Effects of age and feeding history on structure-based UV ornaments of a jumping spider (Araneae: Salticidae)

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Recent studies have shown for birds that females sometimes choose mates on the basis of condition-dependent variation in ultraviolet (UV, less than 400 nm) ornamentation, but there have been few comparable studies on invertebrates. Yet many invertebrates have UV structural coloration. Here, we investigate *Cosmophasis umbratica*, a jumping spider (Araneae: Salticidae) that has sexually dimorphic UV-iridescent ornamentation, and we provide evidence that male UV coloration is condition dependent in this species. Spectral-reflection patterns change with male age and prior feeding history. The position of the UV band (i.e. UV hue) of the carapaces of younger (field-collected as subadults and matured as adults in laboratory) males shifted, relative to older (field-collected as adults) males, significantly towards longer wavelengths. Food deprivation significantly decreased the spectral intensity of the abdomen, but not the carapace. Questions concerning the mechanisms by which UV ornaments change are highlighted, as are hypotheses concerning the role of condition-dependent UV variation in male–male competition and as a criterion used by females when making mate-choice decisions.

Keywords: UV vision; UV reflectance; body conditions; jumping spiders; structural colour; *Cosmophasis umbratica*

1. INTRODUCTION

Pigment-based ornaments have long been known to be important in intraspecific communication (reviewed by Hill 1999), but recent work is showing that optical interference of biological microstructural characteristics may also play an important role in animal communication. Many animals may have colour vision based in part on sensitivity to ultraviolet (UV) and sometimes these animals also have UV-reflecting ornaments, with these ornaments appearing to function in communication (e.g. Jacobs 1992; Bennett & Cuthill 1994; Tovée 1995; Losey *et al.* 1999; Cuthill *et al.* 2000*a*,*b*; Shi *et al.* 2001). Research on birds, in particular, has shown that structure-based ornaments reflecting in the UV may reveal an individual's state or condition (Keyser & Hill 1999, 2000; Mougeot *et al.* 2005; Doucet *et al.* 2005, 2006; Delhey *et al.* 2006) and function in the context of male–male competition for access to females (Alonso-Alvarez *et al.* 2004; Siefferman & Hill 2005) and in the context of female choice of males with which to mate (Cuthill *et al.* 2000*a*).

Variation in the UV reflectance of bird ornaments may be influenced by both biotic and abiotic factors, including age (e.g. red grouse *Lagopus lagopus scoticus*: Mougeot *et al.* 2005; eastern bluebirds *Sialia sialis*: Siefferman *et al.* 2005; blue tits *Parus caeruleus*: Delhey & Kempenaers 2006; Peters *et al.* 2006), nutritional condition (blue grosbeaks *Guiraca caerulea*: Keyser & Hill 1999; McGraw *et al.* 2002), season (blue tits *P. caeruleus*: Örnborg *et al.* 2002; Delhey *et al.* 2006),

parasite load (red grouse, *L. l. scoticus*: Mougeot *et al.* 2005) and feather-degrading bacteria (Burtt & Ichida 1999). However, despite UV vision and UV-based ornamentation being widespread in invertebrates (Fox 1976; Parker 1999, 2000; Briscoe & Chittka 2001), our understanding of invertebrate UV signalling lags behind avian UV signalling. For example, although feeding regimes of caterpillars are known to affect the ultimate UV-structural ornaments of butterflies (Kemp *et al.* 2006), there have been no studies that test hypotheses about how age or prior feeding might influence these ornaments in the adult stage.

Here, we address the imbalance in our understanding of invertebrate versus vertebrate reliance on UV by presenting findings from a study on a sexually dichromatic jumping spider (Araneae: Salticidae). Salticids are known to have UV-sensitive receptors in the retinas of their principal eyes (Land 1969, 1985; DeVoe 1975; Yamashita & Tateda 1976; Blest *et al.* 1981; Peaslee & Wilson 1989) and male salticids are well known for their often extravagant coloration, and there has been a strong emphasis in the salticid literature on the hypothesis that the mate-choice behaviour of females has driven the evolution of elaborate salticid male ornamentation (Peckham & Peckham 1889, 1890, 1894; Crane 1949*a*,*b*). Besides pigmentary coloration (e.g. red, yellow or black; Townsend & Felgenhauer 1999), some salticids have structural coloration (e.g. blue, green, white or UV; Parker & Hegedus 2003).

