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Odonata colour: more than meets the eye?

Wendy E. Harris[a], Dan W. Forman[b]*, Roy D. Battell[b], Marie T. R. Battell[b], Alan K. Nelson[c] and Paul F. Brain[a]

[a]*Conservation Ecology Research Team Swansea (CERTS), Department of Biosciences, College of Science, Swansea University, Swansea, SA2 8PP, UK;* [b]*Pineham House, Haversham, Milton Keynes, Buckinghamshire, MK19 7DP, UK;* [c]*British Dragonfly Society Buckinghamshire Dragonfly Recorder*

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Interpretations of behavioural visual cues, based on human perception of colour, may mislead because of the difference in our visual range compared to other animals. Investigations into ultraviolet (UV) reflectance have shown that this can be an important mode of communication in many animals. The present study focused on 10 species of British Odonata. Digital photography was used to capture images of UV reflectance of the body using a Schott UV pass filter to eliminate all other portions of the spectrum. Percentage cover of UV reflectance was determined and all but one of the 10 species sampled were found to reflect UV in one or both sexes. Most of the reflectance tended to occur on the ventral surface. Patterns of UV reflectance varied among species suggesting a variety of possible functions that are briefly discussed. A potential evolutionary mechanism for the development of UV reflectance in Odonata is proposed.

Keywords: Odonata; dragonfly; UV; colour; vision; signal of fitness; mistaken identity

Introduction

When assessing relationships between colour and behaviour in animals, human visual pigments have some disadvantages. The human lens and cornea strongly absorb wavelengths in the ultraviolet (UV) region (10–400 nm), preventing these wavelengths from reaching the retina, while the retina itself lacks any photoreceptor sensitive to UV (Tovée, 1995). Numerous studies on a range of vertebrate and invertebrate taxa have depended solely on the human perception of colour (Cuthill et al., 1999; Endler, 1990), meaning that some assumptions linking behaviour and colouration may be flawed (Brunton & Majerus, 1995).

UV plays a significant role in the colour of flowers and other vegetation, and it has long been known that insects see into the UV range (Lubbock, 1882; Silberglied, 1979). The perception of UV wavelengths enables bees to discriminate different flower hues and make economic decisions in terms of foraging and food choice; an action that may have driven changes in the

*Corresponding author. Email: d.w.forman@swansea.ac.uk

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colouration of angiosperms (Chittka & Menzel, 1992; Chittka et al., 1994; Osorio & Vorobyev, 2005). UV patterns on the body or wings may be important in species recognition for closely related, sympatric species of butterfly, and can be used by entomologists as a tool to distinguish between morphologically similar taxa of Lepidoptera (Brunton & Majerus, 1995; Knüttel & Fiedler, 2000). It is energetically beneficial for individual insects to quickly recognise female and male conspecifics, and this is likely to have been the evolutionary driving force behind the development of sexually dimorphic colouration (Figeurola & Green, 2000; Frantsevich & Mokrushov, 1984; Johnson, 1964). Sexual dimorphism in the UV range is apparent in spiders, butterflies, birds and reptiles, and this cue is often used in mate selection and recognition (Lim & Li, 2006; Silberglied, 1979; Tovée, 1995).

The vivid patterns and hues of Odonata are features that characterise these insects. Many distinctive colours (such as the non-iridescent blue produced by light scattering from spheres in the endoplasmic reticulum of epidermal pigment cells) result from pigmentation types found within and beneath the integument (Prum et al., 2004). While pruinescence and iridescence are known to reflect UV, the pigments involved in Odonata colouration have yet to be identified (Corbet, 1999; Hilton, 1986; Prum et al., 2004; Robey, 1975; Silberglied, 1979).

It is known that most Odonata species can see into the UV range; the majority of Odonata having both 11-*cis* retinal and 11-*cis* 3-hydroxyretinal that can pair with different combinations of opsins to give four spectral sensitivities that range from UV to orange (590 nm) (Briscoe & Chittka, 2001; Hilton, 1986; Seki & Vogt, 1998; Silberglied, 1979). It seems likely, therefore, that UV is an integral part of the visual system in most, if not all, Odonata.

