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ULTRAVIOLET DEGRADATION IN CAROTENOID PATCHES: LIVE VERSUS MUSEUM SPECIMENS OF WOOD WARBLERS (PARULIDAE)

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Abstract.—Accurate assessment of color is essential in testing the adaptive significance of color variation in avian plumage. Over the past decade, use of objective methods for assessing color has increased, with particular emphasis on ultraviolet (UV) wavelengths. Researchers have used various source materials, most notably museum specimens, to extend or represent color measurements of individuals in natural populations. Here, we address whether the colors seen in museum specimens accurately represent the colors seen in natural populations. We focus on UV wavelengths and carotenoid-derived colors across 10 species of wood-warblers (Parulidae). Our results indicate an uneven decrease in brightness across the color spectrum, with greater relative decrease in shorter wavelengths in museum specimens. That decrease leads to differences in both hue and chroma between living and museum specimens. The difference from live specimens appears to increase with the museum specimen's age. Our results suggest that caution is needed when using data from museum specimens to test hypotheses on plumage coloration, particularly those involving communication. *Received 18 December 2003, accepted 13 December 2004.*

Key words: carotenoid, color, *Dendroica*, museum, reflectance spectrophotometry, ultraviolet, wood-warblers.

Degradación Ultravioleta en Parches de Carotenoides: Especímenes Vivos versus Especímenes de Museo de Especies de la Familia Parulidae

Resumen.—La determinación exacta del color es esencial para probar la significancia adaptativa de la variación del color en el plumaje de las aves. El uso de métodos objetivos para determinar el color, con un énfasis en las longitudes de onda ultravioletas (UV), ha aumentado durante la última década. Los investigadores han utilizado una variedad de fuentes de material, en su gran mayoría especímenes de museo, para expandir o representar las medidas de color de individuos de poblaciones naturales. En este estudio, determinamos si el color observado en especímenes de museo representa exactamente el color observado en individuos de poblaciones naturales. Nos enfocamos en las longitudes de onda UV y en los colores derivados de carotenoides en 10 especies de la familia Parulidae. Nuestros resultados indican una disminución desigual en el brillo a través del espectro de colores, con una disminución relativamente mayor en las longitudes de onda más cortas en especímenes de museo. Esta disminución conduce a diferencias en el tono y la intensidad entre especímenes de museo y vivos. La diferencia con los especímenes vivos parece aumentar con la edad de los especímenes de museo.

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Nuestros resultados sugieren usar con precaución los datos provenientes de especímenes de museo para probar hipótesis sobre los patrones de coloración del plumaje, particularmente aquellas que se relacionan con la comunicación.

Considerable recent work on color variation in avian plumage has been focused on plumage reflecting in the ultraviolet (UV, 300–400 nm; Burkhardt 1989, Finger and Burkhardt 1994) and perception of those wavelengths (Cuthill et al. 2000). Studies of UV-reflecting plumage suggest that it is widespread in the avian world (Burkhardt 1989, Finger and Burkhardt 1994, Eaton and Lanyon 2003) and exhibits substantial within-species variation (Andersson et al. 1998, Cuthill et al. 1999). Such ubiquity and subtle variation are important, given that birds possess an extra photoreceptor sensitive to violet and UV wavelengths, which increases their hue discrimination and enables them to perceive colors that humans cannot (Finger and Burkhardt 1994). Variation that is relatively subtle to humans may be perceived more clearly by birds, and this variation may be more pronounced when the UV region is considered.

For decades, biologists have relied on subjective descriptions of color from a variety of sources to assess variation in avian plumage. For example, Ridgway's (1886, 1912) system of color standards was long used as a basis for describing plumage coloration. Similar subjective methods, such as ranking or scaling color according to human visual sensitivities, have also been common (e.g. Baker and Parker 1979, Hamilton and Zuk 1982, Read and Harvey 1989, Götmark 1994, Martin and Badyaev 1996). Although such methods have merit in certain applications, caution is warranted. For instance, later editions of Ridgway's standards contained different colors, reflecting changes in the author's perception of colors as he aged (Maerz and Paul 1950).

