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Surveying ultraviolet reflectance in moths: A method and workflow for data capture using open-source tools

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Abstract

Although moths are much more diverse members of the Lepidoptera compared with butterflies, there is a deficit of studies concerning their ultraviolet (UV) reflectance. The Natural History Museum, London (NHMUK), is re-curating its collection of moths occurring in the British Isles as part of the iCollections mass digitisation project. We captured UV images as an addition to the workflow. Through imaging entire drawers in UV and human-visible spectra and applying post-production methodology to standardise the images, we obtained objective and comparable UV reflectance values for 176 species in ten families, totalling 1,760 specimens. We show that usable imaging in UV above 360 nm is possible with conventional photographic equipment. UV reflectance metrics were calculated per species, and compared to usual flying time. Nocturnal species were found to reflect significantly more than diurnal.

We generated a corpus of data for UV and other morphological studies, without the need for additional expensive equipment. Scaling of the images provides for morphometric analysis. This method can be adopted as an additional module to digitisation workflows at NHMUK and other museums

Keywords: collections, digitisation, image processing, Lepidoptera, morphology, open-source software, photography, visual ecology

Introduction

The sensitivity of animals to ultraviolet (UV) light has been known since the time of Lubbock (1882), but the significance of patterns in animals has generally lagged well behind its study in plants, particularly flowers (Knuth, 1898; Chittka, et al., 1993). It was mainly pioneering studies in pierid butterflies, particularly *Gonepteryx* Leach, 1815 (Mazokhin-Porshnyakov, 1957), which highlighted its importance in animals. For example, UV reflectance has been used to resolve closely-related taxa, such as in *Gonepteryx* (Nekrutenko, 1964; Brunton, Russell and Majerus, 1996) and *Colias* Fabricius, 1807 genera (Ferris, 1973; Silberglied and Taylor, 1973; Silberglied and Taylor, 1978).

In butterflies, UV reflective patterns have also been shown to play a role in inter- and intraspecific communication: deterring predators, recognising

conspecifics, and for assessing the quality of mates (Silberglied, 1977). In *Colias eurytheme* Boisduval, 1852, male UV reflectance may be a key signal evaluated by females in assessing mate fitness, as strong reflectance is apparently due to environmental conditions in the male juvenile phase, which contribute to the production of nutritious ejaculate (Boggs and Watt, 1981).

Few studies have investigated moth UV patterns, despite many species being important pollinators and pests. A greater proportion of moths occupy these niches than butterflies within Lepidoptera, and yet butterflies have remained a main focus for UV investigations (Winfree, Bartomeus, and Cariveau, 2011). As for any other colour, interpretation of the UV reflectance as a signal depends on a complex interplay of physiological and environmental factors (Pecháček, et al., 2014). In the case of moths, such factors are, for example, their visual systems and anti-predator strategies, physical properties of reflected light (Johnsen, et al., 2006), the moths' flying and resting postures (Dennis and Shreeve, 1989; Briscoe, et al., 2003), and predator attack techniques (Olofsson, et al., 2013). Night vision also has low signal-to-noise ratios, and factors such as the speed of motion, direction of the stimulus, and chromatic and achromatic contrast are of great relevance (Cronin, et al., 2014; Zapletalová, et al., 2016).

The ongoing iCollections digitisation project (Paterson, et al., 2016) at the Natural History Museum, London (NHMUK) presented an opportunity to study UV reflectance. This project (in which authors EC and SL were involved) is digitising approximately one million specimens in the collection of British and Irish Lepidoptera. During digitisation, spatial, temporal,

and other data is captured at specimen level, providing the data keys which permit the development of a UV survey via digital photography. Recent advances in photography have overcome lighting and sensor variations (Stevens, et al., 2007), preventing artefacts that impede analysis. Sensor arrays provide information about entire areas more quickly than extensive point-sampling with spectrometers (Cuthill, et al., 1999; Endler and Mielke, 2005). Calibration techniques, as well as colourspace conversions to specific animal visual systems, are becoming easily available (Troscianko and Stevens, 2015). To use existing resources, we chose to acquire UV reflectance by photographing entire drawers at the time of digitisation – hence we sampled only species from the British and Irish fauna using a non-specialist but high-resolution camera. Even though such equipment is specifically designed to reduce UV sensitivity, it is our main purpose to show that useful results are still achievable.

Method

The moths examined are pinned specimens of the British and Irish collection of NHMUK, digitised by the iCollections project, with 176 species available at the time: in the Drepanidae Boisduval, 1828, Lasiocampidae Harris, 1841, Endromidae Boisduval, 1828, Saturniidae Boisduval, 1837, Sphingidae Latreille, 1802, Geometridae Leach, 1815, Notodontidae Stephens, 1829, Erebidae Leach, 1815, Noctuidae Latreille 1809 and Nolidae Bruand, 1846. Each drawer holds between 30 and 600 specimens, mounted with their wings open, normally showing the dorsal side; information labels and a Data Matrix barcode are pinned underneath. The drawers were placed next to a scale bar and colour chart and
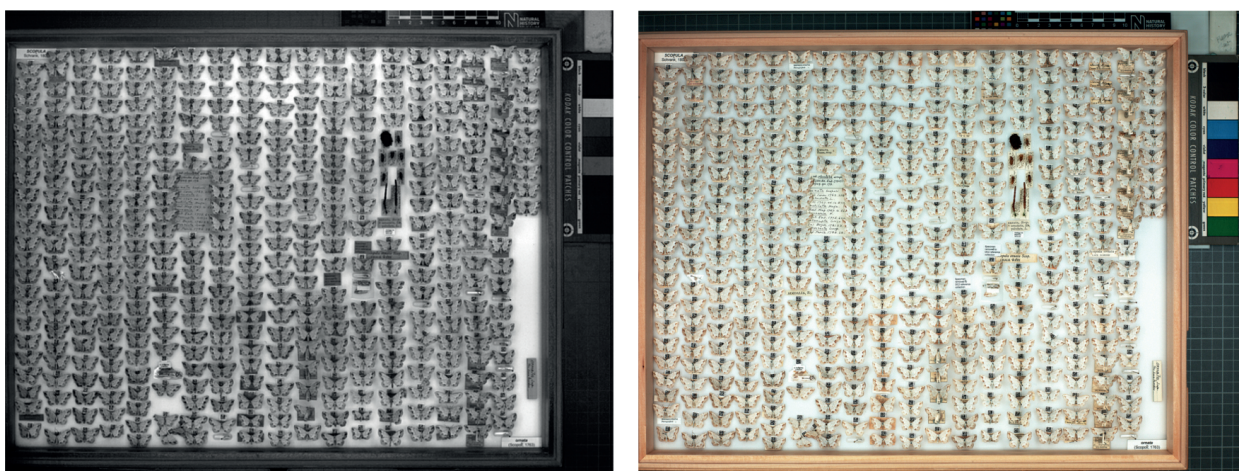

Figure 1: Drawer 70-021-1 (Scopula ornata) showing scales and colour chart in UV (left) and visible (right). Image: NHMUK, 2016.

imaged in batches, refocusing when the illumination was changed (Figure 1). Where a single species filled several drawers in the collection, we imaged only the first one.

