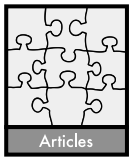

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Effect of feather abrasion on structural coloration in male eastern bluebirds *Sialia sialis*

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We used observations of male eastern bluebirds captured twice within a breeding season to test whether changes in structural coloration are related to feather abrasion. Between first and second broods, the UV chroma and brightness of feathers decreased, while hue shifted towards longer wavelengths. Observed changes were greatest for feathers on the head, least for feathers on the rump, and intermediate for feathers on the back. For head feathers, we found a significant correlation between reduction in barb length and UV chroma. Plumage coloration at first capture was correlated with change in UV chroma such that the most ornamented males tended to lose more coloration. Moreover, the magnitude of UV color change was positively related to the number of days between color measurements.To test whether these changes were caused by abrasive properties of the nesting sites, we randomly increased or decreased the abrasiveness of nesting-box entrances by attaching sand paper or smooth plastic tape. The type of box entrance had no signicant effect on either coloration or barb length change. Our results suggest that feather abrasion is a factor in the seasonal color changes of bluebirds.

Many environmental factors can affect the color of feathers as they are being grown (reviewed by Hill 2006). The period of feather growth is often presented as the only time when feather coloration can be altered because the color of feathers is usually described as fixed once feathers keratinize by the end of molt (Gill 2007). Several studies in the last decade, however, have presented evidence that the color of bird feathers can change between molts, irrespective of the mechanisms of color production (Örnborg et al. 2002, McGraw and Hill 2004, Figuerola and Senar 2005, Avilés et al. 2008). Experimental studies have investigated a variety of agents that may be responsible for changes in the color of grown feathers including accumulation of dirt (Surmacki and Nowakowski 2007), application of uropygial glad secretions (López-Rull et al. 2010), activity of keratinolytic microbes (Shawkey et al. 2007) and sunlight-induced fading (Surmacki 2008).

Feather abrasion is one of the least explored mechanisms of seasonal change in plumage color. Several songbird species have cryptic, dark-or-buffy feather tips on fresh feathers that wear down to reveal a different underlying color (Montgomerie 2006). This form of color change through feather abrasion typically occurs just before onset of breeding, so it is assumed to be an energy-saving alternative to a costly pre-breeding moult (Montgomerie 2006). This strategy for changing feather coloration occurs mainly in species with carotenoid- or melanin-based nuptial (alternate) plumages (Montgomerie 2006, Tökölyi et al. 2008). In some species the process of feather wear is passive; in other species, birds actively rub their plumage against objects to accelerate feather wear (Montgomerie 2006).

To date, only two studies have quantitatively related plumage wear to color change. Møller and Erritzoe (1992) showed that abrasion of whitish tips of ventral feathers enlarges the visible area of the black bibs of male house sparrows *Passer domesticus*, which are honest indicators of male quality. Similarly, in the Lawrence's goldfinch *Spinus lawrencei* grayish and olive-brown barbule tips abrade to reveal more yellow barbs, a process that is sex specific and related to the thicker barbs of males (Willoughby et al. 2002).

Feather abrasion was also proposed as a possible mechanism of seasonal color changes for structural UV/blue crown feather in blue tits *Cyanistes caeruleus* and wing coverts in azure-winged magpie *Cyanopica cyanus* (Solis et al. 2008) The crown of blue tits shows an initial post-moult increase of UV reflectance until the onset of the breeding season, followed by a marked decrease during incubation and chick rearing (Örnborg et al. 2002, Delhey et al. 2006, 2010). In contrast, crown brightness shows a gradual increase as the season progresses, while hue shifts toward longer wavelengths (Örnborg et al. 2002, Mongomerie 2006). The most common explanation for these observed patterns of change in feather coloration is that they are related to changes in feather structure. Initial increases of UV reflectance may result from the loss of dark,

melanized barbules. Later decreases in UV reflectance are likely to be an effect of breakage of barbs and/or dirt and fat accumulation (Örnborg et al. 2002, Delhey et al. 2010). To date, however, there are no studies investigating quantitatively how feather abrasion affects structural coloration.

