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Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament

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After years of investigation into the function of sexually dimorphic ornamental traits, researchers are beginning to understand how bright plumage colour in birds acts as an intraspecific signal. This work has focused primarily on pigment-based ornaments because they are highly variable in patch size, hue and brightness for some species. In contrast, structurally based ornaments have been little studied, in part because they do not appear to be as variable as pigment-based ornaments. We investigated a structurally based plumage ornament in a wild population of blue grosbeaks (*Guiraca caerulea*), a sexually dimorphic passerine. We report plumage variation that extends into the ultraviolet region of the spectrum. The pattern of covariation between four out of five elements of plumage variation suggests that structurally based ornamentation is pushed towards extreme expression of the trait as predicted by the sexual selection theory. The 'bluest' birds have the highest percentage of blue feathers on the body. These ornamental feathers reflect light maximally at the shortest wavelengths (ultraviolet), with the greatest intensity and the greatest contrast. Age may have some effect on expression of blueness. In addition, plumage variables are correlated with growth bars in tail feathers (a record of nutritional condition during moult in a non-ornamental trait). This suggests that the ornament is partially condition dependent. Thus, blue plumage in male grosbeaks may serve as an honest indicator of age and quality.

Keywords: honest advertisement; sexual selection; nutritional condition; ultraviolet reflectance; structural colour; birds

1. INTRODUCTION

Sexual selection theory attempts to explain the evolution and maintenance of ornamental traits, particularly sexually dimorphic traits, in terms of intraspecific signalling functions (Darwin 1871). If exceptional individuals in a population bear extreme expressions of secondary sexual traits, they may be favoured in mate choice or intrasexual competition (Andersson 1986, 1994; Darwin 1871; Kirkpatrick 1982; Kodric-Brown & Brown 1984). If an ornamental trait functions in intraspecific interactions, variation can persist when the trait is costly to produce or to bear such that not all individuals are capable of possessing the most extreme version of the trait (Andersson 1986; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984; Zahavi 1975). When an ornamental trait is correlated with a fitness-related trait and the ornamental trait itself is costly, the trait acts as an honest advertisement of quality that potential mates or competitors can assess (Kodric-Brown & Brown 1984).

Two primary mechanisms produce brightly coloured plumage in birds: pigments deposited in growing feathers and reflective or disruptive feather microstructure. There are two common classes of pigments: melanins, which produce colours from brown to black; and carotenoids, which produce yellow, orange and red. Both are found in ornamental plumage and can be highly variable in hue within and across species. In addition to ornamental functions, melanins provide structural support to feathers (Burtt 1981), and carotenoid pigments are essential vitamin A precursors (Pitt 1971; Underwood 1984). In contrast to pigment-based colours, blue, purple, green, ultraviolet colours and iridescence are produced when physical structures in the reflective keratin of the feather scatter incident light and reflect the shortest wavelengths (Finger 1995; Finger & Burkhardt 1992; Fox 1976; Greenewalt *et al.* 1960). Structural colours occur in many avian taxa (Auber 1957; Fox 1976) and appear to be purely ornamental. Feather microstructure may be species specific (Brush 1978; Dyck 1971, 1978, 1987; Monge-Nájera & Hernández 1994).

There is strong empirical evidence that melanin and carotenoid-based plumage coloration functions in female mate choice and male–male competitive interactions (Andersson 1994). In contrast, structural plumage coloration, while widespread among avian taxa, has generally been viewed as invariant among males and hence uninteresting (Borgia & Collis 1990). Until recently the function of structural plumage coloration has remained virtually unstudied.