Equipment

All the images were taken through Capture One software by a Phase One iXR camera fitted with a Mamiya LS 80mm *f*/2.8 D lens and a Phase One Credo 80 digital back, which has a Teledyne DALSA sensor (53.7 x 40.3 mm) with 5.2 x 5.2 µm pixels. UV images were taken at 50 ISO, *f*/12, 30 sec., and those in visible light at 50 ISO, *f*/12, ¼ sec. UV images were taken through a B+W 403 UV-pass filter.

The UV lighting consisted of four 18-inch T8 25 W fluorescent blacklight tubes with peak at 368 nm (Sylvania Black Light 368), arranged rectangularly. The visible illumination was a HerbScan lightbox (HerbScan Engineering) of 300 LEDs (HIDS4U, cool white, 60 LEDs per metre, nominally 72 W at 62.5 lm W^{-1}, before a white acrylic diffuser). The UV lighting was fitted inside the visible lighting system, and both lit the drawer evenly from directly above.

The overall system spectrum peaks at 375 nm and spans 361-392 nm (10%), with smaller 'leakage' spikes at 405 and 435 nm (Figure 2).
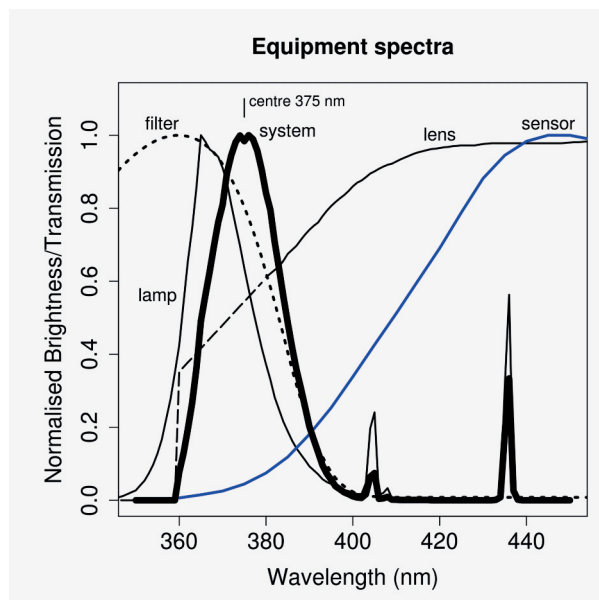

Figure 2. Spectra for lamp emission, filter and lens transmission, and sensor sensitivity, from their respective manufacturers' data. Lens transmission for 360-380 nm is an estimate, extrapolated from the 380-400 nm segment. The thick black line represents the calculated overall estimated system spectrum for the UVA-blue region.

Control images were taken to ensure we captured UV wavelengths: a) samples of aluminium (kitchen foil, polished side), which reflects both visible and UV light (Coblentz and Stair, 1929), and zinc oxide (dental grade powder), which reflects visible light and absorbs UV (Rodnyi and Khodyuk, 2011) (Figure 3); and b) two male specimens of the butterfly *Gonepteryx rhamni rhamni* (Linnaeus, 1758), for visual proof-of-concept comparison with existing studies (Pecháček, *et al.*, 2014) (Figure 4). We also imaged a standard Stemmer A3 test chart.

Image and metadata capture

We used web forms to capture the drawer identification and illumination type, matching these to the captured images through the image and form submission time stamps. This avoided the need to use expensive proprietary software, and made the capture process streamlined.

All the images were captured in the camera's proprietary lossless raw format 'IIQ Large' with accompanying XML metadata ('COS') file. We converted these to an appropriate lossless PNG format for maximum portability, subsequently processing with standard tools (Imagemagick `convert`) and a small number of custom functions, detailed below. Data is kept in an SQL database (MariaDB).

Scaling and noise reduction

The visible light images were converted into linear 16-bit PNG format (`dcraw -4`), and we manually marked a number of control positions: the inside corners of the drawer, and the colour chart registration marks. The white balance was set from the colour chart with matrix colour transformation (`convert -recolor`).

The portion of the image inside the drawer (471 x 361 mm) was then transformed by perspective correction into an image of 9600 x 7360 pixels (`convert -perspective`). Allowing for vertical variation in the positioning of the specimen, this gives a linear scale of 0.05 mm pixel^{-1} ±2%.

The UV images required special treatment. The sensor used, as in most colour digital cameras, has a Bayer filter over a panchromatic sensor. Our images were taken under very low light conditions, and showed considerable salt and pepper noise, defined as highly deviant single pixel bright and dark values on the underlying sensor, normally spread over multiple
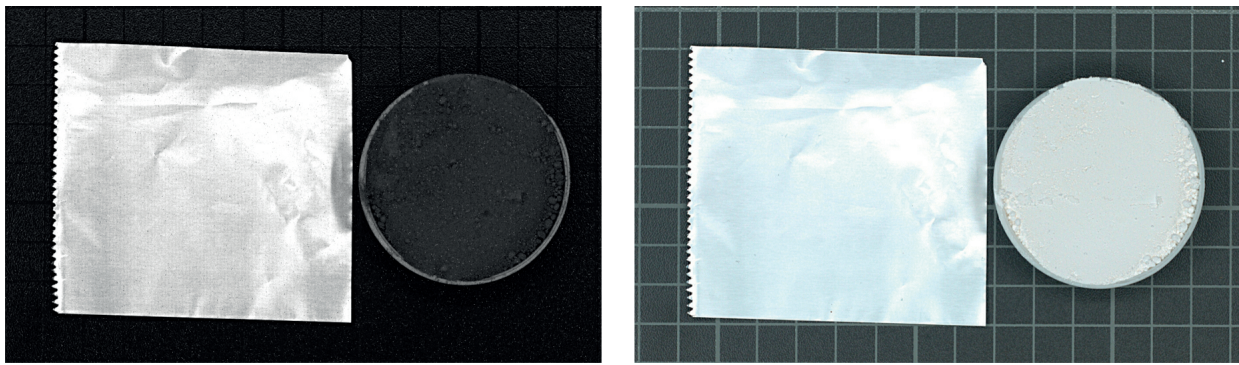
Figure 3: Control images of the aluminium foil (square) and zinc oxide (round) under UV (left) and visible (right) illumination. Note that the zinc oxide is dark under UV and white under visible light. Image: NHMUK, 2016.