Following work by Hilton (1986) on UV wing patterns of dragonflies, this study aimed to reassess the body colours of 10 British odonate species after elimination of the visible portion of the spectrum. The primary aim was to determine if there was any feature of the pigmentation or integument structure of dragonflies that caused UV wavelengths to be detected, in order that a more detailed analysis could follow. Digital photography was chosen as the method by which to gain preliminary data due to its accessibility and the ability to record the entire pattern of each Odonata specimen, as opposed to point analysis recorded by spectrophotometry (Steven et al., 2007). This photographic technique also allowed live specimens to be used; an important factor in contrast with Hilton's study (1986) in which chemicals used to prevent pigmentation deterioration and preserve colouration after death may have affected UV reflectance.

Materials and methods

All fieldwork was performed in the area around Milton Keynes, in the east of England from June 2007 to October 2008. Odonata specimens were gathered from a private wildlife area SP817440, with permission and assistance from the owners, and from other wetland areas in Milton Keynes: Howe Park Wood Site of Special Scientific Interest SP830340, Stony Stratford nature reserve SP785410 and Elfield Park SP584632. Permission to capture dragonflies at these last-mentioned sites was given by The Park's Trust Milton Keynes.

The species studied were *Aeshna cyanea* (Müller 1764), *Aeshna grandis* (Linnaeus 1758), *Aeshna mixta* (Latrielle 1804), *Brachytron pratense* (Müller 1764), *Libellula depressa* (Linnaeus 1758), *Libellula quadrimaculata* (Linnaeus 1758), *Sympetrum striolatum* (Charpentier 1840), *Sympetrum sanguineum* (Müller 1764), *Calopteryx splendens* (Harris 1782) and *Coenagrion puella* (Linnaeus 1758). The aim was to collect several male and female individuals of each species, although this was not always possible due to the poor weather during both summers. Once netted, the subjects were transferred to containers and each container marked with the time and area of capture. The containers were then subjected to a period of cooling to allow the animals

to become torpid in preparation for the photography. No visible colour change was observed during this procedure. Photographs of both dorsal and ventral surfaces were obtained for each specimen in each procedure where possible. The surface temperature of the individual dragonfly was monitored using a Precision Gold Infrared Thermometer N28BJ (Maplin Electronics, Rotherham, UK), to ensure it did not fall below 5 °C.

Each specimen was then removed from cooling and placed on a cream sheet for an identifying photograph, taken at 100 ASA, F22, using the camera's built-in flash. The camera used was a Canon D10 SLR with a Canon 50 mm macro lens (Canon UK, Reigate, UK) mounted to face vertically down, while the subjects were placed on the table surface. The specimens were then transferred onto black velvet for the UV and colour photographs. Black velvet was used to provide a non-reflecting background. When necessary, an ice-block was placed under the velvet to maintain the temperatures and prevent the insect from warming up too quickly. An initial image was recorded at ASA 800 F22-F32 to focus on the subject, to use for comparison to the UV image and to aid identification of specular reflections in order that they could be excluded from analysis.

A 52 mm Schott glass SG1 UV pass filter (Schott UK, Stafford, UK) held in a "Cokin A" filter holder (Cokin, Rungis, France), was used to exclude the visible wavelengths of light from 400 to 700 nm. Several photographs were taken on manual focus, each with small, systematic changes to the focus in order to compensate for the addition of the filter and the lens focus, as UV does not match natural light, and to provide a spread of focus options. The images were taken at ASA 800, and 1/180 second with synchronised flash; F4 was used for dragonfly specimens with distance of 48 cm between dragonfly and lens, and F5.6 for damselfly specimens with a distance of 32 cm. Flash was used in order to minimise the infrared portion of the spectrum, because the SG1 filter allows some infrared to pass through it. A Mecablitz 36C-2 (Metz-Werke, Zirndorf, Germany) flashgun was used at maximum output for UV images and on auto setting for colour images. The camera was set for "daylight" colour balance and images were recorded at maximum resolution as .jpg files. A male *L. depressa* was the first dragonfly species to be photographed in order that the expected UV reflection of the pruinescent blue portions of the body were clear on the UV photographic image produced. Once each set of photographs was completed, the dragonflies were given time to warm up, returned to their containers, and then released back into the area in which they were originally caught. The same camera settings were used to produce analogous UV photographs of a Kodak Q13 grey scale (Kodak, Hemel Hempstead, Hertfordshire) with densities in 20 increments, from 0 to 19 (white to printer's black, respectively), at both 32 cm and 48 cm from the camera. These images were used to quantify the brightness of UV reflection on the bodies of Odonata. The relative presence of UV reflectance on the body of each dragonfly was determined as a percentage of the total body area for both the dorsal and ventral surfaces of the head, thorax and abdomen using a simple 1 × 1 mm grid system.