Researchers have collected color data from various source materials, including museum specimens, feathers found in aviaries, and drawings in field guides (e.g. Burkhardt 1989, de Repentigny et al. 1997, Badyaev et al. 2002, Bleiweiss 2004). Caution may be warranted in the use of such materials, particularly if the intent is to represent natural color variation. This is perhaps best exemplified by studies on the use of UV-reflecting plumage in bird communication. First, humans are blind to UV wavelengths, which makes methods derived from human visual sensitivities inaccurate (Endler 1990, Bennett et al. 1994). Second, the color displayed on the body of a live individual is the color perceived by potential mates, rivals, or predators. Thus, it is important to address more rigorously whether commonly used alternative sources, such as museum specimens, adequately represent natural color variation, particularly by considering the UV region.

Here, we use reflectance spectrophotometry to examine the congruence of color in the UV region between live and museum specimens of 10 wood-warbler species (family Parulidae). We focus on presumedly carotenoid-based colors and UV, for three reasons. First, carotenoid colors are strongly represented in the family Parulidae. Second, these colors are often isolated in discrete patches that function in communicative displays (reviewed by Morse 1989), which suggests that their accurate characterization is crucial for understanding their biological and evolutionary importance. Third, UV is common in many carotenoid colors, yet it is a commonly neglected component in carotenoid color production. Carotenoid colors may also be important in honest signaling and mate-choice decisions (Olson and Owens 1998, Hill 2002). We examined carotenoid colors (all of which reflected UV), noncarotenoid (structural–melanin) colors reflecting UV, and noncarotenoid colors not reflecting UV. Wood-warblers lack structurally based iridescent colors, so those colors are not addressed.

Methods

Study Specimens

We measured plumage coloration in the following species: American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Black-throated Blue Warbler (*Dendroica caerulescens*), Black-throated Green Warbler (*D. virens*), Canada Warbler (*Wilsonia canadensis*), Common Yellowthroat (*Geothlypis trichas trichas*), Chestnut-sided Warbler (*D. pensylvanica*),

Magnolia Warbler (*D. magnolia*), Yellow-rumped Warbler (*D. coronata coronata*), and Ovenbird (*Seiurus aurocapillus*). We obtained measurements of live specimens during spring 2001 in Huntington Forest at the Adirondack Ecological Center, Essex County, New York. We captured males in mist nets, using taped playbacks of conspecific song, and obtained color spectra of plumage patches using reflectance spectrophotometry. Individuals were color-banded to avoid recapture and released at the site of capture following all measurements.

Museum skins were measured in April 2002 at the American Museum of Natural History, New York. Specimens were also measured at the San Diego Museum of Natural History and the Natural History Museum of Los Angeles; measurements from those locations (data not presented) were similar to data presented here. To minimize differences associated with geographic variation, we restricted our data to specimens from the New York metropolitan area. To minimize differences associated with seasonal variation, we used only skins from specimens caught in spring (April–June). Further, we used only specimens that appeared to be in the best condition. Although it would be desirable to include a more extensive treatment of the effect of age of museum specimens on plumage coloration, we found few new specimens (i.e. <30 years old) in the three museums visited. Effects associated with museum age are represented using nine new specimens (1983–2001), five *D. c. coronata* and four *G. t. trichas*. All other specimens measured were collected between 1878 and 1934. Species names, sample sizes, and body regions measured are presented in the Appendix.