Figure 4: Control images of male Gonepteryx rhamni rhamni under UV (left) and visible light (right). Note the bright UV patches on the forewings, corresponding to Pecháček, et al. (2014). Image: NHMUK, 2016.

pixels during demosaicing, and only the blue-filter pixels provided useful results under UV illumination. Our principal reflectance measurement was quantile-based; it was unaffected by pepper noise, which was therefore ignored. The raw IIQ files were converted to linear 16-bit PNG files without any colour interpolation (`dcraw -D`), and the blue-filter pixels extracted to give a half-width, half-height image, corrected for noise (custom programs `debayer` and `denoise`). This latter is a simple decision-based median filter (Astola and Kuosmanen, 1997), where each pixel is replaced by the median of its eight neighbours if its value exceeds the largest neighbour by p standard deviations of the neighbours, or an absolute q; this second condition being required for many very dark regions where the neighbour pixels have identical value. We used $p = 1.5$ and $q = 5.0$, which identified 1.9% of the pixels as salt noise. Figure 5 shows a portion of the aluminium control image, where the three shaded pixels were replaced by the median of their neighbours. Finally, images were level-converted to give densities of 20% and 80% to the black and white patches of the colour

chart, and scaled to 4800 x 3680 pixels, giving a scale of 0.1 mm pixel^{-1} ±2%.

Specimen extraction and processing

For each drawer, we generated ten coordinates at random and manually selected the nearest specimens which had a) unobscured barcodes, b) were not artificially bred, and c) were not visibly damaged. As the specimens are densely positioned in columns and are of the same species, bias towards larger specimens was considered negligible. Their barcodes were read (79% with dmtxread, remainder manual) and stored.

Attempts to use computer vision (OpenCV) for image segmentation were unsuccessful because: a) the specimens often overlapped a barcode, labels, or other specimen, b) lighting artefacts obscured specimen edges, and c) the background polyethylene foam material (Plastazote) is UV-reflecting. We therefore created mask files manually by drawing outlines over multilayer SVG files (Inkscape), allocated at random to several technicians who were instructed

Figure 5: Salt noise filtering detail with values from centre of aluminium sample, as 16-bit integers, before (left) and after (right) filtering. A decision-based median filter was used to reduce this noise: shaded values are much brighter than their eight neighbours, and thus considered as noise and replaced: eg pixel value 7032 > max(neighbours)+sd(neighbours)*1.5, so it is replaced by the higher of the central two values (as proxy for median) of the neighbours, 6541.

to err on the side of omitting portions of the specimen. This process was the most time-consuming, with an average of 10.4 minutes per specimen, in contrast to 16 minutes per drawer for imaging.

Specimen pixels were normalised to floating point in (0, 1) for statistical processing in R, producing values for each specimen: mean, standard deviation, and each centile. In order to disregard patterning, we wished to allocate the same reflectance value to species which have highly-reflective patches as those with high reflectivity overall. We therefore chose the 75th percentile brightness value as our principal metric of reflectance, *R*. The value for a species is simply the mean of the values for the specimens.

Results

Survey

This dataset comprises species belonging to ten families with varying species richness (Table 1). The reflectance quantified with this method is summarised in Table 2 (see Appendix I). Three species of varying reflectance are shown in Figure 6. The brightest species are *Euproctis similis* (Fuessly, 1775), *Scopula ornata* (Scopoli, 1763), *Jodis lactearia* (Linnaeus, 1758), *Euproctis chrysorrhoea* (Linnaeus, 1758), *Leucoma salicis* (Linnaeus, 1758), *Idaea*

subsericeata (Haworth, 1809), *Utetheisa pulchella* (Linnaeus, 1758), *Cilix glaucata* (Scopoli, 1763), *Lithostege griseata* (Denis & Schiffmüller, 1775), *Nola aerugula* (Hübner, 1793), and *Cosmorhoe ocellata (Linnaeus, 1758)*. These are strictly nocturnal species, with the exception of *U. pulchella,* which is both diurnal and nocturnal. Five of these top reflective species belong to the Geometridae and four to the Erebidae, both nocturnal pollinators (Winfree, Bartomeus and Cariveau, 2011; LeCroy, Shew and VanZandt, 2013). The other two known nocturnal pollinator families, Noctuidae and Sphingidae (Winfree, et al., 2011; LeCroy, et al., 2013) were amongst the lowest reflectance, but were also poorly represented in this dataset: *Diloba caeruleocephala* (Linnaeus, 1758) was the only species representing Noctuidae and only five species represented Sphingidae of the 18 species present in UK. Moreover, one of these five species, *Hemaris fuciformis* (Linnaeus, 1758), has partially transparent wings and *Macroglossum stellatarum* (Linnaeus, 1758) is a diurnal species.

UV reflectance and activity time

We compared the relationship between UV reflectance and usual flying time of the species (Figure 7). We excluded those species where females and males differ in the time of daily activity or where one

Table 1: The families and numbers of species in the survey (total is as given as present in the British Isles in Agassiz et al., 2013).

Family	Surveyed	Total	Coverage (%)
Drepanidae	11	16	68.8
Lasiocampidae	6	12	50.0
Endromidae	1	1	100.0
Saturniidae	1	1	100.0
Sphingidae	5	18	27.8
Geometridae	109	307	35.5
Notodontidae	13	29	44.8
Erebidae	20	88	22.7
Noctuidae	1	368	0.30
Nolidae	9	12	75.0
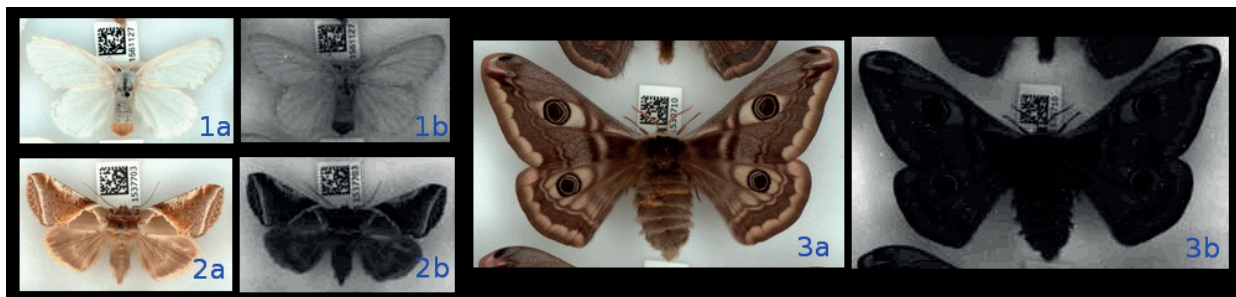
Figure 6: Images in visible light and UV respectively of Euproctis similis, BMNH(E)1561127, 1a and b, Habrosyne pyritoides (Hufnagel, 1766), BMNH(E)1537703, 2a and b, and Saturnia pavonia (Linnaeus, 1758), BMNH(E)1530710, 3a and b, selected as most, medium and low UV reflectant species. Images: NHMUK, 2016.