Results

Table 1 summarises the mean percentage cover of UV reflectance of the dorsal and ventral surfaces of each odonate species investigated in this study. Table 2 presents the strength of UV reflectance recorded that corresponds to features of odonate male and female visible colouration. UV reflectance is quantified by the density increment that the reflectance most resembles (0 to 19). Colour and UV images are presented in Figures 1 and 2.

Both *B. pratense* males and females exhibited greater UV reflection on the dorsal surface than on the ventral side (see Figure 1a, b). The dense hairs covering the body appeared to reflect UV in both sexes.

Table 1. A comparison of UV reflectance in different species of Odonata.

Suborder Family	Species	Sex	Number sampled	Mean % cover of UV reflectance (± S.E.) Dorsal	Ventral
Anisoptera: Aeshnidae	*Brachytron pratense*	M	1	43.5	45.8
		F	2	19.0 (±6.9)	13.9
	Aeshna mixta	M	3	25.1 (±7.5)	60.0 (±3.6)
		F	2	43.1 (±11.3)	42.8 (±7.2)
	Aeshna cyanea	M	4	34.5 (±7.6)	42.7 (±7.46)
		F	2	27.5 (±8.0)	46.25 (±3.8)
	Aeshna grandis	M	1	22.7	76.2
		F	1	17.9	48.0
Anisoptera: Libellulidae	*Libellula depressa*	M	2	61.3 (±1.3)	0
		F	1	0	0
	Libellula quadrimaculata	M	1	0	0
		F	1	0	0
	Sympetrum striolatum	M	4	50.7 (±16.4)	53.1 (±11.4)
		F	4	12.5 (±3.6)	47.7 (±7.9)
	Sympetrum sanguineum	M	4	25.1 (±12.7)	31.3 (±12.9)
		F	1	0	5
Zygoptera: Calopterygidae	*Calopteryx spendens*	M	1	100	100
		F	1	0	0
Zygoptera: Coenagrionidae	*Coenagrion puella*	M	3	37.3 (±11.3)	54.6 (±17.2)
		F	2	23.8 (±1.2)	70.2 (±9.7)

Table 2. Equivalent density increment for UV reflectance of specific features.

Species	Feature	Density increment Male	Female
Brachytron pratense	Green, yellow (♀♂); blue (♂) markings	9	9–13
	Ventral surface	13	13
Aeshna mixta	Yellow (♂);white and lilac markings (♀)	6–7	8–12
	Blue marking on abdominal segment 2	5	
	Ventral surface segments (♂), midline (♀)	6–11	7
Aeshna cyanea	Blue markings	5–7	
	Yellow markings (and green ♀)	7–15	6–9
	Midline of ventral surface	8–10	5–8
Aeshna grandis	Blue marking on abdominal segment 2	4	
	Yellow markings	6	6
	Midline of ventral surface	7	5
Libellula depressa	Pruinescent blue	3–9	
	Yellow markings	8–15	none
Sympetrum striolatum	Dorsal surface	9–12	12–17
	Ventral surface	7–12	5–12
Sympetrum sanguineum	Dorsal surface	13–16	17
	Ventral surface	6–15	6
Calopteryx splendens	Iridescent blue (♂) or green (♀)	7	none
Coenagrion puella	Blue (♂) or green (♀) dorsal surface.	7	8
	Ventral surface	7	2