We experimentally tested the effect of feather abrasion on UV/blue coloration in male eastern bluebird *Sialia sialis*. The entire dorsal plumage of the male eastern bluebird exhibits non-iridescent UV/blue coloration produced by coherent light scattering from barb microstructure (Shawkey et al. 2003). UV/blue coloration of males signals their quality and plays an important role in antagonistic behaviors and territory acquisition (Siefferman and Hill 2005a, b). Like other species with structural coloration, the blue coloration of eastern bluebird fades over the breeding season (Siefferman et al. 2005). We confined our study to males for two reasons. First, the majority of evidence confirming the role of structural coloration come from males (Siefferman and Hill 2005d). Second, only males provide an opportunity to compare abrasion effect across different plumage sections because in females structurally colored blue feathers are confined to the rump.

The goal of our study was to test whether seasonal changes of structural coloration are related to feather wear. First, we manipulated the abrasive environment to which birds were exposed at their nest boxes and tested whether the abrasiveness of the environment determined the degree of change in feather coloration during a breeding season. Second, we tested for correlations between aspects of feather wear and the magnitude of color change. Third, we used a passerine visual model to determine whether the color changes caused by feather abrasion could be perceived by birds.

Methods

Study area and general methods

Observations were conducted in 2010 on a population of eastern bluebirds in Lee County, Alabama (32°35′N, 82°28′W; Siefferman and Hill 2005b for descriptions of the study area). The eastern bluebird is a cavity-nesting species that readily uses artificial nest boxes. Within a breeding season, eastern bluebirds can successfully raise multiple successive broods in the same box.

We caught males at their nest boxes during both their first (28 April–6 May) and the second (23–29 June) broods using mist nets set at the entrance to nest boxes and traps set inside nest boxes. Males were lured to nets by placing taxidermic mounts of male bluebird behind a mist net while playing a recording of a bluebird song.

We measured the ultraviolet-blue color of feathers from the head, back, and rump region of each bird using a portable reflectance spectrometer. We plucked two feathers from each feather region to measure feather wear. We captured 40 males during their first brood, and we were able to recapture 23 of these males at the same boxes during their second brood. The 23 recaptured males became the focus of this study.

Field experiment design

At the beginning of the study, each nest box was randomly assigned to one of three groups. For two treatment groups, entrance holes were modified to either increase or decrease plumage abrasion when bluebirds entered and exited the nest box. The third group of nest boxes had their entrance holes unchanged and served as controls (hereafter 'control boxes'). To increase feather abrasion, strips of sand paper (coarseness number 80) were taped to box entrances (hereafter 'rough boxes'). The sand paper covered the upper one-third of the circumference of the entrance. In this group of nest boxes we expected increased feather abrasion due to rubbing plumage against the surface of the sand paper. In the second treatment group of nest boxes (hereafter 'smooth boxes'), we attached Scotch duct tape in the same manner as the sand paper in 'rough boxes'. The duct-tape treated boxes had much less abrasive entrances compared to control boxes that had the semi-abrasive rough entrance of unsanded wood that had been exposed to the elements for several years. Sample sizes for three groups of boxes were as follows: control boxes: $n = 8$, rough boxes: $n = 7$, smooth boxes: $n = 8$.

Feather wear

We quantified feather wear by measuring changes in barb length throughout the season. We measured four barbs on each collected feather, two on each side of the feather shaft. All measured barbs were located in the distal quarter of the feather shaft. Barbs were measured with a digital caliper (0.01 mm) under a dissection microscope (10× magnification). We used the average length from eight barb measurements to characterize the feathers from each plumage region for samples collected during both the first and the second broods. We calculated the amount of feather wear for each individual as the percentage difference in the mean barb lengths between feathers collected during the first brood and feathers collected during the second brood.

Spectrometry

We took five reflectance measurements from the feathers at the middle of each of three body regions (head top, back and rump) using a USB2000 spectrometer and a pulsed xenon lamp (PX2) connected with a fibre-optic measuring probe (R 200-7-UV/VIS; Ocean Optics, USA). Using a 90° incident and measurement angle, we fixed the distance from the feather surface at 5 mm. Before measuring each individual, we standardized measurements using a white standard (WS-1-SL, Labsphere, USA) while the dark standard was taken by turning off the light source and covering the probe.