or both sexes fly both in day and night time (Townsend and Waring, 2011; Newland et al., 2013; UKMoths, n.d.), species for which activity time could not be found, and subspecies. We see that in our sample, the strictly nocturnal species are more reflective of UV, and also much more numerous ($n =$ 126) than the strictly diurnal ($n = 10$).

An independent samples Welch's *t*-test was performed, to compare the UV reflectance value of diurnal and nocturnal species. There was a significant difference in the reflectance of diurnal species ($m =$ 0.255, $sd = 0.066$) and nocturnal species ($m = 0.381$, $sd = 0.113$); $t(13.7) = -5.45$, $p<0.001$, which is significant at the 0.1% level.
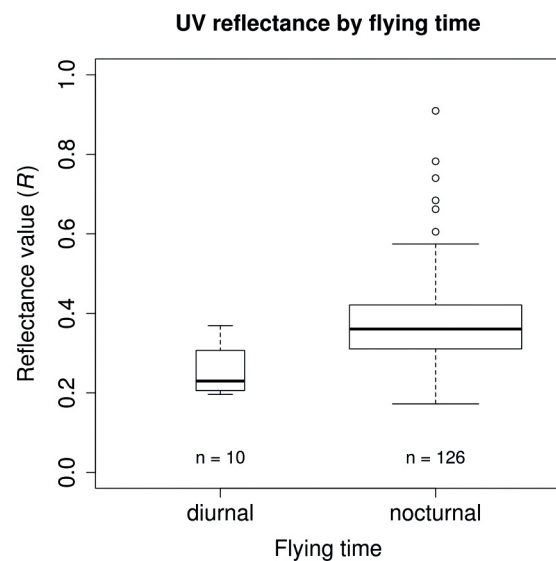
Figure 7: UV reflectance by flying time of strictly diurnal and strictly nocturnal species.

Discussion

The methodology presented in this paper resulted in two major outputs: the survey of a phenotypical character (UV reflectance) in a group of invertebrates (Lepidoptera) where its taxonomic distribution has been largely unknown, and the establishment of a workflow for exploiting digitised collections for the purposes of large-scale morphological surveys.

The quantification of reflectances presented in Table 2 (see Appendix I) adds to knowledge of wing reflectance in these species, which is potentially useful for morphologically-based systematics and for behavioural studies.

Specimen barcodes can be used to link the UV reflectivity of individual specimens to spatial, temporal and other collecting information captured during digitisation at NHMUK. This information will allow correlations between reflectance and possible distribution patterns across the UK, such as perhaps latitude, or, as in Brooks, et al. (2016), correlation with meteorological data for monitoring phenological changes of butterflies. Reflectance gradients could correspond geographically to abiotic factors, such as the amount of UV radiation reaching the land surface at given times of year (Herman, et al., 1999).

We found that, in the species we surveyed, UV reflectance is generally higher in nocturnal than diurnal species, which is consistent with a study of Finnish moths (Lyytinen, et al., 2004).

Detailed interpretation of these values is beyond the scope of the current survey, and needs to take into account many factors involved in intra- and interspecific communication. We nevertheless attempt to provide a basic context to some of the results.

Interspecific communication

The portion of the UV spectrum we studied corresponds in general to the visual range of passerine birds (Cuthill, et al., 2000; Lind, et al., 2014), which are expected to predate diurnal and crepuscular moths. Notably, in our dataset, the exclusively-diurnal species (10 geometrid species plus the sphingid *Macroglossum stellatum*) have similar levels of reflectance, significantly lower than nocturnal species. In human vision, these diurnal species have very dull colours that are presumably useful as camouflage to a range of vertebrates. It is difficult to speculate on the role of UV reflectance as a defence mechanism in nocturnal moths, as few potential nocturnal predators are known to have night vision. Rodents are apparently the only nocturnal group with UV vision (Jacobs, et al., 1991), with bats relying on echolocation and birds of prey on acoustic cues at night (Honkavaara, et al., 2002). UV perception is not necessarily concomitant with colour vision: some owls and bats (Winter et al., 2003) apparently perceive UV achromatically in low light (Parejo, et al., 2010). The nightjar *Caprimulgus europaeus* Linnaeus, 1758 may use the same mechanism in deep crepuscular and nocturnal hunting of moths (Sierro, et al., 2001).

Intraspecific signals

Signalling using markings only differentiated in UV has been demonstrated in *Heliconius* Kluk, 1780 butterflies (Bybee, et al., 2011), and perhaps this is the case for *D. elpenor* (Linnaeus, 1758) (Figure 8). This species shows UV-reflective patches corresponding to only some of its pink markings. It has UV-blue-green trichromatic vision (Schwemer and Paulsen, 1973; Kelber, et al., 2002; Kelber and Roth, 2006), with peaks at 345 nm, 440 nm, and 520 nm (Hamdorf, et al., 1971; Schlecht, 1979; Schwemer and Paulsen, 1973). Johnsen, et al. (2006) show that longer wavelengths
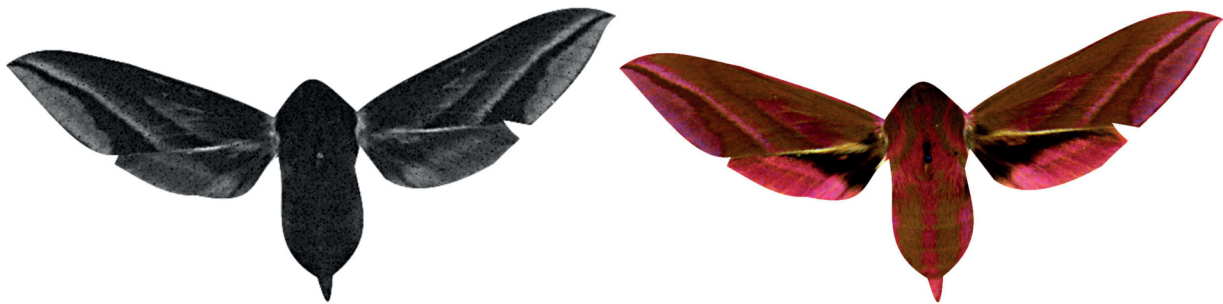

Figure 8: Deilephila elpenor, specimen BMNH(E)1640207, showing UV reflectance (left) corresponding to pink portions of the wing (right) but not body stripes. Images: NHMUK, 2016.

become relatively more visible during moonlight and starlight.

