

Studies on UV reflection in feathers of some 1000 bird species: are UV peaks in feathers correlated with violet-sensitive and ultraviolet-sensitive cones?

PETER MULLEN* & GEORG POHLAND

Alexander Koenig Zoological Research Museum, Leibniz Institute for Terrestrial Biodiversity, Research Group: Biology and Phylogeny of Tropical Birds, Adenauerallee 160, 53113 Bonn, Germany

Nine hundred and sixty-eight bird species, covering all orders, were studied in search of distinctive ultraviolet reflections. All species in the following orders were completely surveyed: Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Galbuliformes, Upupiformes, Coliiformes, Apodiformes and Musophagiformes. The coloured plumage regions in particular exhibited high proportions of UV-reflecting feathers. Bird orders with species which are believed to possess VS (violet-sensitive) cone types mostly had their UV maxima between 380 and 399 nm while orders with species which are assumed to have UVS (ultraviolet-sensitive) cone types contained significantly species which had their UV maxima between 300 and 379 nm. With an emphasis on non-passerine birds the present study provides evidence that birds of many more groups may see UV light than have been studied to date. Ecological aspects related to UV reflection and perception, as well as sexual dimorphism visible only in the UV, are discussed.

Keywords: avian vision, colour, feather, fluorescence, light environment, plumage, sexual dimorphism, signalling, ultraviolet vision, UV reflection [Keywords added after online publication 17 July 2007].

Ultraviolet (UV) perception in a bird was reported for the first time by Huth and Burkhardt (1972). In contrast to humans with only three cone receptors, many birds potentially have tetrachromatic colour vision and are able to perceive the UV portion of the light spectrum. Many further investigations have been carried out since 1972, establishing that near-ultraviolet light hues (300–400 nm) in avian plumage function in intra-specific signalling and that UV detection also influences foraging behaviour (Silberglied 1979, Burkhardt 1982, Bennett & Cuthill 1994, Viitala *et al.* 1995, Church *et al.* 1998, Koivula & Viitala 1999, Pearn *et al.* 2001). Electrophysiological and behavioural experiments as well as microspectrophotometric measurements of single avian cones and a new molecular method which estimates the colour sensitivities of a bird by sequencing a part of the gene coding for the ultraviolet- or violet-absorbing opsin in the avian retina have provided positive evidence of UV vision in at least 57 species of birds (Koivula & Viitala 1999, Cuthill *et al.*

2000, Probst *et al.* 2002, Siitari *et al.* 2002, Ödeen & Håstad 2003, Hart & Vorobyev 2005).

According to the system of classification of avian taxa established by Sibley and Monroe (1990), representatives of 15 out of 23 bird orders have been proven to see or are most likely to see UV light (Table 1). Several studies reported UV reflection by feathers to be a widespread phenomenon, and it is well known that all feathers, except the most deeply black, reflect UV light to some extent, contributing to their overall brightness (Cuthill *et al.* 2000, Hausmann *et al.* 2002, Eaton & Lanyon 2003). In particular, plumage regions used in courtship display exhibit high amounts of UV reflection. Indeed, they often show a peak between 300 and 400 nm, mainly due to carotenoid-based colours which have a peak in the UV (Hausmann *et al.* 2002). The present study focuses on such UV reflections. Furthermore, many behavioural experiments have demonstrated that UV light plays an important role in mate choice. The iridescent green feathers of the Common Starling *Sturnus vulgaris* (Bennett *et al.* 1997), the bright blue breast plumage of the Bluethroat *Luscinia svecica* (Andersson & Amundsen 1997, Johnsen *et al.*

*Corresponding author.
Email: p.mullen.zfmk@uni-bonn.de

Table 1. A summary of the bird orders studied and the species with UV phenomena with amplitudes between 380 and 399 nm or 300 and 379 nm and bird orders containing species with proven UV vision ability through either a violet-sensitive (VS) or an ultraviolet-sensitive (UVS) cone type. Dashes indicate when no data were available. The classification follows the systematic list of Sibley and Monroe (1990).

Order	Total no. of species	Total no. of species measured	% of species measured	No. of species with UV phenomenon	% of species measured with UV phenomena	% of species with UV phenomena with an amplitude between 380 and 399 nm	Species with evidence for UV vision ability detected in this order	VS or UVS cone type according to Ödeen and Håstad (2003)*
Craciformes	69	69	100	0	0	0	–	–
Turniciformes	17	17	100	0	0	0	–	–
Bucerotiformes	56	28	50	0	0	0	–	–
Coliiformes	6	6	100	1	17	100	–	–
Cuculiformes	143	24	17	5	21	80	–	–
Apodiformes	103	103	100	0	0	0	–	–
Musophagiformes	23	23	100	18	78	56	–	–
Tinamiformes	47	47	100	0	0	0	No ²	–
Strigiformes	291	52	18	0	0	0	No ^{7,14,26}	VS
Coraciiformes	152	42	28	14	33	21	Yes ¹⁶	VS
Piciformes	355	36	10	13	36	54	–	VS
Galbuliformes	16	16	100	2	12	100	–	VS
Upupiformes	10	10	100	8	80	100	–	VS
Trogoniformes	39	13	33	13	100	61	–	VS
Gruiformes	196	26	13	3	11	100	–	VS
Galliformes	214	37	17	20	54	75	Yes ^{3,4,5,15,17}	VS
Anseriformes	161	25	16	10	40	60	Yes ⁶	VS
Columbiformes	313	40	13	11	27	54	Yes ^{3,22,23,24}	VS
Ciconiiformes	1027	65	6	11	17	72	Yes ^{2,3,8,9,15,16,25,27,35}	VS (UVS)
Trochiliformes	319	40	13	16	40	87	Yes ^{18,19,20,21}	–
Struthioniformes	10	10	100	0	0	0	Yes ^{2,35}	VS, UVS
Passeriformes	5712	96	1,7	63	65	17	Yes ^{2,7,10,11,12,13,16,28–35}	UVS (VS)
Psittaciformes	358	143	40	140	98	8	Yes ^{3,17}	UVS
TOTAL	9637	968		348				

