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SHORT COMMUNICATION

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Multiple UV reflectance peaks in the iridescent neck feathers of pigeons

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Abstract Recent studies of colorful plumage signals in birds have been aided by the finding that birds can see ultraviolet (UV) light and thus may communicate using colors invisible to humans. Some of the pioneering and more pivotal work on avian color vision was performed with domestic pigeons (*Columba livia*), yet surprisingly there have been few detailed reports of the UV-reflecting properties of pigeon feathers. Here, I use UV-VIS fiber-optic spectrometry to document the full-spectrum reflectance characteristics of iridescent purple and green neck plumage in pigeons. Neck feathers that appear purple to the human eye exhibit four reflectance peaks—two in the UV and one in the blue and red regions—and thus exhibit a UV-purple hue. Neck feathers that appear green to the human eye are characterized by five spectral peaks: two in the UV (UVA and UVB), a predominant green peak, and secondary violet and red peaks, conferring a UV-purple-green color. Such elaborate UV coloration suggests that birds may use an even more complex and 'hidden' UV signaling system than previously thought.

Introduction

The color communication systems of birds are among the most well developed in vertebrates. Among its many functions, color signaling plays a role in locating and acquiring food (Kilner 1997; Maddocks et al. 2001), attracting mates (Hill 1999), mediating aggressive competitions (Senar 1999), and avoiding predation (Götmark 1999). At a mechanistic level, the retinal complexity and visual sensitivity of birds surpass those of most animals (Hart 2001). Thus, to truly appreciate the variation in and significance of avian color signals, it is critical to quantify color patterns as they are perceived by the birds themselves (Bennett et al. 1994; Cuthill et al. 1999).

A particularly noteworthy feature of avian visual communication is the ultraviolet (UV) waveband. Many birds, unlike humans, perceive UV wavelengths of light (Bennett and Cuthill 1994; Cuthill et al. 2000) using specialized UV-sensitive cones that are accompanied by UV-transparent oil droplets (Bowmaker et al. 1997; Vorobyev et al. 1998). Accordingly, birds often develop UV-reflecting colors in their feathers that are used as social or sexual signals (e.g., Andersson et al. 1998; Hunt et al. 1998; Keyser and Hill 1999).

Some of the earliest work on avian UV color vision was completed in the domestic pigeon (*Columba livia*) (e.g., Blough 1957; Wright 1972; Bowmaker 1977; Kreithen and Eisner 1978). The visual properties of this species are now among the most studied in birds (Bowmaker et al. 1997). Using both behavioral and electroretinogram experiments, it has been shown that pigeons perceive UV light with a wavelength as low as 320 nm (reviewed in Kawamura et al. 1999). Given the long-standing notion that pigeons can see into the UV, it is surprising that no studies have investigated the potential UV-reflecting properties of pigeon plumage. Evolutionary biologists have shown interest in the role that plumage colors from different, genetically controlled pigeon strains (e.g., blue checker, blue bar, ash red) play in mate selection (Burley 1981a; Johnston and Johnson 1989), but to my knowledge the spectral properties of pigeon colors remain undocumented.

In this study, I used UV-VIS fiber-optic spectrometry to determine the full-spectrum reflectance characteristics of a colorful plumage trait in pigeons—the iridescent neck feathers. Three observations suggest that iridescent coloration may serve an important sexual signaling function in pigeons (Johnston 1992): (1) the body plumage of adult males and females looks quite similar to humans, except for a notable decrease in neck iridescence in females, (2) juvenile pigeons contain either no (in females) or much reduced (in males) iridescence,

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and (3) as part of agonistic and courtship 'bow-coo' behaviors, males inflate their crop and display their iridescent neck feathers directly at conspecifics. Iridescent neck feathers are described in the literature as having a 'glossy yellowish, greenish, and reddish-purple' color (Johnston 1992). Such color variability is likely due to the characteristically changing appearance of iridescent feathers when viewed from different light angles (Prum 1999). The patch of iridescent feathers can be divided more specifically into two differently colored regions: (1) feathers that appear green in color and (2) feathers that appear purple in color (personal observation). I scored green and purple plumage regions from 14 wild-caught adult pigeons and examined (1) the extent to which each reflected in the UV, (2) differences in reflectance intensity (or brightness; see Endler 1990) among spectral peaks to identify the predominant plumage color(s), and (3) similarities in reflectance intensity among spectral peaks to determine whether birds that reflected light more strongly in one spectral region did so in others as well. Throughout this paper, I work under the assumption of Andersson (1996), defining a color as a "deviation from uniform reflectance", and search for discrete peaks that exist above baseline levels of reflectance for each sample.