Spectral measurements were expressed as percent of light reflected at different wavelengths. We calculated hue, UV chroma, and brightness for each body region following the method described in detail in Siefferman and Hill (2003). Hue is the principal color reflected by the feather and was calculated as the wavelength of maximum reflectance. UV chroma was calculated as the proportion of light reflected in the UV region of the spectrum (300–400 nm) relative to

the total reflectance (300–700 nm). Brightness was calculated as a mean reflectance for each wavelength (1 nm) between 300 and 700 nm. We processed spectral data using RCLR ver. 0.9.28 software (Montgomerie 2008).

Most of the analyses performed in this study focused on UV chroma and brightness of the head plumage region. We excluded hue because it changed only marginally compared to UV chroma and brightness, and changes in head hue were significantly and negatively correlated with UV chroma ($r = -0.72$, $p < 0.01$, $n = 23$). There was no significant relationship between change in UV chroma and brightness of head feathers ($r = 0.01$, $p = 0.95$, $n = 23$), so we analyzed these variables separately. We focused our analyses on head feathers because we found the greatest changes both in coloration and barb length and because we expected that the head would experience the greatest exposure to the abrasive nest box entrance. Male bluebirds tend to repeatedly place their the heads in and out of the nest boxes when feeding mates and offspring.

Statistical analysis

We tested each variable for normality of distribution using the Shapiro–Wilk test. We tested for differences in color variables and barb length between measures taken from the same bird early and late in the breeding season using either paired t-tests (when data were normally distributed) or Wilcoxon matched pair tests (when data deviated from normality). To test the effects of the abrasiveness of the nest box on length of feather barbs and color, we used an ANOVA with repeated measurements. Repeated measures were percentage differences between the first and the second measurement of UV chroma, brightness and barb length recorded at three plumage regions in the same individual (head, back and rump). Separate models were created for changes in UV chroma, brightness and barb length. All percentage values were arcsin transformed before analysis. To test how box abrasiveness affects changes in coloration between the first and the second measurement, we included nest box type as a grouping variable. We used Pearson correlation for testing across individual asociation of color variables between the first and the second measurements. Distribution of data for visual contrast deviated from normality, therefore we used Friedman ANOVA to test between plumage region differences. We corrected alpha level using sequential Bonferroni method whenever multiple testing occured. To test the effects of feather wear, initial coloration, and time between measurements on change in plumage coloration we used multiple regression models. We created separate models for UV chroma and brightness changes as dependent variables, and initial color, degree of feather wear and the number of days between measurements as explanatory variables. To assess repeatability (Lessells and Boag 1987) of spectrometer measurements, we calculated within-region repeatibility of head measurements done for males at the 1st broods ($n = 23$). Repeatabilities (R) of all color parameters were significant: UV chroma: $R = 0.66$, $F_{1, 22} = 9.80$, $p < 0.001$, brigtness: $R = 0.62$, $F_{1, 22} = 8.23$, $p < 0.001$, hue: $R = 0.87$, $F_{1, 22} = 31.80$, $p < 0.001$.

Visual modeling

To assess how bluebirds perceive changes in structural colors, we calculated chromatic (ΔS) and achromatic contrast (ΔL) between feathers collected during first and second broods. The chromatic contrast (ΔS) is expressed in units called just noticeable differences (jnds). It is assumed that ΔS values > 1.0 can be distinguished by birds (Vorobyev et al.1998). Increasing values of ΔS suggest an increasing ability of birds to detect differences between two color patches. We calculated chromatic contrast (ΔS) in the following way. For average reflectance spectra from each region (i.e. head, back and rump) and for each individual, we computed cone quantum catches (Q_i) for each cone type using the formula provided by Vorobyev et al. (1998):

$$Q_i = \int_{\lambda} R_i(\lambda) S(\lambda) I\lambda O(\lambda) d(\lambda)$$

where: λ = a wavelength, $R_i(\lambda)$ = the sensitivity of cone type i, $S(\lambda)$ = the reflectance spectrum, $I(\lambda)$ = the irradiance spectrum, $O(\lambda)$ = the transmittance of the ocular media.