The 12 dimorphic species surveyed, six of which are apterous, reflected a moderate to low amount of UV, and did not show any significant correlation relating the reflectance either with the sex, nor the fact that they are wingless.

Many of the species surveyed here exhibited a moderately low UV reflectance, which nonetheless may play a considerable role. It is known that some moths can be very sensitive to small UV signals, as some species are lured to the webs of orb spiders which have minute UV-reflective spots (Chuang, et al., 2008; Blamires, et al., 2012).

We observed apparent differences in UV reflectance in the green colouration in Geometridae versus Nolidae. The pigmentary green of the geometrid subgroup emeralds (Cook, et al., 1994) is known to fade after emergence in three of the five species we examined (*Pseudoterpna pruinata atropunctaria*, *Jodis lactearia,* and *Hemithea aestivaria)* but not *Geometra papilionaria* or *Comibaena bajularia*, and in fact, after many years, colour is still vivid in the specimens of the latter. All these five species have moderately high UV reflectance, and *J. lactearia* was the third most reflective species in the entire dataset. In the Nolidae, we surveyed three green species: *Earias chlorana*, *Bena bicolorana* and *Pseudoips prasinana britannica*. Remarkably little is known about the green colouration in this family, but it seems to be produced by pigments, as in the case of the Emeralds, but of different chemical composition (Ford, 1972), and fading is unreported. In this survey, nolids reflected considerably less UV than the emeralds.

If the individuals in these species can distinguish UV, blue, and green, as shown in other moths (Briscoe and Chittka, 2001), being UV- and/or green-reflective might function as an intraspecific signal. Furthermore, considering that *J. lactearia* is even more UV-reflective after losing its green colouration, the green pigments may actually mask some physically UV-reflective structure, and the fact that these species lose the colour at different rates may even mediate different interspecific signalling.

Light directionality is a potential concern, because it is known that the structural colour which generates the UV reflectance can be angle-dependent (Nekrutenko, 1964; Ghiradella, et al., 1972; Kemp, 2006). Specimens have uncontrolled orientation: we

note in this respect the review of Kemp and Rutowski (2011), in which they described the presentation of iridescent patterns on the nymphalid and pierid male butterfly dorsal surface "*via highly ritualised aerial courtship routines*", with orientation clearly significant for signalling.

Considerations for assessing UV reflectance in museum collections

To qualify our results, it is important to understand some characteristics of the underlying collection. The British and Irish Lepidoptera collection at NHMUK originates from an amalgamation of donated collections of both wild-trapped and captive-bred moths and butterflies, collected between approximately the 1880s and 1970s. Some of the captive-bred specimens in particular were labelled as aberrations, a rank of no current taxonomic standing used by collectors attempting to describe polymorphism (Salmon, et al., 2000). These were often the result of experiments and so not relevant for systematic and ecological studies. There is also some bias towards rare forms in the wild-trapped specimens, and collecting methods and sampling effort vary substantially between collectors, some being caught using UV light traps, whilst others were netted or, more recently, attracted with pheromones. Brooks, et al. (2016) found that in the butterfly species of this collection, there is a geographical bias towards the South East of England: the same is not yet reported for the moth collection, but may well exist. A final point regarding colouration is variation in killing and preserving chemicals, some of which are known to alter pigment colours (Martin, 1977). In the case of UV reflectance, which is structurally produced, we might be concerned with naphthalene, which is UV-absorbing, and paradichlorobenzene, which is reported to re-crystallise on specimen wings when used in excess (Martin, 1977).

Conclusions

Museum collections and digital photography offer the opportunity to survey morphology rapidly and on a large scale. Our survey concentrates on a feature that is intrinsically difficult to detect and to interpret in its ecological role. Standardisation of images nowadays confers a great degree of freedom in capturing and analysing colour traits. UV reflectance has been generally neglected because of these difficulties, despite being, in nature, just another colour and significant to many animals and plants. We hope that this survey will support future work on validation of species reflectance, live observation of UV display, and

also encourage museums to investigate this trait in their collections and link it to geographical, temporal, and ecological factors.

Data accessibility

Image data, database tables, scripts and program source code are available through NHMUK entry DOI: 10.5519/0019732.

Equipment suppliers

Mamiya Leaf: Mamiya Phase One iXR camera
http://www.mamiyaleaf.com/ixr.html

with Schneider Kreuznach 80 mm LS f2.8 lens
http://www.mamiyaleaf.com/lenses.html
https://captureintegration.com/schneider-ls-lens-mtf-charts-for-phase-one-mamiya/

and Credo 80 back
http://www.mamiyaleaf.com/credo.html

Teledyne DALSA sensor: spectra as given in the datasheets for the slightly smaller FTF9168C
https://www.teledynedalsa.com/public/sensors/datasheets/FTF9168C_datasheet_20130530.pdf

Schneider: B+W 403 filter
http://www.schneiderkreuznach.com/fileadmin/user_upload/bu_photo_imaging/fotofilter/Produktfinder/Infos/B_W_Filter_Info_Transmission_403_UV-Pass.pdf

Sylvania: F25W 18-in. T8 BL368 Toughcoat UV-A lamps
Blacklight brochure 2013. Havells Sylvania Belgium B.V.B.A.