Cosmophasis umbratica, a salticid species that is common in sunlit vegetation in Singapore, is particularly appropriate for investigating UV signals. Males of this

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species have complex iridescent markings, some of which are structural, on various parts of their bodies, but especially on the top and sides of the carapace and on the sides of leg femora (Lim & Li 2006), but females do not reflect UV (Lim & Li 2006). The males' abdomens are mostly black, but with iridescent white lines running anterior to posterior. Earlier work has also revealed that UV reflectance varies considerably among males (Lim & Li 2006), with these findings being the rationale for two questions that we investigate here: (i) does spectral reflectance of structure-based UV ornaments depend on age? and (ii) does prior feeding history affects structure-base UV ornaments?

2. MATERIAL AND METHODS

All spiders were kept individually in transparent cylindrical cages (diameter × height: 6.5 × 8.5 cm) with opaque sides to prevent contact among individuals, and maintained in a laboratory under controlled environmental conditions (relative humidity, 80–85%; temperature, 25 ± 1°C; light regime, 12 : 12 h; lights on at 08.00 h), with the provision, for 4 h daily (09.00–11.00 h; 16.00–18.00 h), of additional lighting (Arcadia Natural Sunlight Lamp) that simulated natural sunlight.

To test whether structure-based spectral reflectance is affected by post-maturity male age (i.e. time elapsing in the natural environment after the male's final moult), we used two groups: 'old' (collected as adults in the field; $n = 25$) and 'young' (collected as subadults from the field and maintained until they matured in the laboratory; $n = 25$). Spiders for the two groups were collected from the same location at the same time. The precise post-maturity age of the old males was unknown, but the important variable in this initial study was simply that we knew they were mature when collected in the field and, therefore, their post-maturity age when we used them in the laboratory was greater than that of the young males and that only old males had spent any time as adults in the field.

Upon collection, these spiders were maintained on a standardized diet of house flies (*Musca domestica*), fruit flies (*Drosophila melanogaster*) and small instars of crickets (*Acheta domestica*) twice per week (Lim & Li 2006). The period in the laboratory before reflectance spectra measurements were obtained was 10 days post-maturity (i.e. 10 days after the final moult) for young males and 10 days for field-collected males (i.e. the post-maturity age of these males was 10 days plus their unknown time as adults in the field).

To explore whether prior feeding history affects the spectral reflectance of males, a separate group of laboratory-matured males (i.e. collected as subadults; $n = 10$) were initially maintained for 10 days, then starved for 10 days and subsequently fed for 5 days, as earlier studies have shown that salticids have low metabolic rate (e.g. Anderson 1996) and are typically maintained in the laboratory by feeding with a few prey items once a week (e.g. Jackson & Hallas 1986). All spiders were first fed fruit flies (*D. melanogaster*) until satiation at day 0, and were then kept without food (only water via a cotton roll was provided ad libitum) from day 1 for 10 days. At day 11, the reflectance spectra of all the spiders were measured (for measurements, see below). From day 12, each individual was fed with 10 fruit flies every day for 5 days, and the reflectance spectra of these same individuals were then

measured again at day 16. Abdominal dimensions (e.g. widths of abdomens and dorsal iridescent line) were not measured as these changes, after 10 days of food deprivation, were too subtle. Therefore, to confirm that starved individuals had successfully fed on provided prey, individual masses were recorded on the same day the reflectance spectra were obtained (i.e. day 11 and day 16). Owing to the extensibility of a spider's abdomen, but not its carapace, here we could assume that an increase in mass should result from abdomen distension.