Color Spectra and Statistics

Plumage color spectra were measured using an S2000 Spectrometer with OOIBASE10 data-acquisition software and a PX-2 xenon light source (Ocean Optics, Dunedin, Florida) attached to a bifurcated optical fiber with reflectance-measuring probe. The probe was mounted inside an aluminum tip that was cut at a 45° angle and provided a 3-mm-diameter illumination area. Measurements were calibrated using a barium sulfate standard that reflects >99% of incidental light. Each spectrum was interpolated to 2-nm intervals and restricted to the 300- to 700-nm spectral range. Three measurements were obtained for each color patch and averaged for a final measurement. Our methods for estimating hue and chroma are adapted from the segment-based method described by Endler (1990), using programs written in MATLAB (MathWorks, Natick, Massachusetts). Our methods approximate the three properties that define color (brightness, hue, and chroma) and accommodate the UV region (J. A. Endler pers. comm). Brightness (total reflectance) is the total amount of light reflected by an object and is measured as the sum of reflected light across each 2-nm interval from 300 to 700 nm. Hue is analogous to the commonly accepted definition of color (i.e. red, green, blue). Estimates of hue were based on the median wavelength value where the brightness to the left and to the right is equalized. Chroma (saturation) refers to the spectral purity of a color. For example, red has higher chroma than pink. We obtained chroma by taking the difference in reflectance between smaller, nonadjacent spectral segments (e.g. $R_{300–400}$ and $R_{500–600}$) and dividing it by the total reflectance. In most situations, segments used in chroma measures should correspond to the spectral sensitivities of the photoreceptors in the receiver of interest. Spectral sensitivity of photoreceptors in warblers has not been reported, but our interest here is in absolute color change rather than change perceived by a particular receiver. All passerines studied to date have four photoreceptors, with sensitivities corresponding roughly to UV–violet, blue, green, and red wavelengths (reviewed in Cuthill 2000). We wanted measurements that reflect the tetrachromacy of avian visual sensitivities but remain receiver-independent. Therefore, spectral segments used here were restricted to four equal 100-nm regions.

Measurements obtained for brightness, chroma, and hue were included in a two-way analysis of variance (ANOVA) with brightness, chroma, and hue as dependent variables and species and source (live or museum) as independent variables. To determine whether brightness degraded evenly across the spectrum, brightness was subsequently broken down into two component parts corresponding to each of the reflectance peaks in the carotenoid patches: UV (300–400 nm) and the human-visible spectrum (400–700 nm). We then ran a three-way ANOVA with a new independent variable (spectrum) reflecting those two peaks. A significant source * spectrum interaction would indicate differences

across the color spectrum (UV vs. human-visible) with respect to source.

We were also interested in assessing degradation related to age. Specifically, we were interested in whether newer museum specimens differed significantly from live individuals. If they did not, new museum specimens could provide a reliable means of using museum specimens to represent natural color. Ideally, we would like to have a model of how a variable like UV brightness varies with age. However, because museum specimens of intermediate ages were not available ("old" specimens = 1878–1934 and "new" specimens = 1983–2001) and data points for new specimens consisted of only nine individuals, a predictive regression model of the data seemed tenuous at best. Therefore, we calculated relative difference scores for old and new specimens for both species in which new specimens were available (*D. c. coronata* and *G. t. trichas*) for both the UV and human-visible regions. Those scores represent the percentage of decrease in brightness of museum specimens as compared with live individuals. Difference scores were then calculated as follows: (species average for live measurement – species average museum measurement)/species average for live measurement × 100). Those means were then used to assess degradation in the old and new museum specimens compared with the live individuals.

Results

Carotenoid Colors

Significant differences according to species occur with all three parameters: brightness, chroma, and hue (Table 1). That is not surprising, given that different colors were measured (e.g. yellow and orange). However, we note that in most cases, the source variable explained more of the variation than species (Table 1). Our primary question is whether live and museum specimens differ. Mean brightness of carotenoid patches differed between live and museum specimens ($F = 105.78$, df = 1 and 118, $P < 0.001$; Fig. 1 and Table 1). Mean chroma and hue also differed significantly between live and museum specimens (chroma, $F = 181.40$, df = 1 and 118, $P < 0.001$; hue, $F = 204.46$, df = 1 and 118, $P < 0.001$). With brightness, there was also a significant species ∗ source interaction, indicating that each species did not exhibit the same pattern of an increase or decrease in brightness ($F = 9.17$, df = 6 and 118, $P < 0.001$). Surprisingly, museum specimens of the Chestnut-sided Warbler were brighter than living specimens

Table 1. ANOVA results on brightness, chroma, and hue in carotenoid patches comparing live and museum specimens (source) across seven warbler species.