Variation in structural coloration may not be absent; however, it may be invisible to human observers. The three retinal cones of the human eye perceive electromagnetic radiation in the range 400–700 nm. In contrast,

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many species of birds can perceive ultraviolet light (Chen *et al.* 1984; Chen & Goldsmith 1986), and a specific retinal cone that is maximally sensitive to ultraviolet light has been characterized for several species (Bowmaker *et al.* 1997; Hart *et al.* 1998; Maier 1994). A comparison of plumage spectra with the tetrachromatic visual system of birds indicates that the signal (feather colour) may be tuned to the receiver (avian eye) and thus could potentially serve a signalling function (Finger & Burkhardt 1994). Some birds that appear dull to humans (and perhaps mammalian predators as well) show ultraviolet ornaments that may serve to make them more apparent to each other (Andersson 1996; Radwan 1993). Variation in these ornaments between the sexes indicates a possible intraspecific signalling function (Andersson *et al.* 1998; Bleiweiss 1994; Hunt *et al.* 1998). The fact that birds have a wider visual spectrum than humans suggests that some plumage signals may go undetected by observers who rely on the human visual system (Bennett *et al.* 1994). Cuthill *et al.* (1999) review the physiology and function of ultraviolet vision in birds.

Results of several recent studies suggest that 'invisible' plumage ornamentation extending into the ultraviolet range may function in social signalling. Female bluethroats (*Luscinia s. svecica*) prefer males with ultraviolet plumage reflectance as both social and genetic mates (Andersson & Amundsen 1997; Johnsen *et al.* 1997, 1998), and female European starlings (*Sturnus vulgaris*) are sensitive to a lack of ultraviolet signal in male plumage (Bennett *et al.* 1997). Male ring-necked pheasants (*Phasianus colchicus*) with bright structural coloration are more successful in dominance interactions than dull-coloured males (Mateos & Carranza 1997). Blue tits (*Parus caeruleus*), which appear nearly monomorphic to humans, are dimorphic when ultraviolet signal is considered and show positive assortative mating based on plumage ornamentation (Andersson *et al.* 1998; Hunt *et al.* 1998).

We studied natural variation of blue-ultraviolet plumage ornamentation in a wild population of blue grosbeaks. At the extremes of trait expression, females are brown and males are bright blue. There is overlap in the distributions for each sex such that some females are more blue than some males. Although variation among individuals in number of blue feathers is conspicuous, humans find it hard to judge differences in hue or intensity of the colour (A. J. Keyser and G. E. Hill, personal observation). Our objectives were to document the extent of natural variation in a structural plumage ornament, to test for condition dependence of this trait and to investigate the potential for male plumage to function in intraspecific signalling.

2. METHODS

This study was conducted in Lee County, Alabama, during the 1997 and 1998 breeding seasons. The study site is located in a highly fragmented, agricultural landscape. Most birds were caught in early May using mist-nets and Potter live traps baited with sunflower seeds. Traps and seed piles were removed from the study area several weeks before reproductive behaviours began. Each bird was banded with an aluminium US Fish and Wildlife Service band and a unique combination of colour bands. Blue bands were not used. Standard morphological data were taken, and the outer two tail feathers were plucked. Animals were handled according to the protocols approved by the Auburn University Institutional Animal Care and Use Committee (PRN no. 9809-R-1025). Detailed plumage information was taken for each individual.

To assess the extent of ornamentation in each body region (amount of coverage), the percentage of of blue feathers was visually estimated on the breast and rump. When possible, each bird was scored independently by a second observer, and repeatability of these estimates was calculated (Lessells & Boag 1987; mean repeatability $= 0.96$; $n = 13$). To assess variation in blueness, between eight and 12 body feathers were plucked from both the breast and rump of each male. These were taped on to a white card in an overlapping pattern that replicated the way the feathers were attached to the bird's body. The result was a small (*ca.* 1 cm^2) patch of coloured feathers that was used for spectral analysis.

Spectral data were taken with an Ocean Optics S2000 fibre-optic spectrometer (range 250–880 nm; Dunedin, Florida, USA) using a 200 micron fibre-optic probe at a 90° angle to the feather surface. Ambient light was excluded with a cylindrical metal sheath affixed to the probe tip. The end of this sheath was placed against the specimen and held the probe tip a fixed distance of 6 mm from the feather surface. The reading area was a circle of diameter 2 mm. The sample was illuminated by a deuterium bulb (ultraviolet light source) and a tungsten-halogen bulb (visible light source; Analytical Instrument Systems, Inc., New Jersey, USA). Reflectance spectra were generated in proportion to a Spectralon white standard (Labsphere, Inc.). Using OOIBase, a spectral acquisition software package (Dunedin, FL, USA), 20 spectra were taken sequentially and then averaged to reduce electrical noise from the collection array within the spectrometer. This was repeated five times. The probe was lifted and replaced at a random location on the feather sample between each scan. The five spectra for each body region (breast and rump) were averaged for every male.