HerbScan lightbox
25 Fairway, Chertsey, KT16 8EB, herbscan@mac.com

Stemmer Imaging: test chart
http://www.stemmer-imaging.co.uk/en/knowledge-base/test-chart

Kodak Color Control Patches
http://motion.kodak.com/IN/en/motion/Products/Lab_And_Post_Production/Control_Tools/KODAK_Color_Separation_Guides_and_Gray_Scales/default.htm

Software

Phase One: Proprietary RAW format
http://help.phaseone.com/en/CO7/Output/File-formats/Capture-One-and-RAW.aspx

DCRAW: image conversion software version 9.26
http://www.cybercom.net/~dcoffin/dcraw

DMTXREAD: Datamatrix barcode decoder version 0.7.4 (with libdmtx version 0.7.4)
http://libdmtx.sourceforge.net

Imagemagick: conversion software version 6.7.7-10
http://www.imagemagick.org

Inkscape: vector drawing package version 0.91
http://www.inkscape.org

MariaDB: server version 10.0.17, client version 5.5.46
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Appendix I

Table 2: UV reflectance by species and grouped by family, the brightest ten species in bold: species names are as printed in the drawers. **Drawer** *gives NHMUK drawer number;* **n**, *number of specimens examined;* **R**, *UV reflectance values;* **Night** *and* **Day**, *time of day activity specified by sex;* **Notes: d**=*dimorphic and* **a**=*apterous (Townsend and Waring, 2011; Newland et al., 2013; UKMoths, n.d.). Dimorphic species are reported separately for each sex with the exception of Pseudoips prasinana britannica (Warren, 1913) which is dimorphic, but the sexes were indistinguishable in our specimens.*

Taxon	Drawer	n	R	Night	Day	Note
Drepanidae						
Watsonalla cultraria (Fabricius, 1775)	65-003/1	10	0.28	mf	m	
Drepana falcataria (Linnaeus, 1758)	65-005/1	10	0.29	mf		
Sabra harpagula (Esper, 1786)	65-006/1	10	0.29	mf		
Cilix glaucata (Scopoli, 1763)	65-007/1	10	**0.56**	mf		
Thyatira batis (Linnaeus, 1758)	65-008/1	10	0.38	mf		
Habrosyne pyritoides (Hufnagel, 1766)	65-009/1	10	0.35	mf		
Tethea ocularis octogesimea (Hübner, 1786)	65-010/1	10	0.32	mf		
Tetheella fluctuosa (Hübner, [1803])	65-012/1	10	0.45	mf		
Ochropacha duplaris (Linnaeus, 1761)	65-013/1	10	0.35	mf		
Cymatophorina diluta hartwiegi (Reisser, 1927)	65-014/1	10	0.41	mf		
Polyploca ridens (Fabricius, 1787)	65-015/1	10	0.38	mf		
Lasiocampidae						
Trichiura crataegi (Linnaeus, 1758)	66-002/1	10	0.35	mf		
Eriogaster lanestris (Linnaeus, 1758)	66-005/1	10	0.32	mf	m	
Lasiocampa trifolii flava Chalmers-Hunt, 1962	66-006/1	10	0.28			
Lasiocampa quercus quercus (Linnaeus, 1758)	66-007/1	10	0.22			
Macrothylacia rubi (Linnaeus, 1758) m	66-008/1	2	0.21	m	m	d
Macrothylacia rubi (Linnaeus, 1758) f	66-008/1	8	0.29	f		d
Euthrix potatoria (Linnaeus, 1758) m	66-010/1	6	0.24	m		d
Euthrix potatoria (Linnaeus, 1758) f	66-010/1	4	0.26	f		d
Endromidae						
Endromis versicolora (Linnaeus, 1758) m	67-001/1	5	0.22	m	m	d
Endromis versicolora (Linnaeus, 1758) f	67-001/1	5	0.32	f		d
Saturniidae						
Saturnia pavonia (Linnaeus, 1758) m	68-001/1	4	0.21		m	d
Saturnia pavonia (Linnaeus, 1758) f	68-001/1	6	0.25	f		d
Sphingidae						
Mimas tiliae (Linnaeus, 1758)	69-001/1	10	0.22	mf		
Hemaris fuciformis (Linnaeus, 1758)	69-009/1	10	0.32		mf	
Macroglossum stellatarum (Linnaeus, 1758)	69-010/1	10	0.23		mf	
Deilephila elpenor (Linnaeus, 1758)	69-016/1	10	0.25	mf		
Deilephila porcellus (Linnaeus, 1758)	69-017/1	10	0.21	mf		
Geometridae						
Idaea muricata (Hufnagel, 1767)	70-002/1	10	0.32	mf		
Idaea fuscovenosa (Goeze, 1781)	70-006/1	10	**0.51**	mf		
Idaea subsericeata (Haworth, 1809)	70-009/1	10	**0.59**	mf		
Idaea aversata (Linnaeus, 1758)	70-016/1	10	0.29	mf		
Scopula ornata (Scopoli, 1763)	70-021/1	10	**0.79**	mf		
Scopula rubiginata (Hufnagel, 1767)	70-022/1	10	0.24	mf		
Scopula imitaria (Hübner, [1799])	70-024/1	10	0.33	mf		
Timandra comae Schmidt, 1931	70-029/1	10	0.36	mf		
Cyclophora pendularia (Clerck, 1759)	70-030/1	10	0.35	mf		
Cyclophora annularia (Fabricius, 1775)	70-031/1	10	0.39	mf		
Cyclophora albipunctata (Hufnagel, 1767)	70-032/1	10	0.39	mf		
Cyclophora puppillaria (Hübner, [1799])	70-033/1	10	0.26	mf		
Cyclophora punctaria (Linnaeus, 1758)	70-036/1	10	0.3	mf		