Evidence of species with UV vision abilities or lack of UV vision abilities in bird orders are based on either microspectrophotometry of avian visual pigments: 1, Wright and Bowmaker (1998, 2001); 2, Sillmann *et al.* (1981); 3, Bowmaker *et al.* (1997); 4, Bowmaker *et al.* (1993); 5, Hart (1998); 6, Jane and Bowmaker (1988); 7, Bowmaker and Martin (1978); 8, Liebmann (1972); 9, Bowmaker and Martin (1985); 10, Maier and Bowmaker (1993); 11, Das (1997); 12, Hart *et al.* (1998); 13, Bowmaker (1979); 14, Jacobs *et al.* (1987) [for details see Cuthill *et al.* (2000)]; 15, Hart (2002); 16, Hart (2004), or behavioural experiments: 15, Siitari *et al.* (2002); 16, Parrish *et al.* (1981); 17, Pearn *et al.* (2001); 18, Huth and Burkhardt (1972); 19, Goldsmith and Goldsmith (1979); 20, Goldsmith (1980); 21, Goldsmith *et al.* (1981); 22, Emmerton and Delius (1980); 23, Emmerton and Remy (1983); 24, Kreithen and Eisner (1978); 25, Viitala *et al.* (1995); 26, Koivula *et al.* (1997); 27, Koivula & Viitala (1999); 28, Bennett *et al.* (1996); 29, Bennett *et al.* (1997); 30, Andersson and Amundsen (1997); 31, Johnsen *et al.* (1998); 32, Andersson *et al.* (1998); 33, Hunt *et al.* (1998); 34, Probst *et al.* (2002); or by sequencing a part of the gene coding for the ultraviolet- or violet-absorbing opsin in the avian retina: 35, Ödeen & Håstad (2003).

1998), the blue crown feathers and yellow breast of the Blue Tit *Cyanistes caeruleus* (Andersson *et al.* 1998, Hunt *et al.* 1998) and the yellow and blue plumage of the Budgerigar *Melopsittacus undulatus* (Pearn *et al.* 2001) have a remarkably high peak in the UV. An exception is the Zebra Finch *Taeniopygia guttata* (Bennett *et al.* 1996), which does not possess plumage colours with a reflection peak in the UV. Interestingly, a recent study has reported the over-estimation of the UV waveband in mate choice in this species (Hunt *et al.* 2001).

The purpose of our study is not to reveal possible correlations between UV phenomena in feathers and bird phylogenetic relationships. This would probably be uninformative because almost all birds studied to date show evidence of being capable of seeing ultraviolet light. They either possess a VS (violet-sensitive) cone with a maximum sensitivity at approximately 400 nm or a UVS (ultraviolet-sensitive) cone with a maximum sensitivity at approximately 370 nm (Ödeen & Håstad 2003). A single amino acid change is known to alter a UVS cone into a VS cone (Yokoyama *et al.* 2000). Therefore, it is very likely that UV vision has evolved independently several times within one taxon. A recent study (Eaton 2006) has successfully shown that this is the case in the Icteridae where UV plumage signals have evolved multiple times from an ancestral condition that lacked UV plumage signals.

The aim of our study was to find evidence for the use of UV cues in intraspecific signalling. UV phenomena should then be more frequent in orders likely to have sensitivity to UV. If that is not the case, UV phenomena should be equally represented in all orders. If UVS species are more sensitive than VS species to UV, then, perhaps UV phenomena should be more frequent in orders with these species and UV peaks, when present, should lie in different regions.

METHODS

Analogous to the proposed comparative approach introduced by Hausmann *et al.* (2002), we define a bird as having distinctive UV coloration (which we refer to as UV phenomena) when the spectrum shows a UV reflectance peak higher than 10% relative to our white standard. In order to include species lacking UV peaks, but with high amounts of UV-reflecting plumage, we also speak of UV phenomena when any part of the UV reflectance spectrum exceeds the lowest reflection in the range of 400–700 nm. On the basis of this definition, white and light-coloured feathers are excluded, despite their

ability to reflect high amounts of UV light, and contribute to overall brightness. With respect to the visual abilities of the birds, reflection in the whole spectrum is a basic characteristic of white (Vorobyev *et al.* 1998) and nearly all white feathers reflect significant amounts of UV (Eaton & Lanyon 2003).

A prescreening of species from different avian orders revealed a lack of substantial UV reflection in most of the black, dark-grey and brown coloured feathers. These findings are supported by the results of previous studies dealing with feather coloration (Burkhardt 1989, Finger *et al.* 1992, Hausmann *et al.* 2002, Eaton & Lanyon 2003).

We therefore included the most colourful species in an order as they are most likely to show distinctive UV reflection (Hausmann *et al.* 2002). The species were randomly selected in orders with many colourful species and orders lacking colourfully plumaged birds, such as the Strigiformes. In orders with few coloured species, such as the Gruiformes, species were randomly selected, but always from a coloured species pool.