Wavelength of peak reflectance, percentage reflectance at the peak, the wavelength of maximum slope of the curve, and the difference in intensity between the peak and the trough of the curve were obtained from spectral data. The spectral peak describes the hue at which the plumage was maximally reflective. Peak shifts represent changes in hue. Reflectance at the peak of the spectrum (expressed as a percentage of white standard reflectance) corresponds to the intensity or brightness of the colour displayed by the bird. Wavelength of maximum slope of the curve describes the point on the spectral curve at which the intensity is changing most rapidly. The difference in intensity between peak and trough is related to colour saturation or contrast. Spectral shape and intensity of plumage reflectance provide an objective and repeatable measure of colour (Endler 1990).

To assess how blueness varied among males, we compared the five elements of plumage ornamentation that we measured (percentage of blue, peak wavelength, intensity, maximum slope, and difference between peak and trough) with non-parametric correlations. Birds with plumage which was maximally reflective above 525 nm were excluded from these analyses because they do not display plumage ornamentation in the 'blue' range of the spectrum. This cut-off was chosen after an examination of the frequency distribution of peak wavelength (figure 1). Since we are concerned with the relationship between variables that describe blue feathers, including brown males in the analysis obscures the pattern. Using the patterns of covariation defined by this analysis, we calculated a single blueness score to use in subsequent analyses (described fully in § 3).

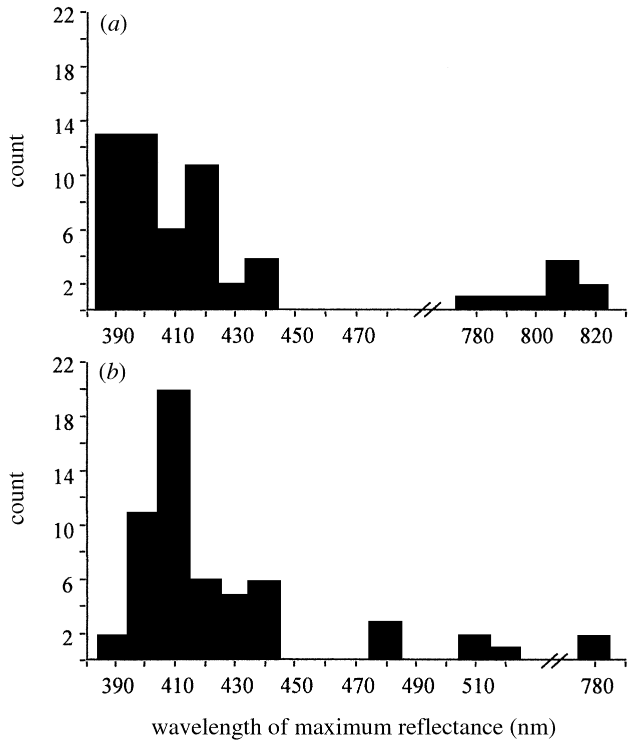

Figure 1. Distribution of peak wavelength reflected by the plumage of 58 male blue grosbeaks on (*a*) the breast and (*b*) the rump.

To test the hypothesis that blue plumage is condition dependent, we used tail feather growth rate as a measure of condition. Rate of new feather growth depends on nutritional condition (Grubb 1989, 1992; Hill & Montgomerie 1994). Light and dark band patterns on tail feathers record daily feather growth (Michener & Michener 1938). In blue grosbeaks, pre-basic moult occurs primarily at the end of the summer on the breeding grounds but may be suspended over migration (Pyle *et al.* 1987). Since tail feathers are non-ornamental in this species, there is no reason to suspect that they are sexually selected (Tobias & Hill 1998). As such, tail feather growth rate is an independent measure of condition that can be compared to ornamental plumage variables.

At the time of capture, the outermost tail feathers of each bird were removed. We measured the length of seven alternations of light and dark bands centred over the midpoint of each feather (repeatability $=0.78$, $n=8$) and averaged the values for the left and right retrices. This measurement yields the feather growth rate (Michener & Michener 1938) and serves as a proxy for nutritional condition during moult in our analyses.

