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**Understanding What We Cannot See:
An Investigation of Research on Signals and Ultraviolet Plumage Reflectance**

With respect to all metaphorical meanings intended in the old cliché “a bird’s eye view,” there are more drastic differences between human and avian visual systems than spatial perspectives. In fact, research on avian vision is very difficult because humans cannot perceive wavelengths of light to which the avian retina is sensitive; collectively called ultraviolet light (UV). Scientists have only begun to understand the ecological significance of this sensory ability. UV wavelength light reflectance is certainly an important component of complex plumage patterns in many species, as determined using technical imaging equipment (Eaton and Lanyon 2002). There is convincing evidence that UV reflectance acts as an intraspecific signal. Of what? Researchers are still in the field, but experiments suggest that UV reflectance conveys information of individual fitness and environmental condition. Recently, ornithologists have begun to tackle an equally complex question; how do information-receiving birds respond to changes in signal strength? This paper is an investigation of such responses to variation of UV reflectance, including a discussion of present hypotheses that describe adaptive explanations for the evolution of such behavior. It is important to keep in mind that UV reflectance participates in an overall image conveyed by plumage in general. Thus, broadly, this is an exploration of the complexity of avian appearance and its significance to relations between birds.

Visual perception is quite a fascinating phenomenon, dependent on more than just the intrinsic properties of the perceived object. Equally significant variables are the

sensory apparatus and neural machinery of the perceiver-organism (Cuthill et al. 2000). In birds, color vision is a complex medium for information exchange and an integral mechanism for sensing behavioral stimuli (Endler and Mielke 2005). It is wrong to anthropomorphically assume that birds see the world as humans do. Indeed, in contrast to humans', avian retinal cones contain oil droplets which cut-off short wavelengths, acting as filters that narrow visual sensitivity range, exaggerating difference in cone-type stimulation and thus enhancing color saturation (Hart 2001). In addition, birds are sensitive to ultraviolet wavelengths. Using a technique called microspectrophotometry biologists have determined four cone classes of rhodopsin pigment on avian retinal cones: a long wavelength sensitive, LWS (max-wavelength, 543-571 nm); a medium wavelength sensitive, MWS (max-wavelength, 497-509 nm); a short wavelength sensitive, SWS (max-wavelength, 430-463 nm); and either a violet sensitive, VS (max-wavelength, 402-426 nm); or an ultraviolet sensitive, UVS (max-wavelength 355-376 nm) (Cuthill et al. 2000). The variation in max-wavelength spectral location of the shortest wavelength-sensitive cone visual pigment (VS or UVS) seems to correlate with phylogeny, with VS likely to represent an ancestral state (Odeen and Hastad 2003). While the ability to see shorter-wavelength light is not unique to birds, the limitations of human vision present a major obstacle to understanding avian visual and behavioral ecology.

Evolutionarily, the visual abilities of birds are closely tied to their plumage patterns. The colors of plumage are produced by chemical pigmentation and structural light scattering. According to Prum et al. (2003) UV wavelengths can be produced from carotenoid pigments *in combination* with human-visible yellows, reds, or oranges. In addition, there are two ways which UV structural colors can be produced: (1) from

coherent scattering of light by a complex of melanin granules in the feather barbule, and (2) from light scattered by the spongy medullary keratin layer of the feather barb¹. As no exclusively UV-colored pigment has been found in birds, short wavelength feather reflection appears to be structural (Prum et al. 1998). The spongy medullary keratin is sufficiently nanostructured to produce ultraviolet colors through coherent light scattering, or constructive interference of light waves (Prum et al. 2003).

VARIATION IN PLUMAGE REFLECTANCE OF UV WAVELENGTHS

Research has provided correlative evidence that enhanced UV reflectance corresponds with individual success. Siefferman and Hill (2005) observed serious competition for pre-excavated nest sites cavities among male eastern bluebirds, which display brilliant structural blue-UV plumage. Variation in experimentally measured UV chroma correlated with nest-box ownership and predicted that brighter-colored males won nest-site competitions. In addition, higher levels of UV chroma reflected reproductive success; brighter males fledged more offspring. These results suggest that (at least a UV component part of) structural coloration in male eastern bluebirds contains visual information about competitive and reproductive ability. Keyser and Hill (1999) studied structural blue plumage in blue grosbeaks, finding the bluest males to have the largest body and territory size, and the highest nestling feeding rate in the first nest of the season. They concluded that in this species, structural blue plumage functions as an honest signal of male quality.