Methods

14 wild-type ('blue-bar') pigeons were captured from the wild in east-central Alabama in 1997. Because of the very subtle differences in morphology between males and females, I was unable to sex these birds (Burley 1981b).

Plumage color was measured from a central location on the two colored regions (green and purple) of iridescent neck feathers. To collect reflectance data, I used an Ocean Optics (Dunedin, Fla.) S2000 fiber optic spectrometer (for detailed methods, see McGraw et al. 1999). Data are presented from 300–700 nm, which spans the range of UV (300–400 nm) and human-visible (400–700 nm) light wavelengths. For each plumage region on each bird, 20 spectra were measured and then averaged without lifting the probe tip from the plumage surface.

I used mixed-model ANOVAs (with peak as a fixed effect and bird number as a random effect) and post hoc paired independent contrasts on least-squares means to examine differences in reflectance intensity among spectral peaks within a plumage region. I used linear Pearson's correlation matrices to test for relationships between reflectance intensity for different peaks within a plumage region.

Results

'Purple' iridescent feathers

General reflectance characteristics

Iridescent neck feathers that appeared purple in color to the human eye exhibited four discrete reflectance peaks in the 300–700 nm range (see Fig. 1a). There were two main peaks in the human-visible spectrum that reflected light maximally (λ_{max}) at 496 and 687 nm, which correspond to predominantly blue and red wavelengths of light, respectively. These dual, blue-red peaks are characteristic of a purple color (as opposed to violet; see Bradbury and Vehrencamp 1998). There were also two peaks that were confined to the UV region of the spectrum: one each at

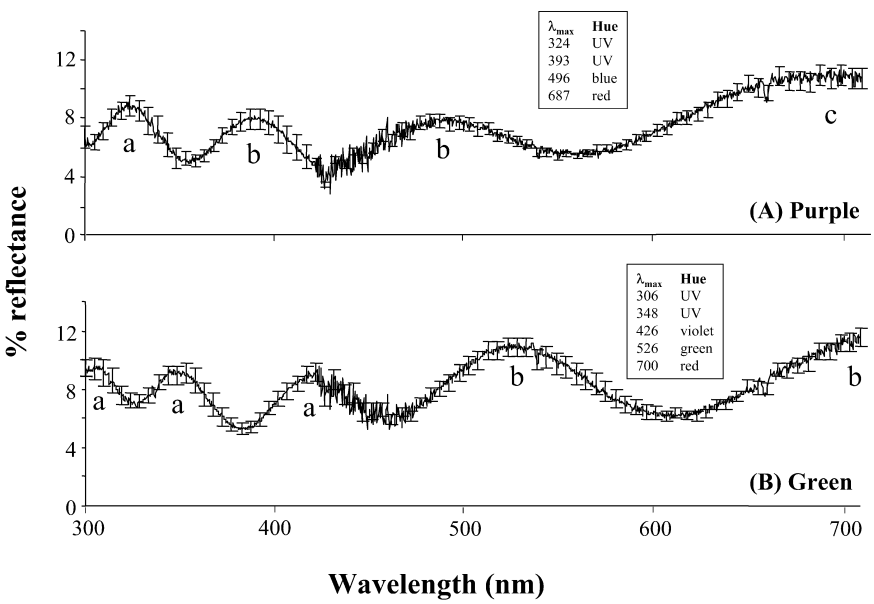

Fig. 1 Mean reflectance curves (±SEM at every 5 nm increment; for clarity) for **a** iridescent 'purple' plumage and **b** iridescent 'green' plumage in *Columba livia*. Boxes in each panel show wavelengths at maximum reflectance (λ_{max}) and the characteristic color assigned to such wavelengths for each peak. *Letters* beneath each peak in the spectrum denote significant differences in peak height (see 'Results). It should be noted that the curve in panel **b** was truncated at 700 nm (near the upper limit of avian vision). In actuality, these curves continued to rise steadily in height past 700 nm until reaching the upper range of the instrument's sensitivity (~760 nm)

