important for a variety of natural behaviours including intra- and interspecific signalling (Stella & Kleisner, 2022), lighting environments containing UV may be attractive because they facilitate these discriminations (Obara et al., 2008).

Understanding what animals want is a key part of understanding their welfare needs (Dawkins, 2003). In that context, the clear preference of butterflies for UV+ environments alone suggests that these should be provided to captive butterflies to improve their welfare. Natural light environments vary between habitats, weather conditions, times of day and seasons (Endler, 1993; Nilsson et al., 2022), and properties of those light environments such as their spectral quality, and the vertical gradient of that spectral quality, may be important for the master control of behavioural states, providing the motivation to perform the right behaviour in the appropriate context (Nilsson et al., 2022). Furthermore, since reflected UV light enables intra- and interspecific signalling underlying courtship and foraging (Cronin & Bok, 2016; Stella & Kleisner, 2022), UV-augmented lighting might be expected to promote efficient foraging and reproduction. These effects would be expected to improve captive rearing, as demonstrated for black soldier flies, *Hermetia illucens*, where provision of UV-enriched lighting enhanced reproduction through significant increases in viable larvae (Oonincx et al., 2016).

Vanessa cardui is a common and widely distributed species often found in relatively open habitats. However, butterfly species vary in their habitat preferences (Seymoure, 2018), and heterogeneous lighting environments within butterfly houses may be essential to provide for the differing needs of the wide variety of species held and would result naturally from vegetation within the house (see Endler, 1993). However, insight from the current study can help to manage butterfly behaviour resulting from unintentional heterogeneity in lighting. For example, screening windows with UV− filters might prevent butterflies from resting inactive on window ledges where windows provide UV bright spots.

Overall, provision of UV-augmented lighting in butterfly houses has the potential to improve butterfly welfare, enhance captive breeding, and provide healthy and active specimens for the benefit of visitors.

Author Contributions

Rowan Thomas: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing – Original draft. **Alan Gay**: Methodology, Writing – review & editing. **Dylan Gwynn-Jones**: Conceptualization, Supervision, Writing – review & editing, Funding acquisition. **Natasha de Vere**: Conceptualization, Supervision, Writing – review & editing, Funding acquisition. **Roger Santer**: Conceptualization, Methodology, Formal analysis, Visualization, Supervision, Writing – review & Editing, Funding acquisition.

Data Availability

Behavioural data are provided as Supplementary material.

Declaration of Interest

At the time this work was conducted, N.d.V. was employed by the National Botanic Garden of Wales, which operated a butterfly house.

Acknowledgments

Supplementary Material

The following is the Supplementary material to this article:

⊞ Download: Download spreadsheet (20KB)

Multimedia component 1.

Recommended articles

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