The ubiquity of avian ultraviolet plumage reflectance

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Although several bird species have been shown to reflect ultraviolet (UV) light from their plumages, the incidence of UV reflectance, and therefore the potential for UV or UV-enhanced signals, across the avian tree of life is not known. In this study, we collected reflectance data from the plumages of 312 bird species representing 142 families. Our results demonstrate that all avian families possess plumages that reflect significant amounts of UV light. The ubiquity of UV reflectance indicates that all studies of avian behaviour, ecology and evolution involving plumage coloration would benefit from consideration of plumage reflectance in the UV portion of the electromagnetic spectrum. Additionally, we demonstrate the existence of cryptic UV plumage patches and cryptic dimorphism among birds.

Keywords: birds; ultraviolet reflectance; plumage; dichromatism; dimorphism

1. INTRODUCTION

Bird coloration figured prominently in *The origin of species* (Darwin 1859) and has subsequently played an important role in the development of theories of speciation (Mayr 1942), sexual selection (Selander 1965), communication (Rohwer 1982) and behaviour (Burt 1986). These theories, and the majority of research on bird plumages, have focused on colours resulting from the portion of the light spectrum visible to humans (400–700 nm). Indeed, this focus constitutes an unstated assumption in avian biology that birds perceive light, and thus colours, in a manner similar to humans. However, visual sensitivity to ultraviolet (UV) wavelengths was probably the ancestral vertebrate condition (Shi *et al.* 2001) and is common across many animal taxa (Jacobs 1992). Over the last two decades, research has demonstrated that all bird species examined (36 species representing eight orders) (Bennett & Cuthill 1994; Cuthill *et al.* 2000) are physiologically capable of seeing UV wavelengths owing to the presence of a fourth type of cone in their retinas (Chen *et al.* 1984) (humans have only three cone types). The fourth avian cone type, often referred to as the 'UV cone', is maximally sensitive at *ca.* 365 or 410 nm depending on the species examined (Bennett & Cuthill 1994; Cuthill *et al.* 2000). Consequently, the human eye is oblivious to a significant portion of the colour communication available to birds.

Research over the last decade has shown that birds employ their ability to detect UV light in behavioural interactions (e.g. Andersson *et al.* 1998; Hunt *et al.* 1998). Several species have been shown to use UV plumage information during mate choice (Andersson & Amundsen 1997; Bennett *et al.* 1997; Hunt *et al.* 1999; Pearn *et al.* 2001). Females can assess small differences in the reflectance curves between males, suggesting that even small contributions of the UV to the colour content of a feather patch can influence the biological significance of that region of the plumage. Although it is not clear whether

UV is a special channel of communication (Hunt *et al.* 2001; Hausmann *et al.* 2003), it is a significant and biologically important portion of the visual information processed by birds.

While few avian biologists today would assume that the visual capabilities of birds are comparable to those of humans, most studies of avian coloration continue to ignore this aspect of visual communication (Irwin 1994; Wolfenbarger 1999; Figuerola & Green 2000; Omland & Lanyon 2000). We contend that this is the result, in part, of our poor understanding of the frequency of UV-reflecting plumages across the avian tree of life.

While recent research has shown that feathers in at least some bird species do reflect UV wavelengths (Burkhardt 1989; Bennett & Cuthill 1994; Hunt *et al.* 1998; Andersson 1999; Doucet 2002; Hausmann *et al.* 2003), the restricted taxonomic sampling of these studies means that no conclusion can be drawn about the phylogenetic distribution of UV reflectance among birds. Furthermore, plumage colour is one of the more evolutionarily labile features (Omland & Lanyon 2000) (hence its importance in the study of behavioural ecology and evolution), which again makes it difficult to extrapolate to all birds from the few studies documenting UV reflectance in single species. Therefore, we conclude that the current knowledge about UV reflectance does not offer adequate guidance for future studies of avian coloration, and hence a gap exists between what is known about the visual capabilities of birds and our knowledge of the ubiquity of UV reflectance in the class Aves. Our study was designed to test the ubiquity of UV reflectance across avian families and thus to inform future experimental work on plumage colours and their signalling functions.