Taxon	Drawer	n	R	Night	Day	Note
Cyclophora linearia (Hübner, [1799])	70-037/1	10	0.3	mf		
Rhodometra sacraria (Linnaeus, 1767)	70-038/1	10	0.39	mf		
Scotopteryx luridata plumbaria (Fabricius, 1775)	70-041/1	10	0.38	mf		
Xanthorhoe decoloraria decoloraria (Esper, [1806])	70-048/1	10	0.37	mf		
Xanthorhoe decoloraria hethlandica (Prout, 1901)	70-048/2	10	0.3	mf		
Xanthorhoe fluctuata fluctuata (Linnaeus, 1758)	70-049/1	10	0.41			
Xanthorhoe spadicearia ([Denis & Schiffermüller], 1775)	70-051/1	10	0.29	mf		
Xanthorhoe quadrifasiata (Clerck, 1759)	70-055/1	10	0.26	mf		
Catarhoe cuculata (Hufnagel, 1767)	70-056/1	10	0.41	mf		
Epirrhoe tristata (Linnaeus, 1758)	70-060/1	10	0.36		mf	
Euphyia biangulata (Haworth, 1809)	70-064/1	10	0.38	mf		
Mesoleuca albicillata (Linnaeus, 1758)	70-068/1	10	**0.53**	mf		
Entephria flavicinctata ruficinctata (Guenée, 1858)	70-071/1	10	0.41	mf		
Entephria caesiata ([Denis & Schiffermüller], 1775)	70-072/1	10	0.41	mf		
Entephria caesiata hethlandicaria (Bang-Haas, 1910)	70-072/2	10	0.37			
Entephria caesiata caesiata ([Denis & Schiffermüller], 1775)	70-072/3	10	0.42			
Hydriomena impluviata ([Denis & Schiffermüller], 1775)	70-075/1	10	0.31	mf		
Thera obeliscata (Hübner, [1787])	70-081/1	10	0.34	mf		
Cidaria fulvata (Forster, 1771)	70-085/1	10	0.39	mf		
Cosmorhoe ocellata (Linnaeus, 1758)	70-087/1	10	**0.54**	mf		
Eustroma reticulata ([Denis & Schiffermüller], 1775)	70-088/1	10	0.36	mf		
Eulithis prunata (Linnaeus, 1758)	70-089/1	10	0.37	mf		
Eulithis testata (Linnaeus, 1761)	70-090/1	10	0.35	mf		
Eulithis populata (Linnaeus, 1758)	70-091/1	10	0.33	mf		
Eulithis mellinata (Fabricius, 1787)	70-092/1	10	0.45	mf		
Ecliptopera silaceata ([Denis & Schiffermüller], 1775)	70-094/1	10	0.37	mf		
Dysstroma citrata citrata (Linnaeus, 1761)	70-098/1	10	0.38			
Colostygia pectinataria (Knoch, 1781)	70-100/1	10	0.41	mf		
Operophtera fagata (Scharfenberg, 1805) m	70-105/1	5	0.48	m		da
Operophtera fagata (Scharfenberg, 1805) f	70-105/1	5	0.3			da
Operophtera brumata (Linnaeus, 1758) m	70-106/1	5	0.39	m		da
Operophtera brumata (Linnaeus, 1758) f	70-106/1	5	0.25			da
Epirrita dilutata ([Denis & Schiffermüller], 1775)	70-107/1	10	0.46	mf		
Epirrita autumnata (Borkhausen, 1794)	70-109/1	10	0.46	mf		
Hydrelia flammeolaria (Hufnagel, 1767)	70-114/1	10	0.34	mf		
Rheumaptera hastata hastata (Linnaeus, 1758)	70-120/1	10	0.27		mf	
Hydria undulata (Linnaeus, 1758)	70-121/1	10	0.33	mf		
Hydria cervinalis (Scopoli, 1763)	70-122/1	10	0.28	mf		
Horisme vitalbata ([Denis & Schiffermüller], 1775)	70-126/1	10	0.34	mf		
Odezia atrata (Linnaeus, 1758)	70-130/1	10	0.2		mf	
Perizoma affinitata (Stephens, 1831)	70-132/1	10	0.36	mf		
Perizoma alchemillata (Linnaeus, 1758)	70-133/1	10	0.4	mf		
Gagitodes sagittata (Fabricius, 1787)	70-140/1	10	0.37	mf		
Chloroclystis v-ata (Haworth, 1809)	70-142/1	10	0.37	mf		
Eupithecia linariata ([Denis & Schiffermüller], 1775)	70-150/1	10	0.32	mf		
Eupithecia venosata venosata (Fabricius, 1787)	70-155/1	10	0.39	mf		
Eupithecia tripunctaria Herrich-Schäffer, 1852	70-160/1	10	0.32	mf		
Eupithecia insigniata (Hübner, 1790)	70-174/1	10	0.34	mf		
Eupithecia extensaria occidua Prout, 1914	70-178/1	10	0.45	mf		
Eupithecia expallidata Doubleday, 1856	70-180/1	10	0.34	mf		
Eupithecia vulgata (Haworth, 1809)	70-183/1	10	0.32	mf		
Eupithecia succenturiata (Linnaeus, 1758)	70-188/1	10	0.38	mf		
Eupithecia subumbrata ([Denis & Schiffermüller], 1775)	70-189/1	10	0.46	mf		

Taxon	Drawer	n	R	Night	Day	Note
Carsia sororiata anglica Prout, 1937	70-191/1	10	0.37	mf		
Aplocera plagiata plagiata (Linnaeus, 1758)	70-192/1	10	0.45	mf		
Aplocera efformata (Guenée, [1858])	70-193/1	10	0.42	mf		
Chesias legatella ([Denis & Schiffermüller], 1775)	70-195/1	10	0.39	mf		
Chesias rufata rufata (Fabricius, 1775)	70-196/1	10	0.35	mf		
Lithostege griseata ([Denis & Schiffermüller], 1775)	70-197/1	10	**0.54**	mf		
Lobophora halterata (Hufnagel, 1767)	70-198/1	10	0.48	mf		
Acasis viretata (Hübner, [1799])	70-200/1	10	0.36	mf		
Archiearis parthenias (Linnaeus, 1761)	70-203/1	10	0.2		mf	
Boudinotiana notha (Hübner, [1803])	70-204/1	10	0.23		mf	
Abraxas grossulariata (Linnaeus, 1758)	70-205/1	10	0.3	mf		
Abraxas sylvata (Scopoli, 1763)	70-206/1	10	0.43	mf		
Ligdia adustata ([Denis & Schiffermüller], 1775)	70-208/1	10	0.41	mf		
Macaria notata (Linnaeus, 1758)	70-211/1	10	0.34	mf		
Macaria carbonaria (Clerck, 1759)	70-216/1	10	0.26		mf	
Chiasmia clathrata clathrata (Linnaeus, 1758)	70-218/1	10	0.25	mf	mf	
Isturgia limbaria (Fabricius, 1775)	70-220/1	10	0.2		mf	
Cepphis advenaria (Hübner, 1790)	70-221/1	10	0.37		mf	
Petrophora chlorosata (Scopoli, 1763)	70-222/1	10	0.45	mf		
Plagodis pulveraria (Linnaeus, 1758)	70-223/1	10	0.25	mf		
Plagodis dolabraria (Linnaeus, 1767)	70-224/1	10	0.3	mf		
Opisthograptis luteolata (Linnaeus, 1758)	70-226/1	10	0.24	mf		
Epione vespertaria (Linnaeus, 1767) m	70-228/1	10	0.25	m	m	d
Pseudopanthera macularia (Linnaeus, 1758)	70-229/1	10	0.19		mf	
Angerona prunaria (Linnaeus, 1758)	70-230/1	10	0.16	mf		
Apeira syringaria (Linnaeus, 1758)	70-231/1	10	0.22	mf		
Ennomos quercinaria (Hufnagel, 1767)	70-233/1	10	0.32	mf		
Ennomos alniaria (Linnaeus, 1758)	70-234/1	10	0.25	mf		
Ennomos erosaria ([Denis & Schiffermüller], 1775)	70-236/1	10	0.25	mf		
Selenia dentaria (Fabricius, 1775)	70-237/1	10	0.31	mf		
Selenia lunularia (Hübner, [1788])	70-238/1	10	0.26	mf		
Selenia tetralunaria (Hufnagel, 1767)	70-239/1	10	0.3	mf		
Odontopera bidentata (Clerck, 1759)	70-240/1	10	0.3	mf		
Crocallis elinguaria (Linnaeus, 1758)	70-241/1	10	0.31	mf		
Ourapteryx sambucaria (Linnaeus, 1758)	70-243/1	10	0.32	mf		
Colotois pennaria (Linnaeus, 1761)	70-244/1	10	0.37	mf		
Alsophila aescularia ([Denis & Schiffermüller], 1775) m	70-245/1	7	0.43	m		da
Alsophila aescularia ([Denis & Schiffermüller], 1775) f	70-245/1	3	0.25			da
Apocheima hispidaria ([Denis & Schiffermüller], 1775) m	70-246/1	7	0.33	m		da
Apocheima hispidaria ([Denis & Schiffermüller], 1775) f	70-246/1	3	0.22			da
Lycia hirtaria (Clerck, 1759)	70-248/1	10	0.3	m		
Biston betularia (Linnaeus, 1758)	70-252/1	10	0.38	mf		
Pseudoterpna pruinata atropunctaria (Walker, 1863)	70-297/1	10	0.37	mf		
Geometra papilionaria (Linnaeus, 1758)	70-299/1	10	0.41	mf		
Comibaena bajularia ([Denis & Schiffermüller], 1775)	70-300/1	10	0.35	mf		
Jodis lactearia (Linnaeus, 1758)	70-303/1	10	**0.72**	mf		
Hemithea aestivaria (Hübner, 1789)	70-305/1	10	0.39	mf		
Notodontidae						
Cerura vinula (Linnaeus, 1758)	71-003/1	10	0.44	mf		
Furcula furcula (Clerck, 1759)	71-005/1	10	0.49	mf		
Furcula bifida (Brahm, 1787)	71-007/1	10	0.47	mf		
Stauropus fagi (Linnaeus, 1758)	71-009/1	10	0.3	mf		
Drymonia dodonaea ([Denis & Schiffermüller], 1775)	71-010/1	10	0.37	mf		