Members of Turdidea family, like the majority of Passerines, use four cone types for color vision that are sensitive to very short (VS), short (S), medium (M) and long (L) wavelengths (Ödeen and Håstad 2003). Molecular analysis of opsins in VS cone types in a related species, the common blackbird *Turdus merula*, demonstrated that they are sensitive to ultraviolet light (peak sensitivity at 369 nm, Ödeen and Håstad 2003). Because no studies on cones sensitivities nor the transmittance of the ocular media have been performed on eastern bluebirds, we used data from blue tit, a species with similar UV-sensitive vision (Hart et al. 2000). We used Endler's Blue Sky spectrum as the irradiance spectrum (Endler 1993).

We calculated discriminability between two spectra using the following equation:

$$\begin{aligned}\Delta S^2 = {} & (\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 \\ & + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 \\ & + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2 \\ & \times (\Delta f_2 - \Delta f_1)^2 / ((\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 \\ & + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2)\end{aligned}$$

where:

$$\Delta f_i = \Delta q_i / q_i$$

where q_i is cone quantum catch (Q_i) normalized for the irradiance spectrum and ω_i represents receptor noise that depends on scaling factor T, the relative abundance of cone types, and Weber fraction for the cone type. Scaling factor relates a proportion of the maximal cone catch to an absolute cone catch. We set T to 10 000 that roughly corresponds to bright illumination. We used a Weber fraction of 0.05 for all cone types and the following relative abundance of cones from blue tit: VS = 0.37, S = 0.70, M = 0.99, L = 1.00 (Hart et al. 2000).

The Vorobyev–Osorio model assumes that color discriminability does not depend on brightness (Vorobyev et al. 1998). We therefore calculated achromatic contrast (ΔL) using the formula provided by Siddiqi et al. (2004):

$$\Delta L = \Delta f_i / \omega$$

where:

$$\Delta f_i = 1n[q_i(spec1)/q_i(spec2)]$$

and q_i indicates double cone quantum catches for two reflectance spectra (spec1 and spec2). Double cones are assumed to be involved in achromatic vision (reviewed by Cuthill 2006). We used double cone sensitivities data provided by Hart et al. (2000). If ΔL values are >1.0, two reflectance spectra are considered to be distinguishable by birds (Siddiqi et al. 2004).

We performed calculations of cone quantum catches and chromatic discriminability using SPEC.01 software (Hadfield 2004).

Results

The structural coloration of the feathers of eastern bluebirds changed over the course of the breeding season such that, in head and back regions UV chroma decreased significantly (Table 1, Fig. 1). On head and back plumage regions, feathers decreased in brightness (Table 1, Fig. 1). In all three regions, we found significant decreases in barb length (Table 1).

Relationships between colors of males scored at the first and second broods were weak and not significant in most cases (Table 3). The exception was hue of the rump (Table 3) and brightness of the head, where the relationship was marginally significant (Table 3).

A multifactorial analysis showed that changes in UV chroma, brightness, and barb length depended significantly on the plumage region (Table 2). For all analyzed traits, the greatest changes in coloration occurred on the head, and the lowest on the rump. (Fig. 2). We found no significant interactions between manipulation of abrasiveness of entrance hole and any of the color or barb changes, suggesting that the magnitude of color and barb length changes were independent of the treatment (Table 2).

Initial color, time between measurements and degree of feather wear were good predictors of changes in UV chroma for the head region ($F_{3,\ 19} = 11.74$, $p < 0.01$, $R^2 = 0.59$)