Since it is likely that plumage blueness increases with age, we would like to be able to distinguish statistically the effects of condition from the effects of age on blueness. Unfortunately, this is impossible because there are few known-age birds in our study population. However, six males were captured in 1997 and 1998, and one nestling hatched in 1997 was recruited into the breeding population in 1998. From these data, we can draw some preliminary conclusions.

3. RESULTS

Thirty males were captured in 1997, of which six were recaptured and 28 were newly banded in 1998. Plumage data were obtained for 58 males. First-capture data were used in all analyses. Most plumage variables were non-normally distributed, and non-parametric statistical tests were used in all analyses. Plumage descriptors were bimodally distributed (figure 1). This distribution of plumage coloration suggests that yearling males delay acquisition of definitive plumage until their second breeding season and supports previous hypotheses regarding delayed plumage maturation in this species (Pyle *et al.* 1987). While our data do not permit a statistical analysis, changes in plumage characteristics for seven males captured in 1997 and 1998 are suggestive. Two males were completely brown in 1997, and the following year both experienced a large increase in their percentage of blue coloration as well as a substantial decrease in peak wavelength. All other males were at least 60% blue and they experienced very moderate changes in plumage colour (three increased in blueness, one decreased and one remained unchanged). We speculate that age may have a strong initial effect on plumage blueness for young birds, but as males age and approach the extremes of the distributions for plumage variables, smaller fluctuations in blueness occur and these may be mitigated by nutritional condition (described fully below). However, this remains to be tested statistically, and the pattern observed here might be due solely to differences between years and not due to age.

Spectral data obtained from males revealed substantial variation in both the location of peak reflectance and intensity (see figure 2 for representative curves). Males which are mostly brown exhibit plumage reflectance similar to that of females. In our sample, two males were maximally reflective above 525 nm on the rump and nine males were maximally reflective above 525 nm on the breast (figure 1). This is outside of the blue portion of the spectrum. However, when the brown males were excluded from consideration, there remained substantial natural variation in peak wavelength and intensity of reflectance among the blue plumages of adult males (figure 2). Descriptive statistics of plumage variables are given in table 1. Brown males are excluded.

When we analysed the pattern of covariance among the five elements of plumage variation, we found that the 'bluest' male grosbeaks have the highest percentage of blue feathers in their plumage, reflect light maximally at the shortest wavelengths, reflect with the greatest intensity, and show the greatest difference in intensity between the peak and the trough of the spectral curve (table 1). Percentage of blue is negatively correlated with peak wavelength and the difference between peak and trough. Peak wavelength is negatively correlated with intensity of reflectance and the difference between peak and trough. Intensity is positively correlated with percentage of blue and the difference between the spectral peak and trough. Wavelength of maximum slope was not related to any other plumage variables. Spearman's correlation coefficients are reported (table 1).

Using the directional relationships described above between percentage of blue, peak wavelength and intensity of reflectance, breast and rump blueness scores were calculated for each male in each year. This score condenses the individual plumage variables and allows us to compare overall 'blueness' to nutritional condition. The difference in intensity at peak and trough is excluded