Further research has provided insight into some proximate physiological and environmental mechanisms that seem to affect the development of the feather barb

¹ Important terminology for reflectance analysis distinguishes between; “hue,” spectral location; “chroma,” spectral purity; and “brightness,” spectral intensity.

structure, evidence that structural plumage is a condition-dependent trait. Prum et al. (2003) warn against exaggeration of this hypothesis, as researchers know little about the development of medullary keratin in molecular detail. However, in a study on brown-headed cowbirds and house sparrows McGraw et al. (2002) found that during molt nutritionally stressed cowbirds grew less iridescent green-black neck and back plumage. In the same subjects, the melanin-based brown hoods stayed constant with nutritional variation. These data suggest isolated signals from distinct plumage components. Structural coloration appears to convey information about individual health, while melanin-ornamentation may reflect other physiological factors, such as hormone levels (McGraw et al. 2002). Ornborg et al. (2002) observed freshly molted blue tits to be UV-shifted, reflecting maximally wavelengths of 359-373 nm. This compared with pre-molt blue-tits, which reflect maximally above 400 nm. Following plumage-molt patterns, there exists seasonal variation in blue-tit structural plumage appearance. This probably results from the conditions of feathers, which rapidly degenerate during the nestling-feeding period (June). Such changes influence establishment of male territory (early spring) and mate attraction (spring) (Ornborg et al. 2002). These recent findings provide evidence that nutritional stress and feather wear are proximate mechanisms of structural UV reflectance variation in plumage.

Plumage development is likely a phenotypic trait affected by parasitism (Loyle and Zuk 1991). In some species, reflectance of specifically UV from plumage seems to convey information about, or signal parasite load. In these cases, infection levels correlate with signal strength. Hill et al. (2005) report parasite treatment-based variation in structural UV reflectance from regions of wild turkey iridescent plumage. Their

results show effects of infection by coccidian parasites on yearling male turkeys; infected birds had duller breast feathers and less UV reflective wing coverts compared with healthy controls. Doucet and Montgomerie (2003) present similar data: juvenile male satin bowerbirds with greater UV chroma were found to have fewer blood parasites than infected males. In related research, nematode parasite load was predicted by UV reflectance of sexual “comb” ornaments on male and female red grouse (Mouget et al. 2005). Combined, these results confirm that structural plumage is affected by parasitic infection and strongly suggest that UV reflectance signals individual health and quality.

RESPONSE TO SIGNALS TRANSMITTED THROUGH UV REFLECTANCE

Great variation is observed in coloration and UV reflectance levels, suggesting that all species do not maximize UV signaling potential. A possible explanation for these observations is that light environment affects perception of appearance, thus the evolution of plumage characteristics reflect historical phylogenetic habitat (Endler and Mielke 2005). Indeed, component elements of bird appearance vary greatly, resulting in a range of overall plumage phenotypes, even among conspecifics. As nutritional fitness, individual health, parasite load and environment influence reflectance of UV, this information seems to be signaled to receiver-birds, with UV sensitive visual apparatus. How individuals receive, integrate, and respond to this signal-information is an important question recently receiving more and more attention.

Male blue tits adjust their aggressive behavior in response to variation in UV reflectance levels of decoy crown feathers (Alonso-Alvarez et al. 2004). In a study on 48 breeding male blue tits, Alonso-Alvarez et al. (2004) found the percent of attacks on controls (with normal crown UV reflectance levels) to be greater than of attacks on UV-reduced decoys. These data show that UV signals affect male-male interactions in

breeding blue tits. Nest-defending males adjust their investment in aggressive behavior depending on the UV properties of an opponent's crown feathers. Such conclusions support hypotheses that males assess individual quality based on signal asymmetry and adjust their own behavior accordingly. When phenotypic traits contain honest information about an individual, opponents can conserve energy by altering behavior based on this information. Thus, a bird may evaluate opponents and, when unequal in ability (whether more favored or un-favored) avoid unfavorable, predicted outcomes. However, this presupposes that individuals have some conception (cognitive or programmed) of personal ability, a (metaphoric) ruler to measure with.