		Brightness		Chroma		Hue	
Source	df	Mean square	*F*-ratio	Mean square	*F*-ratio	Mean square	*F*-ratio
Carotenoid patches							
Species	6	728.13	54.51 [b]	4,221.80	13.43 [b]	1,136.94	28.96 [b]
Source	1	1,413.02	105.78 [b]	57,005.90	181.40 [b]	8,027.30	204.46 [b]
Species ∗ source	6	122.53	9.17 [b]	635.69	2.02	77.40	1.97
Error	118	13.36		314.26		39.26	
Noncarotenoid patches containing UV							
Species	3	3,065.47	551.96 [b]	2915.07	16.07 [b]	9,681.38	101.31[b]
Source	1	201.43	36.27 [b]	4,577.32	25.24 [b]	22,913.80	239.77 [b]
Species ∗ source	3	82.06	14.78 [b]	6,067.46	33.46 [b]	423.78	4.43 [a]
Error	62	5.55		181.36		95.56	
Noncarotenoid patches lacking UV							
Species	1	188.09	51.87 [b]	624.44	0.34	1,527.76	11.24 [a]
Source	1	9.72	2.68	265.75	0.15	30.16	0.22
Species ∗ source	1	1.62	0.45	7,464.53	4.10	468.42	3.45
Error	38	3.63		1,822.44		135.87	

[a] $P < 0.050$.
[b] $P < 0.001$.

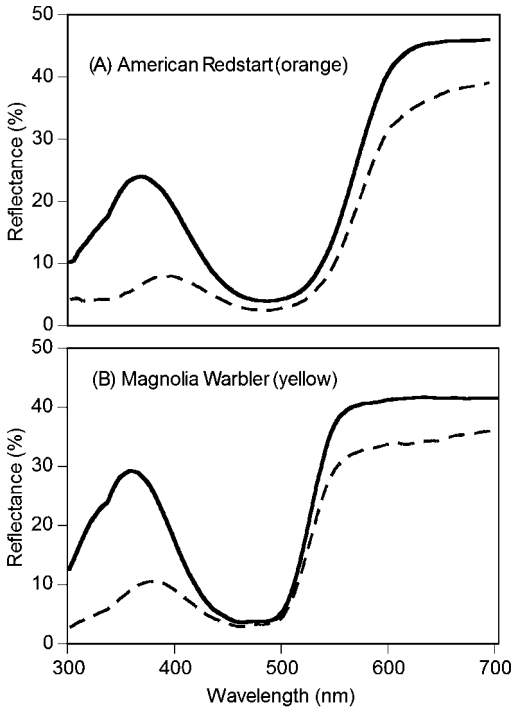

FIG. 1. Live (solid) and museum (dashed) spectra, showing degradation of carotenoid-based colors in two species (American Redstart: live $n = 8$, museum $n = 10$; Magnolia Warbler: live $n = 10$, museum $n = 10$).

($\bar{x} \pm$ SD; live = 10.8 ± 3.30, museum = 13.7 ± 3.06; see Appendix). In the six other species, however, mean brightness was lower in museum specimens. The brighter museum specimens of the Chestnut-sided Warbler contributed to the significant species * source interaction. Omitting that species eliminated the significance of the species * source interaction in brightness ($F = 0.235$, df = 5 and 110, $P > 0.05$).

To determine what contributed to the shift in these parameters, a new variable ("spectrum") was added that corresponded to the reflectance peaks in the UV and human-visible portion (Fig. 1). Greater decreases in brightness in restricted regions of the spectrum concentrate relatively more reflectance at other regions. Therefore, a shift in hue and chroma in museum specimens is indicated by a significant source * spectrum interaction (UV/visible brightness, $F = 10.37$, df = 1 and 236, $P < 0.05$; Table 2). This indicates that live and museum specimens differed in the amount of degradation of UV and human-visible brightness.