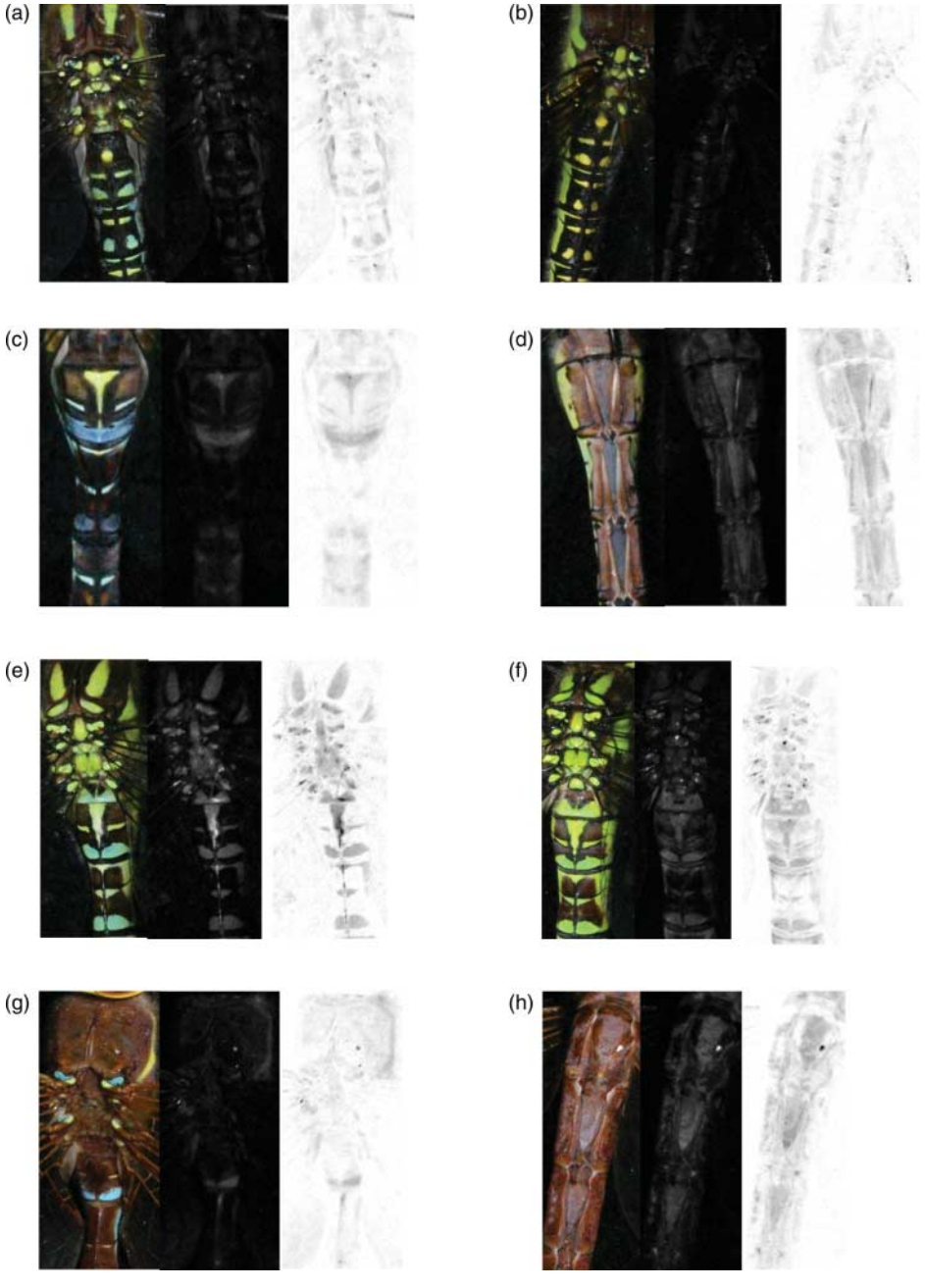

Figure 1. Photographic results. Parts (a) to (h) all comprise colour, UV and UV negative images. (a) Male *B. pratense* dorsal surface; (b) female *B. pratense* dorsal surface; (c) male *A. mixta* dorsal surface; (d) female *A. mixta* ventral surface; (e) male *A. cyanea* dorsal surface; (f) female *A. cyanea* dorsal surface; (g) male *A. grandis* dorsal surface; (h) female *A. grandis* ventral surface.