Table 1 Pearson's correlation matrix for the relationships between reflectance intensity (peak height) for different spectral peaks in the iridescent plumage of feral pigeons. Values at the top of the matrix are for peaks in the green plumage; bottom cells show data for purple plumage; boldfaced cells show statistically significant results after adjusting for multiple comparisons with sequential Bonferroni corrections (Rice 1989). Peaks 1–5 for green plumage are: UV1, UV2, violet, green, and red, respectively. Peaks 1–4 for purple plumage are: UV1, UV2, blue, and red, respectively. Only pairs of UV peaks and groups of visible peaks were significantly intercorrelated in both plumage regions

	UV1	UV2	Violet	Green	Red
UV1	–	**r=0.82**	r=0.08	r=0.15	r=0.08
	–	**P=0.0003**	P=0.79	P=0.64	P=0.80
UV2	**r=0.97**	–	r=–0.06	r=0.15	r=0.17
	P<0.0001	–	P=0.84	P=0.64	P=0.58
Blue	r=–0.04	r=–0.12	–	**r=0.82**	**r=0.66**
	P=0.90	P=0.73	–	**P<0.0001**	**P=0.003**
Red	r=0.01	r=–0.11	**r=0.66**	–	**r=0.94**
	P=0.97	P=0.75	**P=0.009**	–	**P<0.0001**

λ_{max}=324 and 393 nm, which both fall within the UVA waveband.

Among-peak differences in reflectance intensity

I found a significant overall difference in reflectance intensity among spectral peaks from this plumage region (mixed-model ANOVA: $F_{3,35}$=7.4, P=0.0006). Post hoc tests revealed that peaks in the red region were significantly higher than the others (paired independent contrasts on least-squares means, all t>2.2, all P<0.05; denoted by letters in Fig. 1), followed by short-wave UV peaks (both t>2.8, both P<0.02 for comparison with blue and long-wave UV peaks) and finally the blue and long-wave UV peaks (not different from one another; t=0.07, P=0.95). There was also a significant effect of bird in the model, indicating that there is notable variation among individual pigeons in spectral shape ($F_{13,35}$=2.1, P=0.045).

Among-peak correlations in reflectance intensity

There were significant positive correlations between only two sets of peaks in these 'purple' plumage regions: (1) the pair of UV peaks and (2) the pair of human-visible peaks (blue and red) (Table 1). Thus, birds that reflected much light in one UV region also did so for the other UV peak, and feathers reflecting more blue light also reflected more red light.

'Green' iridescent feathers

General reflectance characteristics

Iridescent neck feathers that appeared green in color to the human eye exhibited five discrete reflectance peaks in the UV-VIS range (see Fig. 1b), each of which was different from those found in purple feathers. Again, there were two UV peaks, but in green plumage one was present in the UVB range (λ_{max}=306 nm) and the other in the UVA (λ_{max}=348 nm). Green feathers also reflected light from three main regions in the human-visible portion of the spectrum: violet (λ_{max}=426 nm), green (λ_{max}=526 nm), and red (λ_{max}=700 nm).

Among-peak differences in reflectance intensity

As with 'purple' plumage, there were significant differences in reflectance intensity among the five peaks present in 'green' feathers (mixed-model ANOVA, $F_{4,46}$=6.4, P=0.0003). Using post hoc paired contrasts, I found that the most reflective regions of 'green' pigeon plumage were within the green and red wavelengths (all t>2.0 and all P<0.05 for comparisons with the three remaining peaks; P=0.07 for contrast between red and green peaks), while the two UV and violet peaks were secondary in height (all P>0.45 for contrasts pairing any two of these peaks; also denoted with letters in Fig. 1b). There also were significant interindividual differences in the spectral shape of green plumage in pigeons (mixed-model ANOVA for 'bird': $F_{13,46}$=5.0, P<0.0001).

Among-peak correlations in reflectance intensity

Much like those found in the 'purple' neck feathers of pigeons, the only correlations that existed were between the two UV peaks and then among the three peaks from the human-visible portion of the spectrum (Table 1). 'Green' feathers that reflected more long-UV light also transmitted more short-UV wavelengths, and plumage that was more reflective in the green region also was more colorful at red and violet wavelengths.