Noncarotenoid Colors

Noncarotenoid colors were analyzed in six species; for comparison with carotenoid-based colors, they were broken up into two groups, depending on whether or not they reflected in the UV range (Fig. 2). Color patches in four species reflected in the UV range; those in two species did not (Appendix). Results for those that reflected UV were similar to results for UV-containing carotenoid patches (Table 1). All three parameters differed according to species; but with chroma and hue, source explained more of the variation. Mean brightness differed according to source ($F = 26.45$, df = 1 and 62, $P < 0.001$), as did mean chroma and hue (chroma, $F = 11.57$, df = 1 and 62, $P < 0.001$; hue, $F = 205.21$, df = 1 and 62, $P < 0.001$). Also, there was a significant source * spectrum interaction showing that degradation with respect to source was not uniform across the spectrum ($F = 12.81$, df = 1 and 124, $P < 0.05$; Table 2). Brightness in the UV decreased in noncarotenoid patches of all museum specimens measured, but that was not necessarily the case for human-visible brightness (Appendix).

Noncarotenoid colors not containing UV did not differ in mean brightness according to source ($F = 2.68$, df = 1 and 38, nonsignificant; Table 1). Furthermore, those colors did not differ in mean chroma or mean hue with respect to source (chroma, $F = 0.15$, df = 1 and 38, nonsignificant; hue, $F = 0.22$, df = 1 and 38, nonsignificant).

Specimen Age

Only two species, the Yellow-rumped Warbler and Common Yellowthroat, were represented by newer specimens (years 1983–2001) in the museum collections. In all color measurements, new museum specimens are intermediate between old museum and living specimens (Fig. 3; see Appendix). Hue remains significantly different between live and new museum specimens in the Common Yellowthroat (t-test: $t = -2.92$, df = 12, $P = 0.013$). There is a similar trend in the Yellow-rumped Warbler, though the difference is not significant in that species (t-test: $t = -1.80$,

Table 2. ANOVA results with brightness broken down into a UV and human-visible component (spectrum) in carotenoid and noncarotenoid, UV-containing patches. Data compare live and museum specimens (source) across seven warbler species.

Source	df	Mean square	*F*-ratio
Carotenoid patches			
Species	6	364.06	78.56 [b]
Source	1	706.51	152.46 [b]
Spectrum	1	15,126.76	3,264.27 [b]
Species * source	6	61.26	13.22 [b]
Species * spectrum	6	139.23	30.05 [b]
Source * spectrum	1	32.38	10.37 [a]
Species * source * spectrum	6	5.60	1.21
Error	236	4.63	
Noncarotenoid, UV-containing patches			
Species	3	1,532.74	813.61 [b]
Source	1	100.72	53.46 [b]
Spectrum	1	2,082.41	1,105.39 [b]
Species * source	3	41.03	21.78 [b]
Species * spectrum	3	702.07	372.68 [b]
Source * spectrum	1	24.13	12.81 [b]
Species * source * spectrum	3	8.51	4.52 [a]
Error	124	1.88	

[a] $P < 0.050$.
[b] $P < 0.001$.

df = 12, $P = 0.097$). Again, degradation in the UV seems to contribute to differences, because the peak is significantly different between live specimens and new museum specimens (Common Yellowthroat, *t*-test: $t = 3.68$, df = 12, $P = 0.003$; Yellow-rumped Warbler, *t*-test: $t = 3.50$, df = 12, $P = 0.003$), whereas the human-visible peak is not (Common Yellowthroat, *t*-test: $t = 1.103$, df = 12, $P = 0.29$; Yellow-rumped Warbler, *t*-test: $t = 2.00$, df = 12, $P = 0.68$).