A. mixta males and females had UV reflectance corresponding to the visible colour patterns. The blue stripe at the bottom of the second abdominal segment and the ventral side of abdominal segment three were found to be the most intense UV reflecting region on the male (Figure 1c). These features were absent in the female; however, there was some UV reflectance on the ventral aspect of the abdomen, particularly along the midline (see Figure 1d).

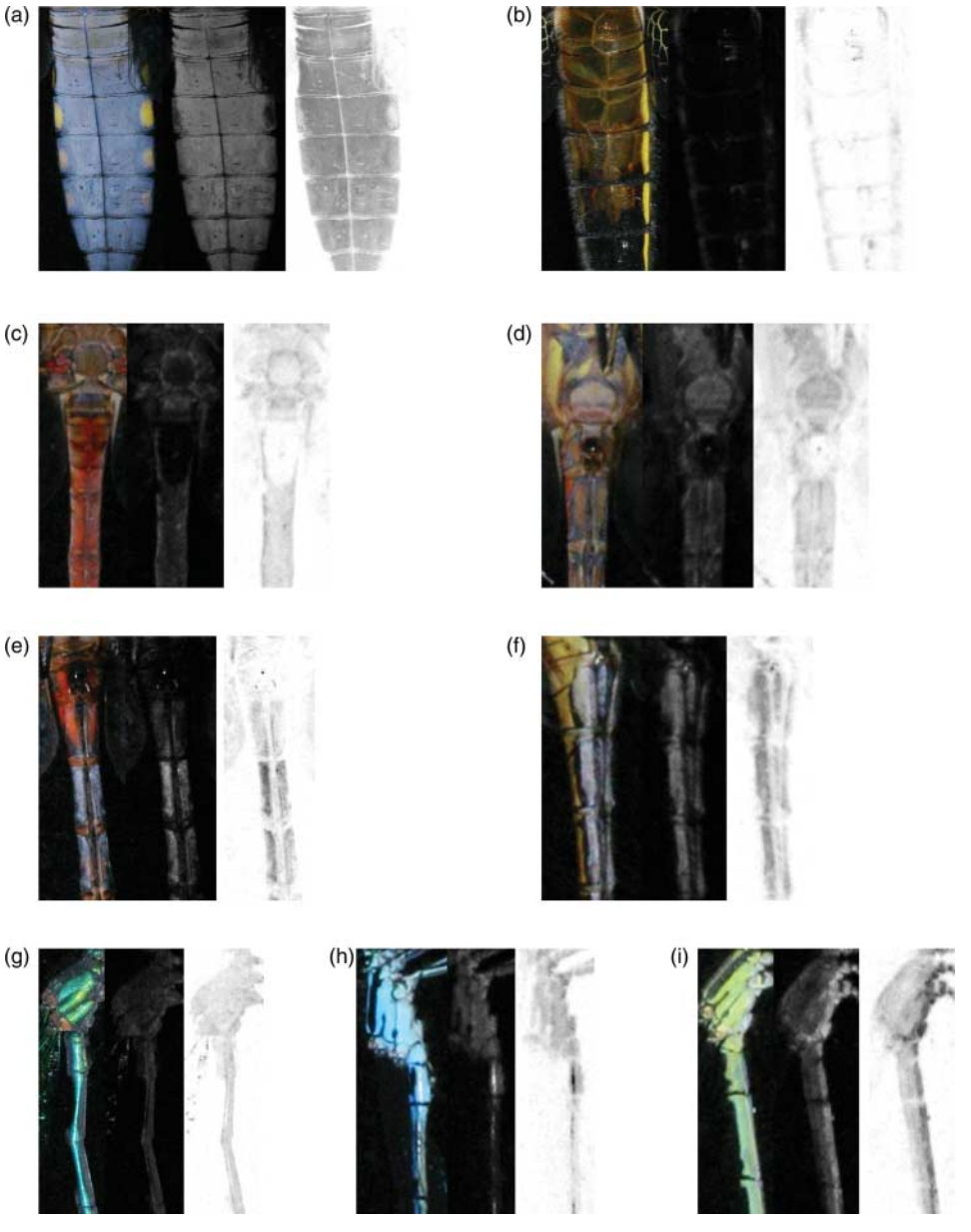

Figure 2. Photographic results. Parts (a) to (i) all comprise colour, UV and UV negative images. (a) Male *L. depressa* dorsal surface; (b) male *L. quadrimaculata* dorsal surface; (c) male *S. striolatum* dorsal surface; (d) female *S. striolatum* ventral surface; (e) male *S. sanguineum* ventral surface; (f) female *S. sanguineum* ventral surface; (g) male *C. splendens*; (h) male *C. puella*; (i) female *C. puella.*

A. cyanea males and females showed UV reflectance associated with the visible colour patterns seen on the thorax and abdomen (Figure 1e, f). The females also showed reflectance on the central portion of the abdomen's ventral surface.

Male and female *A. grandis* showed similar patterns of UV reflectance on both dorsal and ventral surfaces, with the exception of the blue markings only found on abdominal segment two of the male (see Figure 1g). This region had bright UV reflectance not observed on the female.

The female exhibited the brighter region of UV along the midline of the ventral surface of the abdomen also seen in females of *A. cyanea* and *A. mixta* (see Figure 1h).

Individual *L. depressa* males varied in UV reflectance of their pruinescent blue colouration (see Figure 2a). The brown regions of the male ventral surface and the entire female body surface absorbed UV; however, lateral yellow patterns, found on both sexes, were only observed to reflect UV on the males.

Neither male nor female *L. quadrimaculata* showed any UV reflectance on any part of the head, thorax or abdomen on either dorsal or ventral surface. The fine hairs, however, that cover the body of the male and female of this (and other) species reflected UV, and appeared to create a halo of reflectance around the body of each individual (see Figure 2b).