Overall, 5362 reflectance spectra were measured, representing 968 species from approximately 65% of all bird families and from all orders following the taxonomic list of Sibley and Monroe (1990). All species from nine orders were assessed. All colours in all plumage patches of a species were measured. We concentrated mostly on non-passerines, in order to make possible predictions of UV signalling in the less-studied bird orders, given that many studies have shown that UV plays an important role in several behavioural aspects of the passerines (Cuthill *et al.* 2000). For the purpose of this study, bird skins preserved at the Alexander Koenig Zoological Research Museum in Bonn, Germany, the Natural History Museum in Tring, UK, and the American Museum of Natural History in New York were used for data collection. In the main, skins less than 20 years old were used to avoid the problem of possible colour changes in older museum skins (Endler & Théry 1996, Hausmann *et al.* 2002, McNaught & Owens 2002). Where possible, an average of six specimens per species or one subspecies of one geographical region were measured, all adult birds. We selected specimens in good condition which showed well-preserved colours. To find cryptic dimorphism, we measured three males and three female specimens of 50% of half the species, while all specimens of the other half were males. A threshold of 15% difference in the reflectance intensity in the UV range was taken to distinguish a cryptic dimorphism from an artefact.

Additionally, many of the spectra were based on measurements of moulted bird feathers from private feather collections gathered over the last 10 years. None of these feathers had been treated with chemicals for preservation purposes and they had been kept in binders away from the light.

The reflectance spectra were measured using an Ocean Optics USB 2000 spectrometer, with a World Precision Instruments UV-VIS-NIR light source D₂H, containing both a deuterium-halogen and a tungsten-halogen light bulb. A compressed tablet of barium sulphate (BaSO₄) was used as a white reference standard. A black velvet cloth was used as a dark reference. Measurements were made in the ambient light of a darkened room using the bifurcated cable UV/VIS 400UM from World Precision Instruments, illuminating a field of approximately 2–3 mm² with a 100-ms summation time. All reflectance data were considered between the wavelengths 300 and 700 nm. Reflectance spectra for each distinctly coloured area on a feather of each species were calculated from averages of percentage reflectance values from ten measurements.

In many studies, a non-variable measuring angle was used for spectrophotometric plumage or single feather measurements in order not to jeopardize the comparability of the resulting data. The reflection of many colours strongly depends on the angle of illumination and detection (Osorio & Ham 2002). UV reflections in birds are easily overlooked due to the lack of UV sensitivity in human sensory perception. Measurements using a standardized angle might not show UV reflections despite their existence. Therefore, in this study, the angles of detection used were variable. The change in the intensity of the reflection was surveyed simultaneously at the monitor. Only the angles showing the highest amount of UV light reflection were taken. The regions were illuminated at angles of between 35° and 90° to the long axis of

the feather from a top view at a distance of approximately 7 mm. The upper side was used and, in primaries and secondaries, the outer webs were illuminated. The light was collected at the same angle. Black velvet cloth was used as padding to prevent stray light from the coloured surfaces influencing the measurements. The feathers were positioned parallel to the source of illumination and collection, and illuminated from the proximal end, which was orientated to the long axis of the feather, moving only the light source and collector within the stated angles in order to obtain highest UV reflection.

RESULTS

With the exception of the Ciconiiformes and Passeriformes, at least 10% of all species in each of the remaining 21 orders were examined. According to our definition of distinctive UV reflection, 347 species of the 968 surveyed showed UV phenomena in one or more body regions (Table 1). Representatives of 16 out of 23 bird orders exhibited UV phenomena. In bird orders possessing VS cones (Ödeen & Håstad 2003), species of these orders showing UV phenomena most commonly showed highest reflections between 380 and 399 nm (Table 2). By contrast, birds with UV phenomena in the Passeriformes and Psittaciformes – the two orders where most birds were found to possess UVS cones (Ödeen & Håstad 2003) – exhibited UV mainly below 380 nm.

For nine bird orders every single species listed by Sibley and Monroe (1990) was surveyed. In seven of the nine orders, UV phenomena were absent and we assume that UV plays a minor role in intraspecific communication. This was the case in Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Apodiformes, Strigiformes and Bucerotiformes. In the following orders more than 50% of the examined species exhibited UV phenomena: Passeriformes,

Table 2. UV amplitude distribution in feathers and UVS/VS cone correlation. The Fisher exact test was performed on bird orders with known UV/UVS cone types according to Ödeen and Håstad (2003) and orders with UV phenomena assigned to their amplitude position.

	VS	UVS	P
Orders in which more than 50% of the occurring UV phenomena exhibit a max. amplitude between 380 and 399 nm	9 (Piciformes, Galbuliformes, Upupiformes, Trogoniformes, Gruiformes, Galliformes, Anseriformes, Columbiformes, Ciconiiformes)	0	0.045
Orders in which more than 50% of the occurring UV phenomena exhibit a max. amplitude between 300 and 379 nm	1 (Coraciiformes)	2 (Passeriformes, Psittaciformes)	

Galliformes, Upupiformes, Musophagiformes, Trogoniformes and Psittaciformes (Table 1). Of the 143 psittaciform species studied, 140 species showed UV phenomena in at least one feather patch. Most species of the Musophagiformes showed UV phenomena, the genera *Corythaixoides* and *Crinifer* being exceptions. In the genera *Tauraco* and *Musophaga*, only the red patches of the primaries and secondaries exhibited UV phenomena. In the Galliformes and Anseriformes mainly the iridescent feather patches showed UV phenomena. In the Galbuliformes only the Purplish Jacamar *Galbula chalcothorax* and Bronzy Jacamar *G. leucogastra* exhibited UV phenomena, but none was found in the Puffbirds (Bucconidae).