Discussion

Although color measurements from museum specimens have frequently been used in studies of color variation (e.g. Burkhardt 1989, Andersson and Amundsen 1997, Brumfield et al. 2001, Bleiweiss 2004), we report here that museum specimens of wood-warblers may be unrepresentative of natural color. More importantly, the uniqueness of the current study is its demonstration that UV plays a unique role in that discrepancy. Ultraviolet light reflectance exhibits greater and more rapid degradation in museum specimens, which is highlighted by the fact that when plumage lacks UV reflectance, museum-specimen measurements are more accurate representations of natural color variation. However, although our results suggest caution in the use of museum specimens, they do not suggest that museum skins are entirely uninformative in studies of plumage coloration. Use of museum skins to study UV coloration in birds may, in fact, be useful in some situations (e.g. Eaton and Lanyon 2003). But caution may be especially warranted when the aim is to objectively quantify plumage coloration within a species, which may be important when studying communication. One option for minimizing the discrepancy between museum and live specimens would be to ignore the UV region, as many studies have done. However, failing to consider the UV region (300–400 nm) is difficult to justify, given that plumage may reflect in this region and avian visual systems are sensitive to its wavelengths. Also, discrepancies between live and museum specimens might be overcome by using newer museum specimens; however, a similar color discrepancy was shown in one of two species for which newer museum specimens were available. Moreover, newer specimens are scarce in many museum collections.

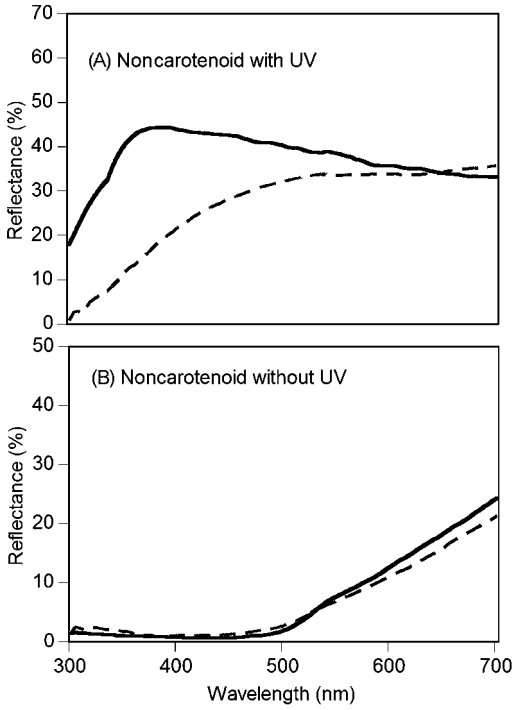

FIG. 2. Degradation from live (solid) and museum (dashed) spectra from (A) noncarotenoid patches that contain UV (white on the eyestripe of the Black-and-white Warbler; live $n = 8$, museum $n = 10$) and (B) noncarotenoid patches that do not reflect in the UV (brownish-orange crown stripe from the Ovenbird; live $n = 10$, museum $n = 10$).

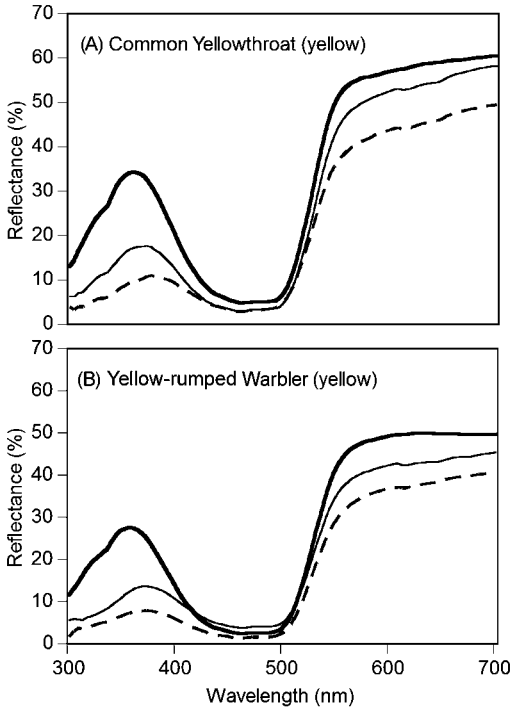

FIG. 3. Age-related differences between live (solid bold line), old-museum (1878–1934; dashed line), and new-museum (1983–2001; solid thin line) spectra in carotenoid-based plumage. (A) Common Yellowthroat (live $n = 10$, museum $n = 10$, new $n = 4$). (B) Yellow-rumped Warbler (live $n = 9$, museum $n = 10$, new $n = 5$).