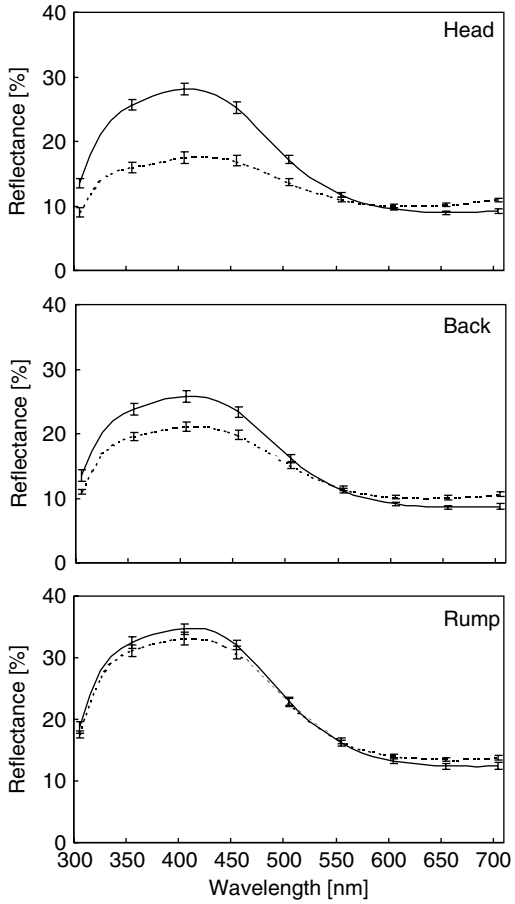

Figure 1. Mean reflectance curves (± SE) of eastern bluebird male plumage regions. Solid and dashed lines represent the first and the second captures, respectively.

but not in brightness ($F_{3,\ 19} = 1.10$, $p = 0.37$, $R^2 = 0.01$). Birds with plumage that reflected relatively greater UV chroma at the beginning of the study tended to lose more UV chroma during the course of the breeding season ($b = -1.60$, $SE = 0.55$, $t = -2.89$, $p = 0.01$, Fig. 4). Similarly, a longer time lag between measurements was related to greater UV chroma reduction ($b = -0.02$, $SE = 0.003$,

Table 1. Color traits and barb lengths [mm] at the first and the second capture. Differences were tested using matched pair t tests or Wilcoxon tests depending on data distribution (normal vs deviated from normal). Presented values are means ± SD or medians with 25–75% quartiles. Alpha level after sequential Bonferroni correction for multiple tests is 0.004.

Trait	First brood	Second brood	t, Z	p
Head				
Brightness	0.18 ± 0.02	0.13 ± 0.02	9.53	< 0.001
UV chroma	0.35 ± 0.02	0.29 ± 0.03	9.37	< 0.001
Hue	405.8 (395.2–415.4)	419.8 (408.4–436.2)	2.68	0.007
Barb length	4.66 (3.75–4.91)	2.90 (2.61–3.08)	4.20	< 0.001
Back				
Brightness	0.17 (0.15–0.18)	0.16 (0.13–0.17)	3.01	0.003
UV chroma	0.35 ± 0.02	0.31 ± 0.02	7.98	< 0.001
Hue	404.6 ± 12.24	410.8 ± 13.82	−2.27	0.033
Barb length	7.74 ± 1.09	5.92 ± 0.92	7.85	< 0.001
Rump				
Brightness	0.23 ± 0.03	0.22 ± 0.03	0.98	0.339
UV chroma	0.34 ± 0.02	0.33 ± 0.02	2.75	0.012
Hue	408.5 ± 12.2	406.9 ± 12.2	0.85	0.406
Barb length	8.73 ± 0.89	7.78 ± 0.76	5.29	< 0.001

Table 2. Results of repeated measures ANOVA comparing changes in UV chroma, brightness and barb length between three plumage regions (head, back, rump) measured on the same individual. *p <0.01.

	DF	UV chroma	Brightness	Barb length
		F	F	F
Test of within-subject effects				
Plumage region	2, 40	32.65*	30.58*	27.77*
Plumage region × box type	4, 40	0.77	2.14	2.52
Test of between-subject effects				
box type	2, 20	0.19	1.44	0.42

$t = -2.90$, $p = 0.01$). On the other hand, the reduction of barb length was positively correlated with a decrease in UV chroma ($b = 0.21$, $SE = 0.07$, $t = 2.94$, $p = 0.01$, Fig. 4).

The effect of initial UV chroma on chroma change could be an effect of a partial correlation (Kelly and Price 2005). We corrected this regression using the method provided by Kelly and Price (2005). We found evidence for differential color loss ($T = -4.59$, $DF = 21$, $p < 0.001$), indicating that our finding was not an artefact.