2. MATERIAL AND METHODS

(a) Data collection

We sampled species from the entire class Aves using familial relationships as a proxy for phylogeny. A computer program was used to select, at random, three genera from each family and one species from each of the chosen genera. Where a family contained fewer than three genera, representatives from all genera

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were included in the study. In total, 312 species were sampled from 142 out of 143 avian families (Raphidae was not sampled) following the taxonomy of Sibley & Monroe (1990). All data were collected from research study skins at the Field Museum of Natural History, Chicago, IL, USA. Where a selected species was not in the Field Museum's collection, we selected the next species from that genus as arranged in the museum drawers. A complete species list is available from the authors upon request.

We took measurements for each specimen from every visually distinct dorsal and ventral colour patch. A colour patch was defined as an area of continuous visual coloration greater than ca. 4 mm² (the limit of the resolution of the equipment). Therefore, finely barred, streaked or mottled plumage was ignored. In total, 3763 plumage patches were sampled across the 312 species. In order to document hidden UV patterns, additional measurements were taken within large continuous-colour patches. These were saved only if they differed markedly from the original reading obtained for that patch. Using an Ocean Optics (Dunedin, FL, USA) S2000 spectrometer with a PX-2 pulsed xenon light source calibrated against a Spectralon white reflectance standard, orientated at 90° to the feather surface, we captured reflectance curves (300–800 nm) from a male and female for each species. The main goal of this research was to determine the frequency of UV-reflecting plumages across a broad taxonomic sample, rather than to quantify rigorously the coloration for each particular species sampled. Therefore, we decided to maximize the number of taxa examined and settled for the examination of one specimen of each sex from each species. Individuals with the freshest looking breeding plumage were chosen.

Hausmann *et al.* (2003) found brightness to be the main component of coloration affected by specimen age; however, they along with other authors (Andersson 1999; Endler & Théry 1996) concluded that the effects of specimen age on UV coloration were not sufficient to cause misinterpretation of their results. In a separate study, we also found a weak correlation between specimen age and UV reflectance in structural colours, with older specimens reflecting at lower levels in the UV (M. D. Eaton and S. M. Lanyon, unpublished data). However, we found that human visual indicators (e.g. dirtiness) were driving this correlation between specimen age and UV levels, and, by choosing specimens with the freshest looking plumage, we avoided this association. Furthermore, if the older specimens included in our sampling for the present study were, in fact, reflecting reduced UV, then this would result in an underestimation of the frequency of UV reflectance among birds.

(b) Data analyses

The visual and UV portions of the 3763 spectra obtained in this study were examined and classified in two ways. First, in order to assess the frequency of UV reflectance as a function of reflectance in the human visual spectrum, each reflectance curve was categorized into one of seven visual colour classes: black, brown, red, yellow, green, blue or white; 218 reflectance curves did not fall neatly into one of these colour classes and were excluded from colour classification. Second, each reflectance curve was classified as having a mean UV reflectance (between 340 and 380 nm) of less than 5%, between 5% and 10%, between 10% and 20%, or greater than 20% of incident light. These four levels of UV reflectance were chosen arbitrarily, because it is not clear what constitutes biologically significant UV plumage reflectance. We examined the distributions of these four levels of UV reflectance across the visual colours and across

all species and families in order to assess the phylogenetic pattern.

To determine the occurrence of cryptic dimorphism (male and female feather patches that look the same to human observers but appear distinct to birds), we examined homologous feather patches for each pair of male and female specimens. Cryptic dimorphism was defined in this study as spectra differing by less than 10% at the peak sensitivities of each of the three human cone types, and differing by more than 10% at the peak sensitivity of the avian UV cone type. Because of the differences in visual capabilities between humans and birds, and the increased sensitivity of the UV cone type, we relaxed our definition of cryptic dimorphism to include spectra differing by more than 5% at the peak sensitivity of the avian UV cone type.