Increased UV degradation associated with museum age is demonstrated, but the mechanisms responsible for that degradation are not entirely clear. Although we measured only specimens that appeared to be in the best condition, physical damage is one possible mechanism, given that it may accumulate with increasing age, perhaps through repeated handling of specimens. Physical degradation has been described in the orange-red and white colors of museum specimens of the Cock-of-the-rock (*Rupicola rupicola*; Endler and Théry 1996) and in the short-wavelength, structurally based color of live Blue Tits (*Parus caeruleus*; Örnborg 2002). Another possibility, as yet untested, is the isomerization of the pigment itself. Carotenoid pigments produce the UV peak in carotenoid-based plumage by minimally absorbing UV wavelengths and absorbing wavelengths outside the UV range to a greater extent, allowing the underlying color of the feather to be reflected. Carotenoids are sensitive to environmental perturbation. In carotenoid-containing foods, for example, trans- to cis-isomerization may result from exposure to light, heat, or oxygen (Chen et al. 1994, Tang and Chen 2000). Cis-isomers characteristically absorb more UV light (i.e. less reflectance) than the more naturally occurring all-trans form (figure 2 in Negro et al. 2001). Whether such isomerization occurs in bird feathers of museum specimens remains to be tested, but that would be consistent with the greater decrease of UV described here.

Geographic and seasonal variation also may contribute to differences in color, and efforts were made to avoid those influences. All our live specimens were measured in the spring in New York; similarly, all museum specimens were collected in spring in the New York

metropolitan area. Geographic variation in UV reflectance has not been studied, though seasonal variation has been reported in the structurally based UV of the Blue Tit (Örnborg et al. 2002). However, when one region is focused on to minimize geographic variation, effects associated with locality necessarily become more pronounced. One possible influence attributable to locality is air pollution. Eeva et al. (1998) reported a decreased abundance of caterpillars, a pigment-rich food source for the Great Tit (*P. major*), associated with more polluted areas. Although we cannot exclude this as an influence in our measurements, we observed similar UV degradation at two other museums, which suggests that it is not a locality effect. Moreover, it seems unlikely that the indirect mechanism of decreased food abundance, as identified by Eeva et al. (1998), would specifically affect UV wavelengths.

Ultimately, the uneven decrease in reflectance across the color spectrum from living to museum specimens, with greater degradation in the UV, emphasizes two things: (1) the importance of objective and accurate measurement of color, particularly when UV reflectance is strong or the interest is to describe more subtle variation in color; and (2) the need for caution in applying such measurements to hypotheses on color variation.

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Appendix. Species, plumage patch and color (in parentheses), sample size according to source (see text; mus = museum), and color variables (mean ± SE). Plumage patch abbreviations: bk = back, flk = flank, wng = wing, tl = tail, es = eye stripe, cr = crown, thr = throat, rmp = rump.

Species	Total brightness	UV	Human-visible	Chroma	Hue (nm)
		Carotenoid			
Setophaga ruticilla (flk–wng–tl, orange)					
live: $n = 8$	23.8 ± 1.32	5.1 ± 0.61	18.7 ± 0.84	175.3 ± 7.21	594 ± 3.2
mus: $n = 10$	16.35 ± 0.54	1.3 ± 0.17	15.1 ± 0.41	224.1 ± 4.43	614 ± 1.3
Dendroica virens (es, yellow)					
live: $n = 12$	21.7 ± 0.86	4.0 ± 0.21	17.8 ± 0.71	195.4 ± 4.66	588 ± 1.6
mus: $n = 10$	17.5 ± 0.47	1.1 ± 0.10	16.4 ± 0.48	233.4 ± 4.37	601 ± 1.2

Appendix. Continued.