The spectral reflectance of two body parts, the dorsal cephalothorax (hereafter carapace) and the dorsal abdomen (hereafter abdomen), which are extensively displayed during intraspecific interaction in *C. umbratica* (Lim & Li 2004), was measured. Spectral measurement followed that of Lim & Li 2006, which was modified from previous well-established standard protocols (Endler 1990; Endler & Théry 1996; Andersson & Amundsen 1997; Cuthill *et al.* 1999). To facilitate accurate measurement of reflectance, spiders were temporarily immobilized by exposure to carbon dioxide (*ca* 5 min). A stable and continuous source of full-spectrum light (215–1700 nm) was provided by a DH-2000 deuterium tungsten halogen light source (Ocean Optics Inc., Dunedin, FL, USA) that illuminated a round area of approximately 1 mm in diameter, at a distance of 2 mm, from the reflection probe to the body region. A reflection probe that housed a single fibre, surrounded by six hexagonally arranged illuminating fibres, recorded reflected spectra from the surface under study. The distance between the specific body region and the probe was set at 2 mm by clamping the probe to a vertical adjustable translation stage (Creative Stars Electro-Optics Inc., Redmond, WA, USA); this allowed the intended distance to be accurately achieved (with a resolution of 0.01 mm) while maintaining a fixed perpendicular angle between the probe and the plane of the intended area on the spider. All of the spectral reflectance data were captured using a USB2000 UV/VIS miniature fibre-optic spectrometer (Ocean Optic Inc.) and processed using OOIBASE32 spectrometer operating software (v. 2.0.1.3), with a Spectralon white standard (Labsphere, North Sutton, NH, USA), an almost perfect diffuser (more than 95% reflectance from 250 to 2000 nm), and a dark reference (lights off in a dark room) being employed for comparison. Five spectra were repeatedly taken from each body part through a process of resetting the probe's position and obtaining a spectral reading, and the average was used for statistical analyses.

Three standard descriptions of reflectance spectra are commonly used in colour analysis (Hailman 1977), namely brightness (spectral intensity, R), hue (spectral location, λ) and chroma (saturation or spectral purity). For this study, we used only brightness and hue to analyse the recorded spectral data. Measurement of chroma (or spectral purity) was not attempted here owing to the lack of a distinctive trough in the reflectance curve of male *C. umbratica* (Lim & Li 2006) that greatly hindered accurate chroma estimation. Instead, we introduced the use of relative spectral position, termed 'band separation', of both UV and VIS bands to represent spectral purity. This is because the proximity (spectral position) of the UV band relates to the bandwidth of the VIS band in a multilayered reflector system (Land 1972), one type of structural colour mechanism which is proposed in *C. umbratica*, based on the prominence of the VIS and UV reflection bands as those of a main band and oscillating sidebands, respectively (Land 1972). To objectively describe
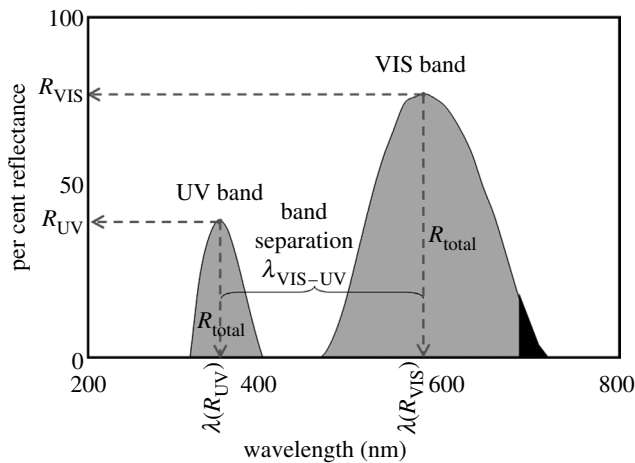
Figure 1. Spectral variables of typical spectral reflectance curve of adult male *C. umbratica*. R_{UV}, UV intensity (%); R_{VIS}, VIS intensity (%); $\lambda(R_{UV})$, UV hue, the spectral position of UV peak (nm); $\lambda(R_{VIS})$, VIS hue, the spectral position of VIS peak (nm); R_{total}, total intensity of reflectance spectra (300–700 nm); λ_{VIS-UV}, band separation (nm), wavelength difference between the peaks of UV and VIS bands.