UV phenomena were primarily found in brightly coloured feather patches. We divided different coloured feather patches into simple colour categories based on their appearance to the human visual system: violet, blue, green, yellow, red (including orange), pink and brown. We found all the non-iridescent blue- and violet-coloured plumage regions to be highly (more than 20%) UV-reflecting. All of these colour patches exhibited UV phenomena with one exception: the light blue to turquoise feather patches of several parrot species showed less than 5% reflection in the UV and therefore lacked UV phenomena. Seventy-five per cent of the green feather patches measured had UV phenomena, as did 50% of the yellow and 40% of the red feathers measured. The brown feathers of only three species exhibited UV phenomena. The species with brown feathers exhibiting UV phenomena were the two parrots Dusky Lory *Pseudeos fuscata* and Brown Lory *Chalcopsitta duivenbodei* as well as the White-bellied Bustard *Eupodotis senegalensis*. Black feathers exhibiting UV phenomena were rarely found. We found dark coloured feathers with UV phenomena only in the whistling thrushes *Myiophonus* spp., the Black Lory *Chalcopsitta atra*, the Dusky Lory, in a few other parrot species and in the Satin Bowerbird *Ptilonorhynchus violaceus*. On the basis of our definition of a UV phenomenon, white and light coloured feathers never exhibited it. However, all white feathers measured showed a significant amount of UV reflection. In no white feather patches examined was UV reflection under 10%, which would have indicated a non-UV/white, where the bird's UV/UVS cones would not be excited.

We did not discover any cryptic sexual dimorphisms. None of the measured feather patches of the species where female and male specimens were measured differed in the ultraviolet range.

DISCUSSION

In contrast to earlier studies on UV reflection in feathers and bird skins (Burkhardt 1989, Finger 1990, Finger *et al.* 1992, Hausmann *et al.* 2002, Eaton & Lanyon 2003), the angles of detection employed in our study were variable and, based on our definition of a UV phenomenon, all birds which did not exhibit more than 10% reflectance in the UV, or did not exhibit a peak in the UV, were considered to be non-UV phenomenon birds. Although we do not know if UV phenomena play a role in visual signalling, they might be more suggestive of a signalling role than the UV reflections which only add to the overall brightness of a bird's plumage (Fig. 1).

However, the association between the position of UV maxima and the possession of VS or UVS cones (Table 2) strongly indicates that UV reflections may be associated more closely with intraspecific signalling than realized previously.

Our studies show that bird orders in which species have been proven to perceive UV wavelengths are very likely to possess highly UV-reflecting plumage. Interestingly, no UV phenomena were found in avian orders which, to date, have not been demonstrated to perceive UV light. It is unlikely that UV plays a role in nocturnal bird groups, e.g. owls and nightjars (Koivula *et al.* 1997, Cuthill *et al.* 2000). Whether it does in the primitive palaeognathous bird orders, Struthioniformes and Tinamiformes, is not clear. Behavioural experiments are the only way to prove UV vision ability. Microspectrophotometric measurements on the Emu *Dromaius novaehollandiae*, the Brushland Tinamou *Nothoprocta cinerascens*, the Chilean Tinamou *N. perdicaria* and the Ostrich *Struthio camelus* did not find any VS/UVS cones (Sillmann *et al.* 1981, Wright & Bowmaker 1998), but a later study on the Ostrich and the Greater Rhea *Rhea americana* (Wright & Bowmaker 2001) and opsin coding genetic studies on the latter two species revealed evidence for UV vision (Wright & Bowmaker 2001, Ödeen & Håstad 2003). Behavioural tests have not yet been conducted on palaeognathous birds but this could be challenging.

The quantity of UV light at night is far less than by day (Endler 1993, 1995). Consequently, it is much more important for night-active birds to perceive contrast than to distinguish colours. This is supported by the large number of rods in owls' retinas compared with the number in birds active during daylight (Bowmaker & Martin 1978, Jacobs *et al.* 1987, Bowmaker *et al.* 1997). However, crepuscularly active

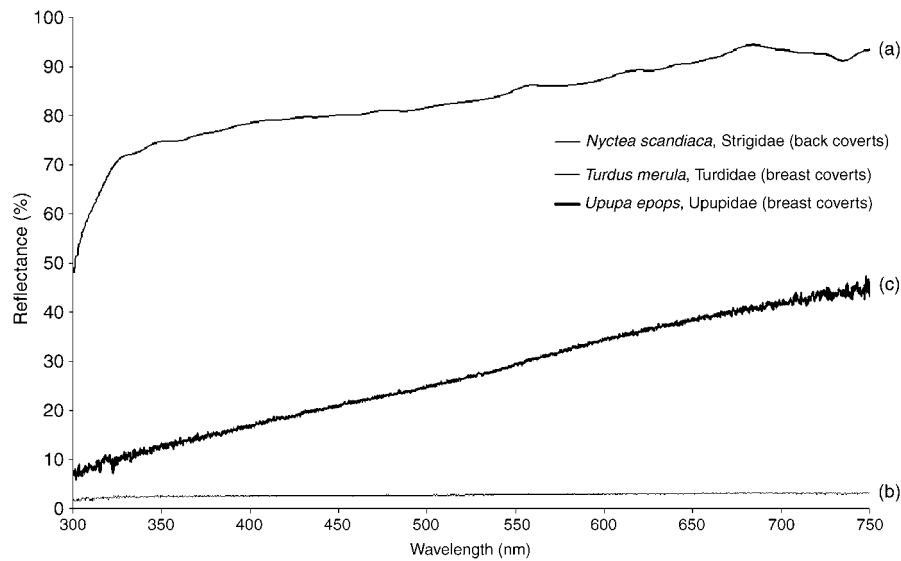


Figure 1. Examples of birds lacking a UV phenomenon. We defined birds as non-UV phenomenon birds with feather patches which did not exhibit more than 10% reflectance in the UV or lacked a peak in the UV. The achromatic and brown feather patches such as (a) the white back feathers of the Snowy Owl *Nyctea scandiaca*, (b) the black breast feathers of a male Blackbird *Turdus merula*, and (c) the brown breast of the Hoopoe *Upupa epops* show characteristic spectra with UV reflection adding to overall brightness or simply being part of broadband reflectance. The spectra were taken on one specimen of each species.