Species	Total brightness	UV	Human-visible	Chroma	Hue (nm)
D. pensylvanica					
(cr, yellow)					
live: *n* = 12	10.8 ± 0.95	1.8 ± 0.21	9.1 ± 0.77	197.9 ± 6.43	589 ± 2.4
mus: *n* = 10	13.7 ± 0.97	1.2 ± 0.16	12.5 ± 0.82	217.5 ± 7.43	598 ± 2.0
D. magnolia					
(rmp–thr, yellow)					
live: *n* = 10	26.7 ± 1.04	6.7 ± 0.41	20.0 ± 0.82	147.3 ± 6.92	570 ± 2.9
mus: *n* = 10	19.5 ± 0.99	1.8 ± 0.18	17.7 ± 0.86	197.5± 5.89	589 ± 1.8
Wilsonia canadensis					
(thr, yellow)					
live: *n* = 5	33.5 ± 2.76	7.5 ± 0.95	26.1 ± 1.98	161.7 ± 6.37	576 ± 2.7
mus: *n* = 6	23.92 ± 0.92	1.8 ± 0.17	22.2 ± 0.79	208.3 ± 4.96	593 ± 1.5
Geothlypis t. trichas					
(thr, yellow)					
live: *n* = 10	36.7 ± 2.42	8.0 ± 0.73	28.7 ± 1.78	164.1 ± 7.71	579 ± 2.9
new mus: *n* = 4	29.8 ± 1.69	3.5 ± 0.41	26.3 ± 1.31	204.6 ± 7.56	593 ± 2.8
old mus: *n* = 10	24.56 ± 1.18	1.9 ± 0.15	22.6 ± 1.06	213.7 ± 3.36	596 ± 0.7
D. c. coronata					
(cr–flk–rmp, yellow)					
live: *n* = 9	29.0 ± 0.97	6.3 ± 0.62	22.7 ± 0.43	181.6 ± 4.51	583 ± 1.7
new mus: *n* = 5	24.0 ± 1.00	2.6 ± 0.31	21.5 ± 0.88	196.4 ± 13.87	590 ± 4.4
old mus: *n* = 10	19.7 ± 0.72	1.5 ± 0.12	18.2 ± 0.64	227.9 ± 2.56	600 ± 0.8
		Noncarotenoid			
Mniotilta varia					
(es–wng, white)					
live: *n* = 8	38.0 ± 1.03	9.4 ± 0.43	28.6 ± 0.68	25.0 ± 3.35	484 ± 2.6
mus: *n* = 10	28.3 ± 1.19	2.3 ± 0.19	26.0 ± 1.02	71.0 ± 2.41	535 ± 1.4
D. caerulescens					
(cr, blue-gray)					
live: *n* = 11	8.2 ± 0.86	2.8 ± 0.38	5.4 ± 0.51	81.0 ± 4.83	451 ± 3.0
mus: *n* = 10	7.6 ± 0.68	1.5 ± 0.17	6.1 ± 0.55	50.0 ± 2.74	482 ± 2.9
Wilsonia canadensis					
(bk, gray)					
live: *n* = 10	6.4 ± 0.57	1.6 ± 0.20	4.8 ± 0.47	18.7 ± 5.10	505 ± 5.8
mus: *n* = 10	3.6 ± 0.20	0.50 ± 0.08	3.1 ± 0.17	65.0± 6.13	539 ± 3.3
D. magnolia					
(cr, gray)					
live: *n* = 10	7.3 ± 0.51	1.8 ± 0.27	5.4 ± 0.30	35.0 ± 6.30	485 ± 4.6
mus: *n* = 10	6.2 ± 0.23	0.9 ± 0.06	5.4 ± 0.22	40.8 ± 4.25	518 ± 2.9
D. pensylvanica					
(flk, brown)					
live: *n* = 12	4.2 ± 0.54	No UV	–	249.1 ± 20.33	633 ± 5.6
mus: *n* = 10	2.8 ± 0.18	–	–	270.8 ± 9.34	641 ± 2.3
Seiurus aurocapilla					
(cr, brown-orange)					
live: *n* = 10	8.0 ± 0.98	No UV	–	268.2 ± 7.12	627 ± 1.8
mus: *n* = 10	7.5 ± 0.32	–	–	236.4 ± 5.05	622 ± 1.6