Table 1. Definition of spectral variables in the reflectance spectra of a *C. umbratica* male.

variables	definition
UV intensity (R_{UV})	percentage reflectance (%) of UV reflection band
VIS intensity (R_{VIS})	percentage reflectance (%) of VIS reflection band
total intensity (R_{total})	area under reflectance graph (from 300 to 700 nm)
UV hue ($\lambda(R_{UV})$)	spectral position of UV band peak: wavelength (nm) of maximal reflectance in UV range (300–400 nm)
VIS hue ($\lambda(R_{VIS})$)	spectral position of VIS band peak: wavelength (nm) of maximal reflectance in VIS range (400–700 nm)
band separation (λ_{VIS-UV})	wavelength difference (in nm) between UV hue and VIS hue

variation in spectral shape ('colour': hue) and intensity ('brightness'), we described seven colorimetrics based on the reflectance spectra recorded from *C. umbratica* adult males (figure 1 and for definitions see table 1). For convenience, we used brightness and intensity interchangeably.

3. RESULTS

For abdominal spectral reflectance traits, young males were not significantly different from old males in brightness (UV, VIS and total intensity), UV and VIS hues or band separation (λ_{VIS-UV}; figure 2a and table 2). However, old males' carapace UV hue shifted, relative to young males, significantly towards shorter wavelengths, and young males had brighter carapaces in the VIS range and greater overall intensity than old males. There was a suggestion of a small shift in the VIS hue of the carapace towards shorter wavelengths in old males, but this was not significant. Carapace band separation (λ_{VIS-UV}) of young was not significantly different from that of old males (figure 2b and table 2).
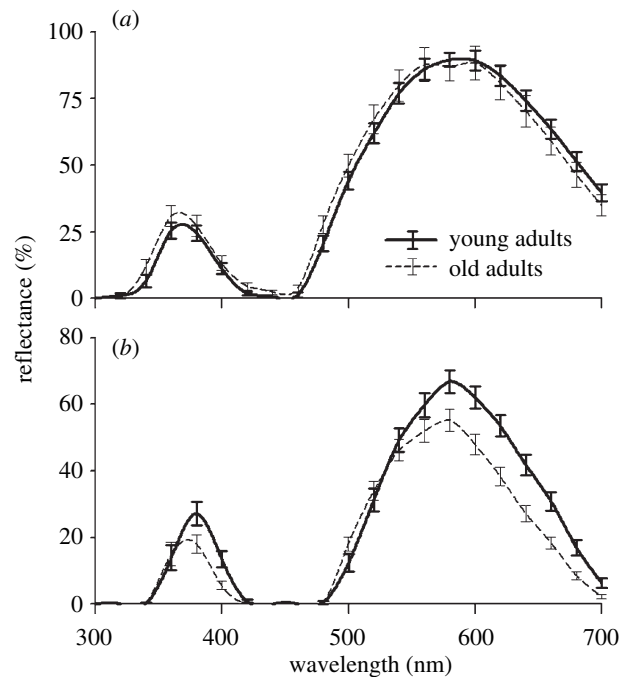
Figure 2. Reflectance spectra for (a) dorsal abdomen and (b) dorsal carapace of young (solid line) and old (dashed line) *C. umbratica*. Error bars represent standard errors, mean ± s.e.

When males were fed again after a fast, there was a significant increase in mass (0.0127 ± 0.0003 g; paired t-test: $t = -3.836$, $p = 0.003$) and prior feeding history had a pronounced effect on abdomen, but not carapace, spectral reflectance (figure 3a and table 2). There was a significant increase in the intensities of UV and VIS bands, as well as the overall abdomen brightness, when spiders were fed again after starvation. However, the abdominal hues (i.e. UV, VIS and band separation) did not change with starvation. Nor did prior feeding history affect carapace spectral reflectance variables (figure 3b and table 2).