species such as some nightjars (e.g. the Common Nighthawk *Chordeiles minor*) are sexually dimorphic and show a distinctive white feather patch on the primaries, the male showing a much brighter patch than the female. Although the difference is clearly visible in normal light, differences persist well into the UV spectrum. Whether UV light plays a role in mate choice remains speculative. Yet, the proportion of UV in the spectrum is actually higher at dawn and dusk than it is during daytime. Additionally, opsin coding genetic studies have revealed evidence for the expression of a VS cone in the European Nightjar *Caprimulgus europaeus* but only a behavioural test can establish UV vision (Ödeen & Håstad 2003).

A remarkably high percentage of species in the Psittaciformes (140 out of 143 surveyed) exhibited highly UV-reflective plumage patches in at least one body region. The three species lacking UV phenomena were the White Cockatoo *Cacatua alba*, the Blue-eyed Cockatoo *C. ophthalmica* and the Long-billed Cockatoo *C. tenuirostris*. According to our definition of UV phenomena, none of these unicoloured white-plumaged birds could exhibit UV phenomena. Nevertheless, their white plumage showed a considerable amount of UV reflection, as was the case in almost all white feathers we measured. Thus, we did not find a single parrot species lacking considerable amounts of UV-reflecting plumage, which makes

this order interesting for further investigations, especially taking into account recent studies of feather pigments found only in parrots and the extraordinary phenomenon of fluorescence found in 52 species of parrots (Pearn *et al.* 2001, Stradi *et al.* 2001, Arnold *et al.* 2002, Masello *et al.* 2004, McGraw & Nogare 2004).

We found most of the UV phenomena in the coloured feather regions. Therefore, any black, brown or dull coloured bird lacking brightly coloured feather patches would most likely not show UV phenomena, and thus would only reflect UV to a certain extent as a contribution to overall brightness (Fig. 1). One of the few exceptions was the non-iridescent black feathers of the Black Lory *Chalcopsitta atra*. The intensive UV reflection stems from light scattering by the spongy structure consisting of quasi-ordered arrays of keratin separated by air vacuoles (Finger *et al.* 1992, Prum & Torres 2003). Put simply, UV reflection in iridescent feathers is caused by light reflected from the interfaces of regular stacks of higher and lower density material, such as rows of regularly orientated keratin rods (Cuthill *et al.* 2000).

In general, the spectra of iridescent feathers are similar to non-iridescent coloured feathers. However, brightly coloured iridescent feathers, such as the green breast plumage of the Purple-bibbed

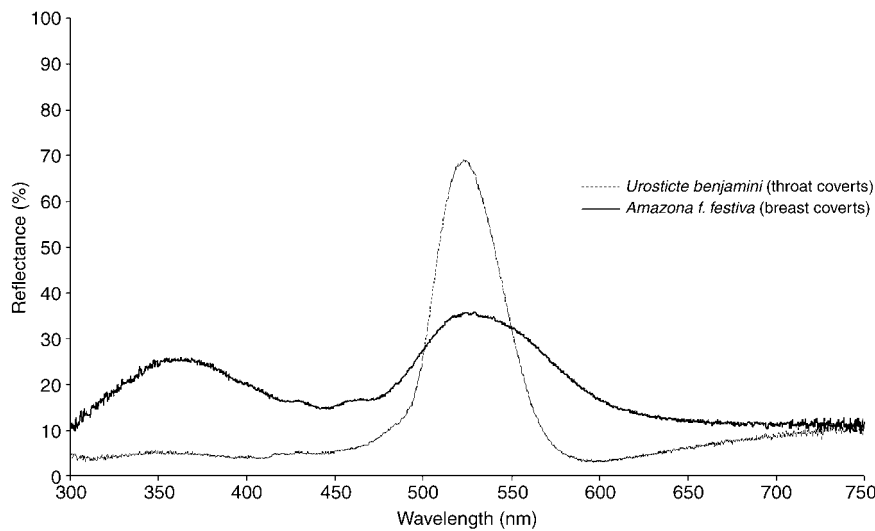


Figure 2. Comparison of spectra of iridescent and non-iridescent feather patches. The iridescent green throat feathers of the hummingbird Purple-bibbed Whitetip *Urosticte benjamini* show a clear peak, being much narrower than peaks of non-iridescent feathers of the green breast of the Red-backed Amazon *Amazona festiva*. The latter additionally shows a significant peak in the UV, a UV phenomenon. The spectra were taken on one specimen.

Whitetip hummingbird *Urosticte benjamini*, always exhibit a characteristic peak, being much narrower than the peaks of non-iridescent feathers such as the green breast of the Red-backed Amazon *Amazona festiva*, which also exhibits a UV peak (Fig. 2). Blue-coloured feather patches, found in many species of different orders, always exhibited distinctive amounts of UV. This is due to the fact that blue and violet lie next to the UV waveband and always extend into the UV to some degree. Blue and violet iridescent feather patches do not necessarily extend into the UV, due to their much narrower peaks compared with non-iridescent colours. Blue and violet spectra either increase in the proportion of the UV waveband, with their maximum lying in the UV, as in Josephine's Lorikeet *Charmosyna josefinae*, or decrease in intensity in the UV as is the case in the dorsal feathers of the Hyacinth Macaw *Anodorhynchus hyacinthinus* (Fig. 3). We assume that peaks in the UV and high amounts of UV reflection are more likely to play a specific role in courtship or other intraspecific behaviours than UV reflectance, as shown in Figure 1.