Chromatic visual contrast (ΔS) observed between two consecutive measurements differed significantly across plumage regions (Friedman ANOVA, $\chi^2 = 15.91$, $DF = 2$, $p < 0.001$, Fig. 3). The highest scores were obtained for head, intermediate for back and the smallest for rump (Fig. 3). The percentage of individuals for which color change was at a perceivable level ($\Delta S > 1.0$) was 91% for head, 56% for back and 26% for rump. Achromatic visual contrast did not differ among plumage regions (Friedman ANOVA, $\chi^2 = 1.13$, $DF = 2$, $p < 0.001$, Fig. 3). The percentage of individuals for which changes in brightness change could be visible ($\Delta L > 1.0$) at head, back and rump was 74, 78 and 69%, respectively.

Discussion

We observed that the UV/blue structural color of the feathers of male eastern bluebirds changed significantly over only a few weeks during the breeding season. In all of the plumage regions that we studied, hue shifted towards longer wavelengths and UV chroma and brightness decreased. However, the changes in rump coloration were not statistically significant. In light of previous studies (Siefferman and Hill 2005a, b, c), the observed color changes represent a decrease in color quality, so our observations indicate that the showiness of structural coloration declines as feathers wear. Similar changes in hue and UV chroma were observed in blue tits late in the breeding season, but the blue tits experienced an increase in brightness whereas we found a reduction in the brightness of eastern bluebird feathers (Örnborg et al. 2002). On the other hand, the same directions of change in all three color variables (i.e. UV/blue

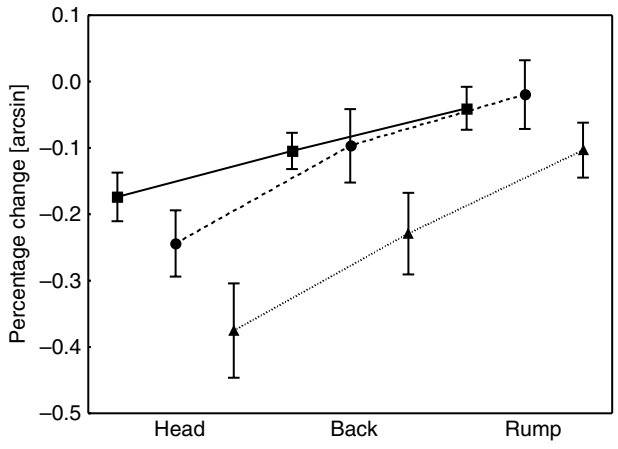

Figure 2. Mean UV chroma (squares), brightness (circles) and barb length (triangles) change (± 95% CL) in relation to plumage region.

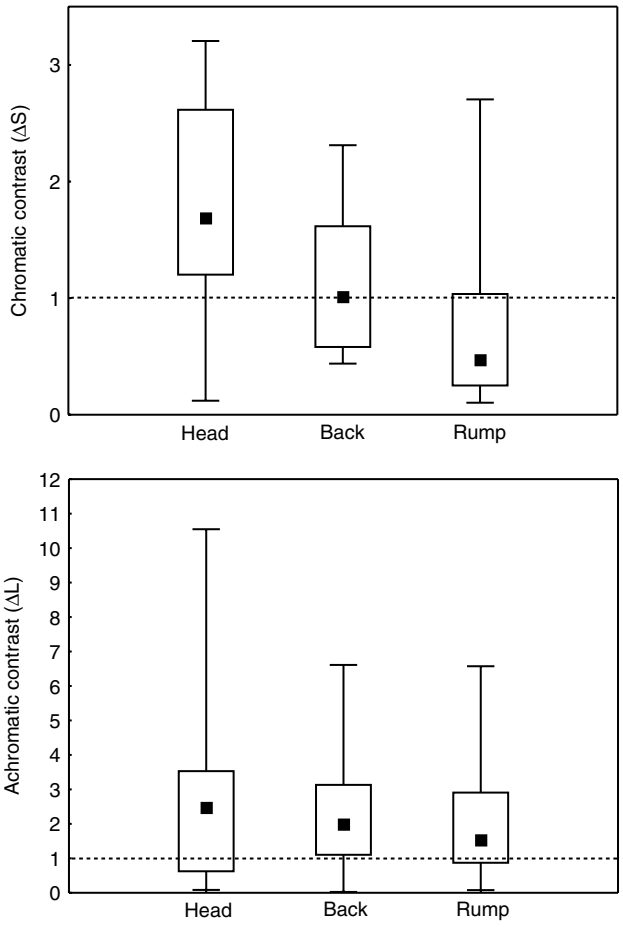

Figure 3. Mean chromatic (ΔS) and achromatic (ΔL) color contrast between measurments done at first and second broods. Shown are medians (points), 25–75% percentiles (bars) and minima and maxima (whiskers). Dotted line indicates a threshold of contrast perceived by birds (1.0 for ΔL and ΔS).