3. RESULTS

Our results demonstrated that reflectance of incident UV radiation varied markedly across the range of plumage patches sampled in this study: 63.3% of sampled feather patches reflected a significant proportion (more than 5%) of UV light, with 34.6% reflecting greater than 10% and 13.6% reflecting in excess of 20% of incident UV wavelengths.

We confirmed that no visual colour class represented in bird plumages was always associated with UV reflectance, just as no visual colour class always lacked UV reflectance (Burkhardt 1989). Nonetheless, some generalizations emerged (figure 1). The majority (more than 50%) of black, brown and red feathers that we sampled reflected less than 5% of the UV wavelengths. By contrast, 50–75% of yellow and green patches examined had greater than 5% UV, and more than 75% of blue patches had a UV reflectance of higher than 5%. Nearly all white feather patches reflected UV wavelengths, with very few (2%) reflecting less than 5% of UV light, and a high proportion of both white and blue feather patches reflected greater than 10% UV (690 out of 781 and 55 out of 88, respectively).

UV reflectance was widespread across all 142 families in our study, regardless of the threshold used to define its presence (figure 2). We were concerned that this phylogenetic ubiquity of UV reflectance might be the result of white feather patches. More than 98% of white feathers reflected at least 5% of the UV wavelengths (figure 1), and 75% of specimens examined had at least one white feather patch. Therefore, we excluded white feather patches from our analysis to investigate the possibility of a phylogenetic pattern in the distribution of UV reflectance in other visual colours. UV reflectance in excess of 5% somewhere on the non-white plumage was still found in 140 out of 142 families, and in all but 15 out of the 312 (95.2%) species examined (figure 2). One of the two families lacking significant UV reflectance from non-white plumage, the Chionididae, has no non-white plumage. Therefore, the Rheidae, for which we examined *Rhea pennata*, is the only avian family in our study that appears to lack significant UV reflectance from non-white plumage patches.

Virtually all species examined (310 out of 312) had a UV reflectance greater than 5% somewhere on their plumage. This estimate of the proportion of species with UV-reflecting plumage is higher than the 72% estimate

Figure 1. UV reflectance across the visual colours in birds. The proportion of feather patches in each of seven colour classes (defined by the human visual system) with differing levels of UV reflectance. Feather patches were sampled from one male and one female in each of 312 species representing 142 out of 143 recognized avian families (Sibley & Monroe 1990). The number (n) of feather patches included in each class is given below the colour. Key: black bars, more than 20% UV reflectance; dark-grey bars, 10–20% UV reflectance; light-grey bars, 5–10% UV reflectance; open bars, 0–5% UV reflectance.

Figure 2. UV reflectance across taxa in birds. The proportion of 142 families and 312 species with differing levels of UV reflectance. Nearly all families and virtually all species examined possessed UV-reflecting (minimum of 5% of incident UV light reflected) plumage patches even when white plumage patches were excluded. Key as in figure 1.

obtained in a taxonomically more restricted study by Hausmann *et al.* (2003). However, these authors used a more conservative definition of UV-reflecting plumage. Under a criterion of 10% defining the presence of UV reflectance, our results still indicate that 91% of species examined have UV coloration in at least one location on the body (figure 2).

We were able to identify only two possible examples of cryptic UV patches (variation in UV reflectance within a visual colour patch) in the 3763 colour patches examined (orange nape in *Amblyornis subalaris* and violet throat in *Malurus cyaneus*). However, cryptic dimorphism was more common. Out of 1304 homologous feather patches on conspecific males and females that differed by less than 10% reflectance at the peak sensitivities of each of the human cone types (437, 533 and 564 nm), 10 patches (0.8%) differed between the sexes by more than 10% at

the peak sensitivity of the avian UV cone type. Given that the UV cone type is extremely sensitive in birds (Maier 1994), we also determined the frequency of cryptic dimorphism at the 5% level. Out of these same 1304 homologous feather patches, 104 (8%) demonstrated a sexual dichromatism of greater than 5% at the peak sensitivity of the avian UV cone type. In order to determine how the observed differences between males and females compare with variation within the sexes, we examined 10 males and 10 females for each of five species in which we identified cryptic dimorphism. Figure 3 shows that variation in UV reflectance between males and females is larger than variation within sexes.