S. striolatum males showed variation in the brightness of their red colouration. They also showed great variation in dorsal UV reflectance (ranging from zero to 77.2%) (see Figure 2c), while the ventral reflectance ranged from 38.3% to 72.6%. *S. striolatum* females also showed variation in dorsal and ventral UV reflectance (see Figure 2d).

Male *S. sanguineum* exhibited variation in the brightness of their visible colour that paralleled differences in the UV reflectance of their dorsal (ranging from zero to 58.6%) and ventral (ranging from zero to 62.5%) surfaces (see Figure 2e). In these insects, the greatest percentage cover of UV reflectance on dorsal (a mean of 25.1%) and ventral surfaces (a mean of 31.5%) was evident in individuals with no wing damage. Conversely, individuals with extensive wing damage had markedly reduced reflectance on both dorsal (a mean of 6.3%) and ventral (a mean of 13.8%) surfaces. The female *S. sanguineum* had low UV reflectance on her dorsal surface, but there was some reflectance in the ventral surface associated with a grey area of colouration (see Figure 2f).

The male *C. splendens* had UV reflectance over the entire body, corresponding to the visible iridescent blue colouration (see Figure 2g). The female *C. splendens*, that appears iridescent green to the human eye, showed no detectable UV reflectance.

The male *C. puella* showed similar levels of UV reflectance on dorsal and ventral surfaces (see Figure 2h), while the female displayed more UV reflectance on the ventral than on the dorsal surface (see Figure 2i). The female *C. puella* has large areas of black pigmentation on the dorsal surface that absorbed UV wavelengths.

All of the species sampled, with the exception of *L. quadrimaculata*, appear sexually dimorphic to the human eye (evident in colouration or pattern) and demonstrated sexual dimorphism in the observed strength or bodily distribution of UV reflectance (see Table 3). The only non-territorial species included was *C. puella*, yet this species also showed dimorphism in both visible and UV spectra, suggesting a potentially different function of colour cues in this species. There is a general

Table 3. A comparison of the appearance of sexual dimorphism in the visible and UV spectra in a range of dragonfly species.