Table 3. Matrix of corrlelation of color variables (UV chroma, hue and brightness) between first and second measurements. Sample sizes in all cases is 23. Alpha level after sequential Bonferroni correction for multiple tests is 0.006.

	UV Chroma 2		Hue 2		Brightness 2	
	r	p	r	p	r	p
Head						
UV chroma 1	0.13	0.571				
Hue 1			−0.16	0.46		
Brightness 1					0.55	0.007
Back						
UV chroma 1	0.31	0.155				
Hue 1			0.51	0.013		
Brightness 1					0.51	0.013
Rump						
UV chroma 1	0.06	0.752				
Hue 1			0.76	<0.001		
Brightness 1					0.45	0.032

chroma, hue and brightness) were reported in structurally colored wings of another cavity nesting species, the azure-winged magpie (Avilés et al. 2008).

Using vision data from other passerine species, we calculated visual contrasts for the observed changes in color. The values that we obtained generally supported results from analysis of traditional color variables. Chromatic visual contrast, which roughly corresponds to changes in chroma and hue, was the highest for head region and the lowest for rump, where changes in color were barely visible. Achromatic contrast was well above visible threshold for all plumage regions. Unlike the changes in brightness, however, we found no differences between plumage regions. It is important to stress that results of visual modelling should be treated with caution, because they were developed based on anatomical and physiological data from other species and small numbers of individuals (Hart et al. 2000).

Our initial hypothesis was that feather abrasion is responsible for seasonal changes in plumage coloration in bluebirds. Two observations from our study support that hypothesis. First, there was a positive correlation between the reduction in the length of feather barbs on the head – caused by feather abrasion – and the reduction of the UV chroma of feathers. Second, there was an among-region positive correlation between the magnitude of barb shortening and the decrease in UV chroma (Fig. 2).

Gradual shortening of feather barbs was proposed as a mechanism for the reduction in hue and chroma of blue tit crown feathers during the late breeding phase (Örnborg et al. 2002). In bluebirds, as well as in blue tits, barbs with UV/blue coloration are located along the distal 1/3 of the feather shaft. The proximal 2/3 of the feather is dark gray and presumably pigmented by melanin. As these blue feathers are abraded, their most distal barbs with UV/blue coloration shorten, revealing underlying melanin-colored barbs. As a consequence, the proportion of shorter-wavelength reflection decreases while longer-wavelength reflection increases and hue shifts toward longer wavelengths.

Other micro-scale processes may also change feather color in concert with gross wear of barbs. The surface of UV/blue barbs erode at a microscopic scale, which affects the reflectance properties of nanostructures and hence the color of feathers. In a study of the effect of keratinolytic bacteria on eastern bluebird plumage coloration, nano-scale degradation of the cortex and spongy layer of barbs caused a decrease in UV chroma but left hue unchanged and increased brightness (Shawkey et al. 2007).

The observations from our study provide the first evidence that, within a coloration type (UV/blue structural coloration), the degree of feather abrasion and associated color changes vary among feather patches on different regions of the body. The rump appeared to be exposed to the least wear, while the head was the most abraded surface of the body. Results of our field experiment, however, did not support feather abrasion at the cavity entrance as the mechanism of color change. Males breeding in 'rough' nest boxes showed only a small and non-significant tendency to have more feather damage on their heads compared to controls. Moreover, the changes that we observed in UV chroma were not related to the abrasiveness of the box entrance. An alternative explanation for the increased abrasion on head feathers compared to other body regions is that it occurs mainly during activities that demand use of the bill such as foraging or nest building. The eastern bluebird commonly forages by dropping from a perch to the ground leading to frequent contact with vegetation which may abrade head feathers (Hill 2010).