4. DISCUSSION

The distribution of UV reflectance across the visual colour classes provides general guidance as to where UV reflectance is likely. For example, brown and black feather patches are less likely to have high levels of UV reflectance than are colour patches such as green, yellow and blue (figure 1). However, UV-reflectance values measured in the laboratory do not necessarily indicate their functionality as plumage signals. An interpretation of the biological significance of these reflectance values requires consideration of the light environment in which birds exist and the manner in which their plumages interact with that environment (Endler 1993). Experimental studies are needed to determine the current function of particular colorations and to identify specific plumage signals. Nonetheless, the overall coloration of a bird undoubtedly serves some biological function, and our results show that UV reflectance can be a significant component of nearly any feather patch, and must be accounted for during future studies.

Avian behavioural research has repeatedly shown that variation in the UV component of coloration can function as a signal to conspecifics (Bennett *et al.* 1997; Hunt *et al.* 1999; Pearn *et al.* 2001). Spectral-sensitivity curves for

Figure 3. Examples of cryptic sexual dichromatism.

Reflectance curves from homologous feather patches of 10 males and 10 females of the following species: (a) *Hirundo smithii*—back; (b) *Nyctyornis athertoni*—throat; (c) *Irena cyanogaster*—crissum; (d) *Ptilonopus cinereus*—crissum; (e) *Atelornis pittoides*—collar ($n = 5$ males and 2 females). In all graphs, the upper curve represents average male reflectance for that feather patch and the lower curve represents average female reflectance for that feather patch, with error bars indicating the 95% confidence intervals for reflectance values every 50 nm. Each pair of homologous patches was defined as cryptically dimorphic.

behavioural studies in blue tits (*Parus caeruleus*) (Andersson *et al.* 1998), European starlings (*Sturnus vulgaris*) (Bennett *et al.* 1997), pied flycatchers (*Ficedula hypoleuca*) (Siitari *et al.* 2002) and bluethroats (*Luscinia svecica*) (Andersson & Amundsen 1997) have demonstrated that differences in UV plumage reflectance of as small as 5% can influence intraspecific interactions. The biological significance of these small UV differences implies that the distribution of UV-reflectance levels shown in figure 1 represents a huge amount of potential information available to birds, yet not apparent to human observers.

If UV reflectance was taxonomically restricted, then only studies on UV-reflecting lineages would need to be concerned with the possibility of UV signalling. However, our results indicate that UV reflectance is widespread across all taxa in our study (figure 2). The distribution of UV-reflecting plumage across the avian tree indicates that there is no phylogenetic pattern at the family level, which suggests that the potential impact of UV reflectance on avian research is far reaching.

Comparative analysis of UV reflectance indicates that the ancestor of modern birds, and the ancestors of all modern bird families, possessed plumages that reflected significant UV. However, the high frequency of white feathers in avian plumages (75% of species examined had at least one white feather patch) could be responsible for the ubiquity of UV reflectance across the avian tree of life, considering that nearly all white feathers reflected highly in the UV (figure 1). Re-analysis with white feathers excluded did not change our conclusion regarding the phylogenetic distribution of UV reflectance. Our results clearly indicate that UV reflectance has been evolving in modern birds for much of their history, and should become an integral part of avian research. However, the selective forces driving UV evolution are beyond the scope of this study. Light environment most probably plays a role in the evolution of colour patterns (Endler & Théry 1996; Fuller 2002; McNaught & Owens 2002), as do other aspects of a given species biology. Hausmann *et al.* (2003) concluded that UV coloration in Australian birds is associated with those areas of the plumage involved in courtship displays. Clearly, much more extensive sampling of species within each avian family is needed to illuminate the causative factors in the evolution of UV coloration.