Although in many cases both female and male bird were measured, we did not discover any cryptic sexual dimorphisms, visible only in the UV. In brightness, the spectra show considerable variance (up to 10% across the spectrum), so that, especially with museum skins, spectra varying only in brightness have to be considered with caution due to colour changes which

usually are invisible to the human eye. After having examined nearly 1000 species of birds and not having found a single hidden sexual dimorphism, as has been detected in Blue Tits (Andersson *et al.* 1998, Hunt *et al.* 1998), we consider easily detectable cryptic dimorphisms as rare. If there are more cryptic dimorphisms, they are most likely to be discovered when dealing with totally fresh skins or live specimens and by comparing a substantial number of birds.

As suggested in earlier studies, we share the view that UV plays an important role but one that is no more prominent than any other plumage colour involved in avian courtship behaviour (Cuthill *et al.* 2000, Hunt *et al.* 2001). However, UV-reflecting plumage should be treated in the same way as any coloured feather patch visible to humans. The high level of UV phenomena found in this study which correlated with coloured feather patches throughout the class Aves underlines the possibility of UV playing an extraordinary role in mate choice. In contrast to pigment-based plumage, structurally based ornaments, such as ultraviolet coloured plumage parts, have been little studied, in part because they do not appear to be as variable as pigment-based ornaments. However, several recent studies indicate that structurally based ornaments serve as an honest indicator of age and quality and communicate different sets of information from pigment-based ornaments (Keyser & Hill 1997, McGraw *et al.* 2002). Furthermore, all behavioural

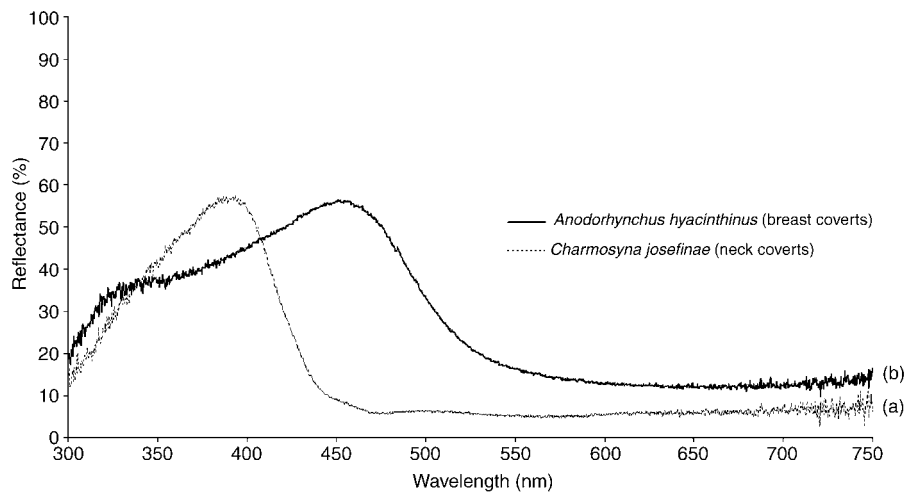


Figure 3. Blue/UV-coloured feather patches with different amounts of UV reflectance. The maximum excitation of the spectra of (a) the blue neck feathers of Josephine's Lorikeet *Charmosyna josephinae* extends well into the UV, in contrast to (b) the blue breast feathers of the Hyacinth Macaw *Anodorhynchus hyacinthinus*, in which the excitation intensity in the UV decreases. Both species show clear UV phenomena: in both species reflectance in the UV spectrum exceeds the lowest reflection in the range of 400–700 nm. The spectra were taken on one specimen.

mate choice experiments involving UV to date show a significant role for UV signalling (Bennett *et al.* 1996, 1997, Andersson & Amundsen 1997, Andersson *et al.* 1998, Hunt *et al.* 1998, Johnsen *et al.* 1998). Due to the considerable numbers of bird species with UV phenomena in coloured feather patches, we suggest more UV-related behavioural studies on birds of the following orders might be promising: Psittaciformes, Passeriformes, Trogoniformes, Musophagiformes, Upupiformes, Trochiliformes and Piciformes.

We thank Karl-Ludwig Schuchmann for his advice and his supporting ideas, and Georg Meyer-Wiel for his assistance with feather identification. We also thank Joel L. Cracraft, Paul R. Sweet, Shannon Kenney and Peter Capainolo from the American Museum of Natural History in New York, Nate Rice and Leo Joseph from the Academy of Natural Sciences in Philadelphia, and Peter Jones from the Natural History Museum in Tring, UK, for support and for allowing access to the collections. We are also grateful to Alexander Mullen and Brian Hillcoat for their critical overview of the manuscript. This study was made possible by grants from the Heinrich Hertz Foundation of the State Department of Science and Research of North Rhine-Westphalia, Germany, and the Collection Study Grant of the American Museum of Natural History.