For the head region, the UV chroma at first capture was a good predictor of the extent of color change over the subsequent weeks – males with more UV chromatic coloration experience the greatest reduction in UV chroma. One possible explanation is that there is a tradeoff between barb coloration and barb strength. For example, barbs that are flatter and express more color may be thinner and thus more prone to breaking (Hill 1994). Another possibility is that males with brighter coloration spend more time on activities that promote feather abrasion or/and soiling. Earlier studies showed that males with higher UV chroma and overall brightness provide more food for chicks (Siefferman and Hill 2003) and incubating females (Siefferman and Hill 2005c). If foraging is a main cause of plumage wear and brighter males spent more time foraging, this would explain observed color change.

Our study provides the first evidence that feather wear is responsible for the seasonal decline of the quality of structural coloration. It is likely that a variety of interacting factors (e.g. soiling, keratinolytic bacteria, sunlight UV

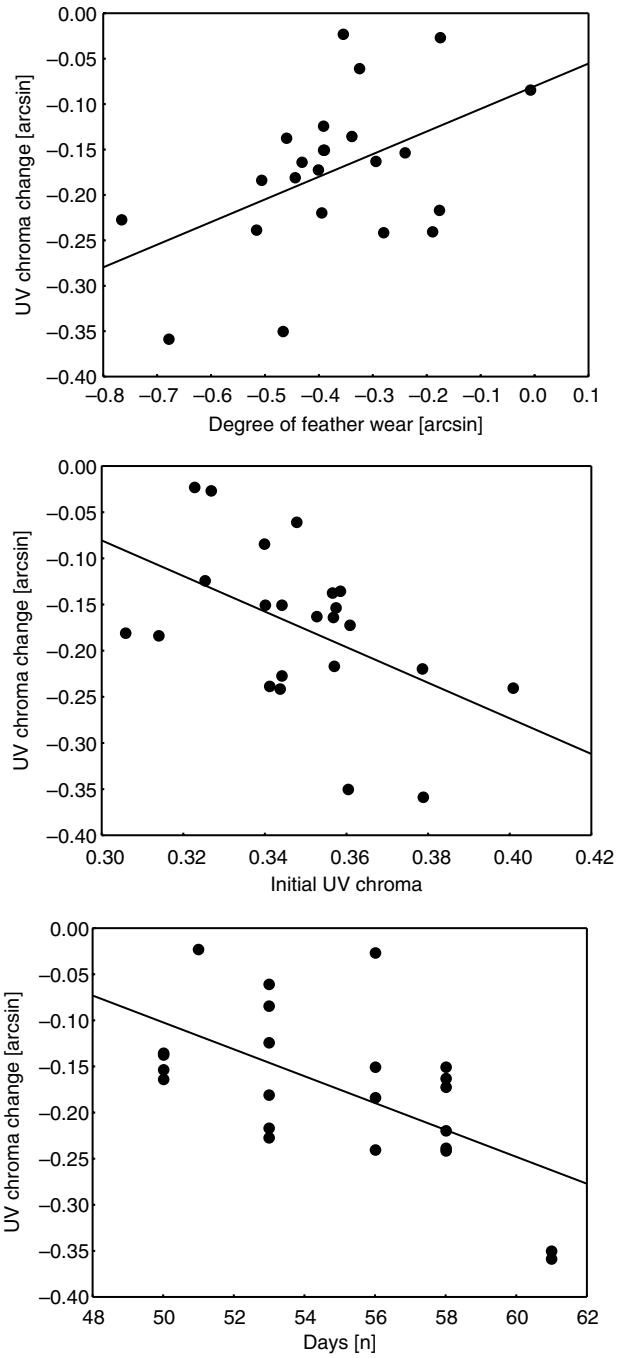

Figure 4. Relationship between head UV chroma change, degree of feather abrasion (upper plot), initial UV chroma (middle plot) and number of days between measurements (lower plot).

radiation) caused the observed changes in coloration. Our study revealed that even within the same type of ornamental coloration, seasonal changes may differ in their magnitude depending on plumage region. These differences were likely not caused by rubbing plumage against cavity entrances but were probably an effect of general foraging activity of birds. We found that the degree of color change was not equal for all males and that males with superior initial color quality lost the most coloration. This relationship could be related to their greater investment in provisioning to mates and offspring. Whether seasonal changes in structural coloration can be used by conspecifics as a signal of quality warrants further research.

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