Discussion

The visible-light (400–700 nm) reflectance characteristics of iridescent plumage in feral pigeons were well-matched to the broad color categories assigned by humans. Neck feathers that appear purple in color to the human eye show dual peaks in the red (primary peak) and blue (secondary peak) regions of the visible spectrum, which typifies purple hues (Bradbury and Vehrencamp 1998). In fact, the predominance of red light reflectance from these regions may help to explain why some researchers describe pigeon iridescence as having a 'reddish-purple' appearance (Johnston 1992). Green neck feathers contained predominant green and red peaks, accompanied by a secondary violet peak, which cumulatively should appear a purple-green color to humans. In fact, upon close inspection of these 'green' feathers, it is evident that they can exhibit a purplish tint (personal observation).

The 'hidden' UV-reflecting properties of these same feathers, however, were quite unusual. Birds and other animals for which UV integumentary colors have been described contain a single peak that is confined to or extends into the UV region (e.g., Burkhardt 1989; Fleishman et al. 1993; Cuthill et al. 2000). This is true even for iridescent feathers in other species, as in the European starling (*Sturnus vulgaris*; Bennett et al. 1997). In pigeons, however, multiple peaks of UV reflectance were noted in both the 'green' and 'purple' regions of iridescent neck feathers. To my knowledge, this is the first demonstration of multiple UV peaks contained within a single color patch in any animal. This UV reflectance does not seem to be universal for all pigeon feathers and colors either. Burkhardt (1989) found low UV transmission from both the white and gray wing primaries of pigeons. This supports the hypothesis that UV colors in iridescent plumage may serve an important signaling function in this species. It is unclear, however, to what extent pigeons perceive all of these peaks in neck feathers. The sensitivity of pigeon vision seems to extend only as low as 320 nm (Kawamura et al. 1999), so the UVB peak (λ_{max}=306 nm) in iridescent 'green' feathers may be invisible to pigeons.

Compared to other pigmentary and structural colors, iridescence has been a rather overlooked form of color signal in birds (Bennett et al. 1997; Cuthill et al. 1999). We generally know little about the behavioral or sexual roles of iridescent ornaments, and I am aware of only one study that has characterized the condition-dependence of avian iridescence (in brown-headed cowbirds, *Molothrus ater*; see McGraw et al. 2002). Iridescent coloration is produced in bird plumage by multi-layer interference within feather barbs or barbules (Greenwalt et al. 1960; Land 1972). Specifically, these feathers contain layers of keratin, melanin-pigment granules, and air vacuoles that are arranged in a three-dimensional lattice (Durrer 1962; Lucas and Stettenheim 1972). Light is reflected (and subjected to interference) at the interfaces of these heterogeneous layers that vary in size, shape, spacing, and refractive index (Prum 1999). It is plausible that this complex, multilayered arrangement is responsible for the elaborate sequence of reflectance peaks reported here.

To further investigate the color properties of iridescent pigeon plumage, I tested for correlations between the height (or reflectance intensity) of different spectral peaks. This would allow me to determine whether a given bird can maximally produce all color components in a plumage region or if the expression of different colors may be unrelated and potentially used as different signals. In both 'green' and 'purple' iridescent feathers, I detected significant correlations between the two UV peaks and also among the set of human-visible peaks, but never between any combination of UV-visible peaks. The dissociation between the intensity of UV and human-visible colors, but correlated levels of expression within each spectral region, suggests that (1) there may be unique environmental, nutritional, physiological, or microstructural mechanisms governing the production of UV versus visible peaks in iridescent pigeon feathers, and (2) while the two UV peaks and the visible peaks may, as separate groups, communicate the same information, UV colors in iridescent pigeon feathers may communicate different information than human-visible colors. Several other species similarly exhibit separate peaks of color in the UV and human-visible regions (several listed in Burkhardt 1989), and in future work it will be interesting to determine their intercorrelations, mechanisms of production, and signal content.

Obviously, this study serves as only a preliminary description of the spectral properties of pigeon plumage. Because iridescent colors exhibit unique reflectance characteristics across different angles of presentation, it would seem useful to determine the spectral properties of pigeon neck feathers across a range of angles from 0–90° under more controlled conditions. Moreover, the sexes may differ not only in the extent of iridescence (e.g., number or proportion of iridescent neck feathers) but also in plumage coloration. Follow-up studies should investigate which, if any, of the spectral characteristics documented here are sexually dichromatic or play a role in sexual selection.

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