Taxon	Drawer	n	R	Night	Day	Note
Drymonia ruficornis (Hufnagel, 1766)	71-011/1	10	0.39	mf		
Pheosia tremula (Clerck, 1759)	71-017/1	10	0.42	mf		
Pterostoma palpina (Clerck, 1759)	71-020/1	10	0.32	mf		
Ptilodon capucina (Linnaeus, 1758)	71-021/1	10	0.3	mf		
Ptilodon cucullina ([Denis & Schiffermüller], 1775)	71-022/1	10	0.31	mf		
Phalera bucephala (Linnaeus, 1758)	71-025/1	10	0.38	mf		
Clostera curtula (Linnaeus, 1758)	71-027/1	10	0.33	mf		
Clostera pigra (Hufnagel, 1766)	71-028/1	10	0.26	mf		
Erebidae						
Leucoma salicis (Linnaeus, 1758)	72-009/1	10	**0.65**	mf		
Lymantria monacha (Linnaeus, 1758)	72-010/1	10	0.43	m		
Lymantria dispar (Linnaeus, 1758) m	72-011/1	4	0.26	m	m	d
Lymantria dispar (Linnaeus, 1758) f	72-011/1	6	0.47			d
Euproctis chrysorrhoea (Linnaeus, 1758)	72-012/1	10	**0.67**	mf		
Euproctis similis (Fuessly, 1775)	72-013/1	10	**0.89**	mf		
Orgyia antiqua (Linnaeus, 1758) m	72-017/1	5	0.21	m	m	da
Orgyia antiqua (Linnaeus, 1758) f	72-017/1	5	0.23			da
Orgyia recens (Hübner, [1819]) m	72-018/1	7	0.19	m		da
Orgyia recens (Hübner, [1819]) f	72-018/1	3	0.19	f		da
Coscinia cribraria bivittata (South, 1900)	72-032/1	10	0.37	mf		
Utetheisa pulchella (Linnaeus, 1758)	72-034/1	10	**0.58**	mf	mf	
Miltochrista miniata (Forster, 1771)	72-035/1	10	0.39	mf		
Cybosia mesomella (Linnaeus, 1758)	72-038/1	10	0.46	mf		
Pelosia muscerda (Hufnagel, 1766)	72-039/1	10	0.38	mf		
Lithosia quadra (Linnaeus, 1758) m	72-041/1	6	0.41	m		d
Lithosia quadra (Linnaeus, 1758) f	72-041/1	4	0.33	f		d
Atolmis rubricollis (Linnaeus, 1758)	72-042/1	10	0.22	mf	mf	
Eilema depressa (Esper, 1787)	72-043/1	10	0.35	mf		
Eilema griseola (Hübner, [1803])	72-044/1	10	0.42	mf		
Eilema lurideola (Zincken, 1817)	72-045/1	10	0.44	mf		
Eilema pygmaeola pygmaeola (Doubleday, 1847)	72-048/1	10	0.41	mf		
Eilema sororcula (Hufnagel, 1766)	72-049/1	10	0.34	mf		
Setina irrorella (Linnaeus, 1758)	72-050/1	10	0.4	mf	m	
Noctuidae						
Diloba caeruleocephala (Linnaeus, 1758)	73-033/1	10	0.31	mf		
Nolidae						
Meganola strigula ([Denis & Schiffermüller], 1775)	74-001/1	10	0.39	mf		
Meganola albula ([Denis & Schiffermüller], 1775)	74-002/1	10	**0.52**	mf		
Nola cucullatella (Linnaeus, 1758)	74-003/1	10	0.38	mf		
Nola confusalis (Herrich-Schäffer, 1847)	74-004/1	10	0.47	mf		
Nola aerugula (Hübner, 1793)	74-005/1	10	**0.54**	mf		
Bena bicolorana (Fuessly, 1775)	74-007/1	10	**0.52**	mf		
Pseudoips prasinana britannica (Warren, 1913)	74-008/1	10	0.38	mf		d
Nycteola revayana (Scopoli, 1772)	74-009/1	10	0.33	mf		
Earias clorana (Linnaeus, 1761)	74-011/1	10	0.47	mf		
Controls						
Gonepteryx rhamni rhamni (Linnaeus, 1758)	N/A	2	0.38			
Aluminium	N/A	1	1			
Zinc Oxide	N/A	1	0.41			