Although we cannot report specific selective agents of UV-reflecting plumage evolution, we do present evidence that UV reflectance can evolve independently of visual colours. UV reflectance in feathers results from the micro-structural arrangement of feather keratin as does blue

a passerine, the red-billed leiothrix (*Leiothrix lutea*), revealed that retinal sensitivity to UV wavelengths was 10-fold greater than sensitivity to human-visible wavelengths (Maier 1994). This suggests that relatively small differences in UV reflectance could be detected and perceived as distinct colours by the avian visual system. Indeed,

feather colour (Prum *et al.* 1999). Our results show that all visual colour classes have the potential to be UV-enhanced or UV-lacking, whether 5% or 10% is used to define the presence of UV reflectance (figure 1). Therefore, the ability of feathers to reflect significant levels of UV light appears to evolve independently of visual colours. It follows that two feather patches that look identical to human eyes, whether located contiguously on one bird or on conspecifics, might actually differ in their UV reflectances. This suggests the possibility of cryptic patterns (when UV reflectance changes within a continuous visual colour patch), cryptic variation within sexes (when the level of UV reflectance varies between conspecific individuals of one sex) and/or cryptic dimorphism (when homologous colour patches on conspecific males and females differ only in their UV reflectances). Our methodology did not allow us to analyse UV variation within the sexes.

Although evidence of hidden UV colour patterns was very rare, we did find that cryptic dimorphism, as first discovered in blue tits (Hunt *et al.* 1998; Andersson *et al.* 1998), might be substantially more common among birds. Based on our observations, we could not perceive coloration differences in feather patches whose associated spectra differed in reflectance by as much as 10% across the human-visible portion of the spectrum. Since avian vision is more complex, owing to the presence of a fourth retinal cone and narrower spectral-sensitivity curves for each cone (Varela *et al.* 1993), birds may actually perceive coloration differences in many of these feather patches that showed differing spectral reflectance curves (figure 3) yet appeared visually identical to us (Osorio *et al.* 1999). We identified 104 pairs (8% of homologous feather patches on males and females) of such cryptic sexually dichromatic patches, which is probably an underestimate of the cryptic dimorphism in our data because our definition of this phenomenon may be too conservative. First, there may have been pairs of feather patches whose spectral curves differed by more than 10% across the human-visible wavelengths and yet appeared to be the same colour. These would not be considered under our definition of cryptic dimorphism (see § 2b). Second, our definition would classify as monomorphic those patches that differed by less than 5% at the peak sensitivity of the UV cone, even though research has shown that such small UV differences (less than 5%) can influence behaviour (e.g. Bennett *et al.* 1997; Andersson *et al.* 1998; Hunt *et al.* 1998; Siitari *et al.* 2002). The existence of cryptic dimorphism produced by sexual differences in structural colours that humans are incapable of seeing, suggests that there is a class of sexually selected traits of which human observers have been unaware. This has important implications for our understanding of sexual selection, given that structural colours (e.g. UV) may function as honest indicators of individual quality (Andersson 1999; Sheldon *et al.* 1999; Keyser & Hill 2000).

5. CONCLUSION

We have demonstrated that: (i) UV plumage reflectance is ubiquitous across the avian tree of life; (ii) feathers of all colours can have a biologically significant UV reflectance; and (iii) black, brown and possibly red feather patches are the least likely to reflect high levels of UV.

Combining these data with previously demonstrated UV visual receptivity and behaviour based on UV variability solidifies the need for all avian behavioural and ecological studies to consider explicitly the UV contribution to avian coloration. By demonstrating that UV reflectance is not confined to a subset of bird lineages but is in fact characteristic of nearly all bird species, our results fill a critical void regarding future research. Studies that fail to assess UV plumage reflectance could yield misguided conclusions. In addition, our study revealed exciting possibilities for future research on colour variation. Specifically, more data are required to determine the frequencies of UV-based colour patterns and the sexual dichromatism that is apparent to birds yet undetectable by human vision.

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