Species	Sexual dimorphism in visible spectrum	Sexual dimorphism in UV reflectance	Is the male territorial?
Hairy Dragonfly	Yes	Yes	Yes
Migrant Hawker	Yes	Yes	Yes
Southern Hawker	Yes	Yes	Yes
Brown Hawker	Yes	Yes	Yes
Common Darter	Yes	Yes	Yes
Ruddy Darter	Yes	Yes	Yes
Broad-bodied Chaser	Yes	Yes	Yes
Four-spotted Chaser	No	No	Yes
Banded Demoiselle	Yes	Yes	Yes
Azure Damselfly	Yes	Yes	No

trend for most UV reflectance to occur on the ventral side in both males and females. *L. depressa* males were the only species showing the reverse of this trend, having no UV reflectance on the ventral side, but strong reflectance on the dorsal side.

Discussion

This paper is the first study investigating UV reflectance from the bodies of a range of live Odonata and, although the sample sizes were relatively small, this phenomenon occurred in all but one of the species that were tested. As a range of vertebrate and invertebrate taxa have previously been shown to employ a UV reflecting element in their colouration (Bennett et al., 1996; Cuthill et al., 1999; Hunt et al., 1998; Lim & Li, 2006; Ries et al., 2008; Stapley & Whiting, 2006), this result is, perhaps, to be expected. In all but one of the Odonata species sampled, sexual dimorphism was evident in the UV portion of the spectrum. Sexual selection for UV-mediated body traits may have resulted in it becoming a secondary sexual characteristic that is involved in mate assessment. UV reflectance (perhaps along with visible colours) may not only facilitate species recognition but help these insects to distinguish between males and females of their own species. This would enable territorial males to more effectively identify both potential rivals and mating opportunities. Hilton (1986) also recorded a frequent occurrence of sexual dimorphism of the UV patterns on the wings and bodies of the museum specimens he tested; therefore, a combination of Hilton's results and a study of live specimens may produce the most accurate impression of the sexual dimorphism of odonates in the UV spectrum.

The variation in pattern and coverage of UV reflectance recorded in the range of species studied suggests that this part of the spectrum has other functions in some Odonata species. It is possible that the complex patterns of UV reflectance and colouration seen in the Aeshnidae may provide camouflage when they are hunting over vegetation or roosting. The occurrence of the grey UV reflecting area on the ventral side of both *S. sanguineum* and *S. striolatum* may be a similar adaptation to that producing the blue pruinosity observed on male *L. depressa*. *S. sanguineum* individuals with no wing damage had a greater cover of UV reflectance on both dorsal and ventral surfaces, while counterparts with extensive wing damage had markedly less reflectance in both these areas. As wing damage naturally increases with age, the reduction in UV reflectance may act as an honest signal of fitness in this species, as well as others that exhibit pruinosity, such as *L. depressa*. The bright reflectance of the male *L. depressa* may also provide a form of crypsis against the water surface, protecting them from avian predators that are known to possess UV sensitive photoreceptors. The lack of UV reflectance seen in *L. quadrimaculata* may function to provide the greatest contrast against the background in order to be easily detected by potential mates and rivals, and be conspicuous from members of other species (e.g. *L. depressa*), as observed in *Enallagma* sp. (Schultz et al., 2008). This absence of distinguishing marks may, however, also account for some inappropriate responses of male Odonata towards other species (Schulz & Switzer, 2001). Developments in phylogenetic analysis may help to elucidate the evolution and functions of this phenomenon (Ballare & Ware, 2011).

Evidence suggests that the ancestor of Pterygote insects possessed UV, blue and green receptors (Briscoe & Chittka, 2001), mutations for which may well have occurred during the late Palaeozoic oxygen pulse (Seki & Vogt, 1998). Interestingly, although this change occurred independently, the polymorphism that gives rise to UV vision in insects occurred at the same site in the protein as that generating this phenomenon in birds (Salcedo et al., 2003). It is likely that the mechanism was the same, so it would be interesting to attempt to determine when this change in communication actually occurred in these ancient insects. Evidently more research is required in this area; not only to firmly establish the roles of UV cues on behaviour in Odonata, but to use spectrometry to provide quantitative data in a greater number of Odonata taxa.

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