4. DISCUSSION

Our findings show that the UV structural coloration of *C. umbratica* males varies significantly with male age and male prior feeding history. This is the first demonstration of the expression of structure-based coloration in the jumping spider being condition dependent, but there are studies showing comparable condition dependence of UV coloration in birds (Andersson & Amundsen 1997; Siitari & Huhta 2002; Mougeot *et al.* 2005; Siefferman *et al.* 2005).

The mechanisms responsible for variation in the structural colours of *C. umbratica* are currently unknown. However, as salticid scales are basically chitinous, cumulative periods of exposure to UV radiation may cause changes in the refractive indexes (as related to optical thickness) of the chitin layers and thereby cause the spectral characteristics of old males to diverge from the spectral characteristics of young males. It is of interest that photodegradation has been suggested as a basis of coloration change in birds (Smith 1995; Blanco *et al.* 2005). A particularly interesting area for future research on salticids might be to identify, measure and compare the optical traits of the cuticular scales of young and

Table 2. Effects of age and prior feeding history on the reflectance spectral traits of male *C. umbratica*. (Data are presented as mean ± s.e. and are analysed by independent *t*-tests for age effects or paired *t*-tests for effects of prior feeding history. Boldfaced cells show statistically significant results. *Mann–Whitney *U*-test.)

| spectral variables	body part	age (see figure 2)				prior feeding history (see figure 3)		
		young	old	statistics	comments	change	statistics	comments
UV intensity (%)	abdomen	31.67 ± 2.83; n=25	38.69 ± 3.74; n=23	$t_{46} = -1.511, p=0.138$	no difference	10.79 ± 2.17	$\mathbf{t_9 = -4.977, p < 0.001}$	satiated males are UV brighter
	carapace	32.44 ± 3.42; n=24	25.86 ± 3.17; n=22	$t_{44} = 1.405, p=0.167$	no difference	−0.74 ± 1.56	$t_9 = 0.472, p=0.648$	no change
VIS intensity (%)	abdomen	89.50 ± 3.52; n=25	88.18 ± 6.09; n=25	$t_{48} = 0.191, p=0.850$	no difference	16.93 ± 2.61	$\mathbf{t_9 = -6.486, p < 0.001}$	satiated males are VIS brighter
	carapace	64.38 ± 3.29; n=25	53.20 ± 3.23; n=25	$\mathbf{t_{48} = 2.451, p=0.018}$	young males brighter	−1.14 ± 1.75	$t_9 = 0.650, p=0.532$	no change
normalized total intensity	abdomen	0.61 ± 0.03; n=25	0.60 ± 0.05; n=25	$t_{48} = 0.088, p=0.930$	no difference	0.14 ± 0.02	$\mathbf{t_9 = -6.717, p < 0.001}$	satiated males are brighter
	carapace	0.57 ± 0.04; n=25	0.44 ± 0.04; n=25	$\mathbf{t_{48} = 2.305, p=0.026}$	young males brighter	0.00 ± 0.01	$t_9 = 0.076, p=0.941$	no change
UV peak (nm)	abdomen	369.15 ± 2.18; n=25	366.77 ± 2.29; n=25	$t_{48} = 0.753, p=0.455$	no difference	−0.17 ± 4.34	$t_9 = 0.121, p=0.907$	no change
	carapace	376.62 ± 1.64; n=25	370.57 ± 1.46; n=25	$\mathbf{t_{48} = 2.765, p=0.008}$	UV band shift towards shorter wavelengths in old males	−0.89 ± 3.48	$t_9 = 0.813, p=0.437$	no change
VIS peak (nm)	abdomen	584.20 ± 2.89; n=25	579.23 ± 3.24; n=25	$t_{48} = 1.144, p=0.258$	no difference	−3.38 ± 8.82	$t_9 = 1.211, p=0.257$	no change
	carapace	580.64 ± 1.72; n=25	574.33 ± 2.19; n=25	$Z_{50} = -0.805, p=0.071^*$	no difference	−0.57 ± 5.30	$t_9 = 0.337, p=0.744$	no change
band separation (nm)	abdomen	215.05 ± 1.57; n=25	212.46 ± 1.75; n=25	$t_{48} = 1.133, p=0.263$	no difference	−3.21 ± 9.33	$t_9 = 1.088, p=0.305$	no change
	carapace	204.02 ± 1.11; n=25	203.76 ± 1.39; n=25	$t_{48} = 0.179, p=0.858$	no difference	0.33 ± 6.61	$t_9 = -0.158, p=0.878$	no change
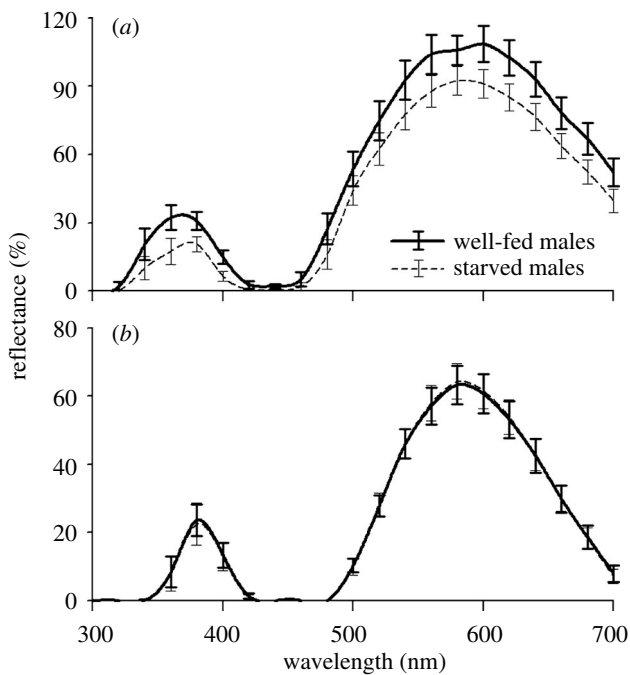
Figure 3. Reflectance spectra of (*a*) dorsal abdomen and (*b*) dorsal carapace of starved (dashed line) and satiated (solid line) *C. umbratica*. Error bars represent standard errors, mean ± s.e.