REFERENCES

- Andersson, S. & Amundsen, T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond. B* **264**: 1587–1591.
- Andersson, S., Örnborg, J. & Andersson, M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. Lond. B* **265**: 445–450.
- Arnold, K.E., Owens, I.P.F. & Marshall, N.J. 2002. Fluorescent sexual signalling in parrots. *Science* **295**: 92.
- Bennett, A.T.D. & Cuthill, I.C. 1994. Ultraviolet vision in birds: what is its function? *Vision Res.* **34**: 1471–1478.
- Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proc. Natl Acad. Sci. USA* **94**: 8618–8621.
- Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Maier, E.J. 1996. Ultraviolet vision and mate choice in zebra finches. *Nature* **380**: 433–435.
- Bowmaker, J.K. 1979. Visual pigments and oil droplets in the pigeon retina, as measured by microspectrophotometry, and their relation to spectral sensitivity of the pigeon. In Granda, A.M. & Maxwell, J.H. (eds) *Neural Mechanisms of Behaviour in the Pigeon*: 287–305. New York: Plenum.
- Bowmaker, J.K., Heath, L.A., Wilkie, S.E. & Hunt, D.M. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retina of birds. *Vision Res.* **37**: 2183–2194.
- Bowmaker, J.K., Kovach, J.K., Whitmore, A.V. & Loew, E.R. 1993. Visual pigments and oil droplets in genetically manipulated and carotenoid deprived quail: a microspectrophotometric study. *Vision Res.* **33**: 571–578.
- Bowmaker, J.K. & Martin, G.R. 1978. Visual pigments and colour vision in a nocturnal bird, *Strix aluco* (Tawny Owl). *Vision Res.* **18**: 1125–1130.
- Bowmaker, J.K. & Martin, G.R. 1985. Visual pigments and oil droplets in the penguin, *Spheniscus humboldti*. *J. Comp. Physiol. A* **156**: 71–77.
- Burkhardt, D. 1982. Birds, berries and UV. *Naturwissenschaften* **69**: 153–157.
- Burkhardt, D. 1989. UV vision: a bird's eye view of feathers. *J. Comp. Physiol. A* **164**: 787–796.

- Church, S.C., Bennett, A.T.D., Cuthill, I.C. & Partridge, J.C. 1998. Ultraviolet cues affect the foraging behaviour of blue tits. *Proc. R. Soc. Lond. B* **265**: 1509–1514.
- Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S. & Hunt, S. 2000. Ultraviolet vision in birds. *Adv. Stud. Behav.* **29**: 159–214.
- Das, D. 1997. *Visual Pigments, Oil Droplets and Opsin Sequences from the Canary, Serinus canaria*. PhD thesis, University of London.
- Eaton, M.D. 2006. A phylogenetic perspective on the evolution of chromatic ultraviolet plumage coloration in grackles and allies (Icteridae). *Auk* **123**: 211–234.
- Eaton, M.D. & Lanyon, S.M. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proc. R. Soc. Lond. B* **270**: 1721–1726.
- Emmerton, J. & Delius, J.D. 1980. Wavelength discrimination in the visible and ultraviolet spectrum by pigeons. *J. Comp. Physiol. A* **141**: 47–52.
- Emmerton, J. & Remy, M. 1983. The pigeon's sensitivity to ultraviolet and 'visible' light. *Experientia* **39**: 1161–1163.
- Endler, J.A. 1993. The color of light in forests and its implications. *Ecol. Monogr.* **63**: 1–27.
- Endler, J.A. 1995. Ultraviolet light environments in forests and shrubs, and some implications for UV-containing color patterns. *J. Am. Soc. Zool.* **145**: 238.
- Endler, J.A. & Théry, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. Nat.* **148**: 421–452.
- Finger, E. 1990. *Spektrale Reflexion von Vogelgefieder*. Thesis. University of Regensburg.
- Finger, E., Burkhardt, D. & Dyck, J. 1992. Avian plumage colors: origin of UV reflection in a black parrot. *Naturwissenschaften* **79**: 187–188.
- Goldsmith, T.H. 1980. Hummingbirds see near ultraviolet light. *Science* **207**: 786–788.
- Goldsmith, T.H., Collins, J.S. & Perlmann, D.L. 1981. A wavelength discrimination function for the hummingbird *Archilochus alexandri*. *J. Comp. Physiol.* **143**: 103–110.
- Goldsmith, T.H. & Goldsmith, K.M. 1979. Discrimination of colors by the Black-chinned Hummingbird, *Archilochus alexandri*. *J. Comp. Physiol.* **130**: 209–220.
- Hart, N.S. 1998. *Avian Photoreceptors*. PhD thesis, University of Bristol.
- Hart, N.S. 2002. Vision in the peafowl (*Aves: Pavo cristatus*). *J. Exp. Biol.* **207**: 1229–1240.
- Hart, N.S. 2004. Microspectrophotometry of visual pigments and oil droplets in a marine bird, the wedge-tailed shearwater *Puffinus pacificus*: topographic variations in photoreceptor spectral characteristics. *J. Exp. Biol.* **207**: 1229–1240.
- Hart, N.S., Partridge, J.C. & Cuthill, I.C. 1998. Visual pigments, oil droplets and cone photoreceptor distribution in the European Starling (*Sturnus vulgaris*). *J. Exp. Biol.* **201**: 1433–1446.
- Hart, N.S. & Vorobyev, M. 2005. Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *J. Comp. Phys.* **191**: 381–392.
- Hausmann, F., Arnold, K.E., Marshall, N.J. & Owens, I.P.F. 2002. Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B* **270**: 61–67.
- Hunt, S., Bennett, A.T.D., Cuthill, I.C. & Griffiths, R. 1998. Blue Tits are ultraviolet tits. *Proc. R. Soc. Lond. B* **265**: 451–455.
- Hunt, S., Cuthill, I.C., Bennett, A.T., Church, S.C. & Partridge, J.C. 2001. Is the ultraviolet waveband a special communication channel in avian mate choice? *J. Exp. Biol.* **204**: 2499–2507.
- Huth, H.-H. & Burkhardt, D. 1972. Der spektrale Seebereich eines Violettöhr-Kolibris. *Naturwissenschaften* **59**: 650.
- Jacobs, G.H., Crognale, M. & Fenwick, J. 1987. Cone pigment of the Great Horned Owl. *Condor* **89**: 434–436.
- Jane, S.D. & Bowmaker, J.K. 1988. Tetrachromatic colour vision in the duck (*Anas platyrhynchos* L.): microspectrophotometry of visual pigments and oil droplets. *J. Comp. Physiol. A* **162**: 225–235.
- Johnsen, A., Andersson, S., Örnborg, J. & Lifjeld, J.T. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (*Aves: Luscinia s. svecica*): a field experiment. *Proc. R. Soc. Lond. B* **265**: 1313–1318.
- Keyser, A.J. & Hill, G.E. 1997. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc. R. Soc. Lond. B* **266**: 711–777.
- Koivula, M., Korpimäki, E. & Viitala, J. 1997. Do Tengmalm's owls see vole scent marks visible in ultraviolet light? *Anim. Behav.* **54**: 873–877.
- Koivula, M. & Viitala, J. 1999. Rough-legged Buzzards use vole scent marks to assess hunting areas. *J. Avian Biol.* **30**: 329–332.
- Kreithen, M.L. & Eisner, T. 1978. Ultraviolet light detection by the homing pigeon. *Nature* **272**: 347–348.
- Liebmann, P.A. 1972. Microspectrophotometry of photoreceptors. In Dartnall, H.J.A. (ed.), *Photochemistry of Vision* Vol. 7 no. 1: 481–528. Berlin: Springer-Verlag.
- Maier, E.J. & Bowmaker, J.K. 1993. Colour vision in the passeriform bird, *Leiothrix lutea*: correlation of visual pigment absorbency and oil droplet transmission with spectral sensitivity. *J. Comp. Physiol. A* **172**: 295–301.
- Masello, J.F., Pagnossin, M.L., Lubjuhn, T. & Quillfeldt, P. 2004. Ornamental non-carotenoid red feathers of wild burrowing parrots. *Ecol. Res.* **19**: 431–432.
- McGraw, K.J., Mackillop, E.A., Dale, J. & Hauber, M.E. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* **205**: 3747–3755.
- McGraw, K.J. & Nogare, M.C. 2004. Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots. *Comp. Biochem. Physiol. B* **138**: 229–233.
- McNaught, M.K. & Owens, I.P.F. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? *J. Evol. Biol.* **15**: 505–514.
- Ödeen, A. & Håstad, A. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* **20**: 855–861.
- Osorio, D. & Ham, A.D. 2002. Spectral reflectance and directional properties of structural coloration in bird plumage. *J. Exp. Biol.* **205**: 2017–2027.
- Parrish, J., Smith, R., Benjamin, R. & Ptacek, J. 1981. Near-ultraviolet light reception in mallards and Passeriformes. *Trans. Kansas Acad. Sci.* **84**: 147.
- Pearn, S.M., Bennett, A.T.D. & Cuthill, I.C. 2001. Ultraviolet vision, fluorescence mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. *Proc. R. Soc. Lond. B* **268**: 2273–2279.
- Probst, R., Pavliciv, M. & Viitala, J. 2002. UV reflecting vole scent marks attract a passerine the Great Grey Shrike *Lanius excubitor*. *J. Avian Biol.* **33**: 437–440.