According to Peters et al. (2006), physiological regulations, such as hormonal levels, may influence UV signals and reproductive behavior in male blue tits. In these males, higher levels of UV reflectance enhance within pair success, while other sexually selected traits enhance extra-pair success. The authors suggest testosterone to be a proximate physiological cause of the trade-off between UV coloration and other sexually selected traits: with higher levels of the hormone correlating with reproductive success in both yearling males (higher testosterone, higher crown UV reflectance) and older males (higher testosterone, lower crown UV reflectance). As the hormone also governs aggressive behavior, a connection between testosterone levels and UV reflectance from plumage is substantial. Perhaps this links hormonally-sustained abilities, such as aggression, with signals that elicit aggressive responses; providing insight into how physiological cycles and sensory abilities in birds combine, to “measure up” self and opponents. Future research will need to investigate this multifaceted relationship in closer detail. For now it is clear that male behavioral response to plumage variation is an

integrated and complex process, regulated in part by physiological and environmental factors, as well as phenotypic appearance.

Does information contained in UV reflectance signals elicit (different) responses in females? It has been hypothesized that mating success and female preference should reflect female response to signals of individual male quality. Indeed, Woodcock et al. (2005) report that female black-capped chickadees can rapidly assess males based on visual cues. Results from spectral analysis reveal that achromatic plumage reflectance of UV chroma is greater in socially dominant males. Tested females demonstrated preference for socially dominant males in the absence of social dominance information, suggesting that variation of UV chroma signals sufficiently for female preference decisions.

According to the differential allocation hypothesis (Burley 1986 as summarized in Johnsen et al. 2005), parents adjust their parental effort in relation to perceived mate attractiveness, represented by visual and auditory signal-information. Limbourg et al. (2004) reduced crown UV reflectance of male blue tits and observed that while females mated to UV-reduced males decreased their offspring feeding rates, male rates did not change. The reduction in feeding rate resulted in skeletal growth problems amongst offspring, exemplifying the significance of behavioral adjustments to UV reflectance information. In a more recent study on mating blue tits, Johnsen et al. (2005) found that yearling females mated to males with UV enhanced phenotype invested more in nest defense than their mates, while the opposite was true of females mated to males with a UV reduced phenotype. They also found that *males* adjust their behavior according to the manipulations. UV reduced males were observed feeding offspring at *higher* rates

than UV enhanced males, suggesting that males cued to the investment levels of their female mates. Johnsen et al. (2005) hypothesize that differences in test results from Limbourg et al. (2004) may reflect natural variation in male investment between separate blue tit populations. Taken together, this information emphasizes the complexity of information exchange between mated individuals. Through constant assessment of visual cues, birds gain information to which they calibrate behavior, theoretically optimizing their energy management and genetic success. Females quickly adjust behavior to manipulated male phenotypes. Their response provides information which males then use in offspring investment activities. Thus, indirectly, UV reflectance signals affect countless individuals who may respond to an information-stimulated behavioral change of an initial signal-receiving bird.

CONCLUSION

UV reflectance is an important and widespread component of plumage and has been measured significant in 142 sampled avian families (Eaton and Lanyon 2003). In the last decade, advances in technology have opened doors for a more comprehensive analysis of visual ecology, revealing complex differences between avian and human visual systems. Building on this knowledge, attention has been given to investigating the importance of what we cannot (naturally) see. There is convincing correlative evidence that variation in UV plumage reflectance is an honest intraspecific signal of certain information about individual fitness. Nutrition, parasite load and feather condition (season/molt) have been experimentally determined to be physiological and environmental generators of reflectance variation. Recent studies with blue tits demonstrate the fantastically complex world of signal output and response, culminating in observation of behavioral adjustments predicted by optimality relationships. But

deciphering the importance of UV reflectance is merely a small advance to understanding avian communication and behavior. UV reflectance is but a component portion of plumage, which is likely perceived as a whole, visual appearance. Thus what is truly necessary is a synthetic model of what a bird sees. The limits of human vision explain why this topic is still rather vaguely understood, a true “bird’s eye view” is impossible for man and woman. But, phenomenal progress has been made and future research promises to reveal fascinating developments on the mechanisms and ecological importance of visual signals and receiver-responses.

I affirm that I have adhered to the honor code on this assignment _____

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