old males using transmission microscopy techniques (Fitzstephens & Getty 2000).

Male–male interactions of *C. umbratica* often entail considerable contact, with the spiders rolling about and biting each other (Lim & Li 2004). Perhaps, these intensive interactions cause abrasive loss of scales, with this possibly accounting, at least in part, for old males having spectral characteristics that differ from the spectral characteristics of young males. Physical contact between interacting males tends to involve especially the anterior region of the spiders' bodies, suggesting that this is a mechanism that may account especially for loss of cuticular scales on the carapace.

It will be of interest to investigate whether, for *C. umbratica*, condition dependence of male UV spectral characteristics functions in the context of sexual selection. Other research (M. L. M. Lim & D. Li unpublished) has shown that *C. umbratica* females rely on cues from male UV spectral characteristics when making mate-choice decisions. However, we do not currently know whether the female gains a fitness advantage by choosing young instead of old males or by choosing well-fed instead of fasted males.

Having found significant increase in the UV and VIS reflectance of the abdomen, but not the carapace, after feeding suggests that abdomen stretching is a mechanism by which feeding changes a male's UV spectral characteristics. The pattern of packing and overlapping of numerous iridescent cuticular scales adorning the abdomens of *C. umbratica* males (Lim & Li 2004) may be sensitive to the level of abdomen distension, which in turn is sensitive to feeding history. It is of interest that *C. umbratica* males actively move their abdomens not only during intraspecific interactions but also during normal locomotion, with these movement patterns most probably making abdomen coloration conspicuous to other conspecific individuals (Lim & Li 2004), suggesting that the effects of feeding history on abdomen UV spectral characteristics may function as an indicator of male quality, or as an amplifier of a male's physical condition (Taylor *et al.* 2000).

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