- Prum, R.O. & Torres, R.** 2003. Structural colouration of avian skin: convergent evolution of coherently scattering dermal collagen arrays. *J. Exp. Biol.* **206**: 2409–2429.
- Sibley, C.G. & Monroe, B.L.** 1990. *Distribution and Taxonomy of the Birds of the World*. New Haven, CT: Yale University Press.
- Siitari, H., Viitala, J. & Hovi, M.** 2002. Behavioural evidence for ultraviolet vision in a tetraonid species – foraging experiment with Black Grouse (*Tetrao tetrix*). *J. Avian Biol.* **33**: 199–202.
- Silberglied, R.E.** 1979. Communication in the ultraviolet. *Ann. Rev. Ecol. Syst.* **10**: 373–398.
- Sillmann, A.J., Bolnick, D.A., Haynes, L.W., Walter, A.E. & Loew, E.R.** 1981. Microspectrophotometry of the photoreceptors of palaeognathous birds – the Emu and the Tinamou. *J. Comp. Physiol.* **144**: 271–276.
- Stradi, R., Pini, E. & Celentano, G.** 2001. The chemical structure of the pigments in *Ara macao* plumage. *Comp. Biochem. Physiol. B* **130**: 57–63.
- Viitala, J., Korpimäki, E., Palokangas, P. & Koivula, M.** 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* **373**: 425–427.
- Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C.** 1998. Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A* **183**: 621–633.
- Wright, M.V. & Bowmaker, J.K.** 1998. Visual pigments and oil droplets in the retinae of palaeognathous birds. *Invest. Ophthalmol.* **39**: 1059.
- Wright, M.V. & Bowmaker, J.K.** 2001. Retinal photoreceptors of paleognathous birds: the ostrich (*Struthio camelus*) and rhea (*Rhea americana*). *Vision Res.* **41**: 1–12.
- Yokoyama, S., Radlwimmer, F.B. & Blow, N.S.** 2000. Ultraviolet pigments in birds evolved from violet pigments by a single amino acid change. *Proc. Natl Acad. Sci. USA* **97**: 7366–7371.

Received 21 September 2006; revision accepted 30 April 2007.