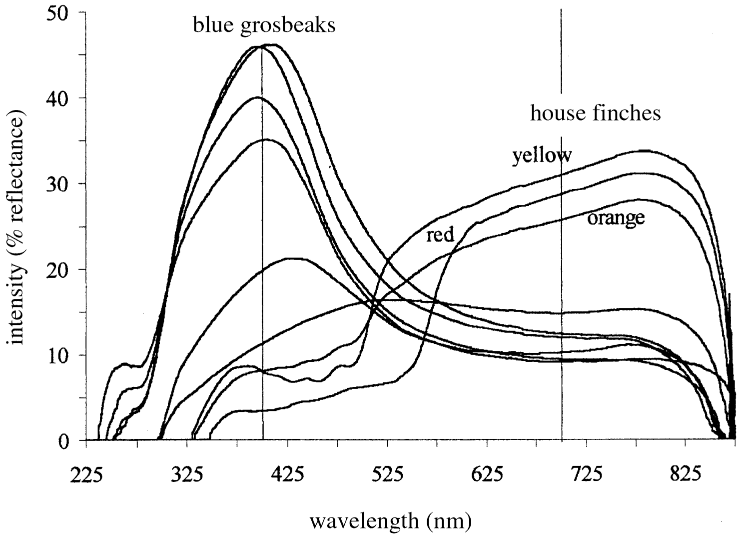

Figure 2. A comparison of reflectance spectra of plumage from the rump region of six adult male blue grosbeaks and three male house finches. The spectral curves shown here span the range of variation in wavelength of maximum reflectance and include the minimum, median and maximum from the population. All blue feathers, with the exception of the minimum curve, appeared equally blue to human observers. Male house finches were uniformly pigmented on the rump but hue varied among individuals from yellow to orange to red as indicated by labels. Vertical lines delineate the range of human visual sensitivity. Error bars omitted for clarity.

Table 1. *Descriptive statistics for plumage variables and correlation between plumage variables for male blue grosbeaks*

($n = 49$ for breast region and $n = 56$ for rump region.)

	breast region							rump region						
	% blue	peak	int	diff	slope	mean	±s.d.	% blue	peak	int	diff	slope	mean	±s.d.
% blue	—	−0.65*	0.59*	0.60*	−0.19	0.80	±0.23	—	−0.63*	0.63*	0.60*	−0.21	0.85	±0.23
peak		—	−0.71*	−0.68*	0.13	406	±15		—	−0.74*	−0.76*	0.17	422	±30
int			—	0.93*	−0.25	29.6	±8.0			—	0.97*	−0.20	30.4	±9.9
diff				—	−0.21	23.5	±5.5				—	−0.16	24.6	±6.7
slope					—	304	±3.4					—	305	±4.9

% blue, percentage of blue plumage on each region of the body; peak, wavelength of maximum light reflectance (peak of reflectance spectrum in nm); int, intensity of reflectance (% reflectance) at the peak wavelength; diff, difference between intensity at the wavelength of maximum reflectance (peak) and intensity at the wavelength of minimum reflectance; slope, wavelength of maximum slope of the spectrum (nm). Spearman's rank correlation coefficients are reported with significant correlations flagged ($^*p < 0.001$).

because it is not independent from maximum intensity. Percentage of blue and intensity values were ranked such that the bird with the highest percentage of blue and greatest intensity received the highest rank. Peak wavelength was ranked in the opposite manner, and the bird with the shortest peak wavelength received the highest rank. These ranks were averaged yielding a single blueness score ranging from 2.3 (brownest) to 54.0 (bluest).

To address whether the expression of blue plumage is condition dependent, we compared average tail feather growth rate to the plumage variables using three slightly different methods. First (method I), the analysis was performed using only males with plumage that was maximally reflective below 525 nm (rationale described above). Second (method II), all males were included in the analysis. Third (method III), the blueness score described above was compared to tail feather growth rate per week. Using method I, no plumage variables were associated with tail feather growth rate on the breast, but on the rump all plumage variables, with the exception of maximum slope, were significantly associated with tail feather growth rate. Using method II, percentage of blue and peak wavelength on the breast were positively correlated with tail feather growth rate, and on the rump the results were similar to those of method I. Using method III, increased feather growth rate was correlated with extreme expression blueness on both body regions (table 2, figure 3).

These three methods yielded somewhat different results on the breast. In part, this is due to the fact that brown feathers reflect maximally at intensity levels similar to those of blue feathers. In general, males showed a higher proportion of brown feathers on the breast than on any other part of the body (A. J. Keyser and G. E. Hill, unpublished data). In the rump-region analyses, fewer males were brown on this part of the body and the relationship between plumage variables that describe blueness and nutritional condition is strong.

4. DISCUSSION

This study documents extensive variation in blue-ultraviolet coloration among males of a single population. We wanted to determine if the variation in the blue plumage of male grosbeaks was sufficient to act as a signal in mate choice and male–male competition. We compared the reflectance spectra of grosbeak plumage to the reflectance spectra of house finches (*Carpodacus mexicanus*). It has been demonstrated that colour variation in the plumage of male house finches acts as a reliable indicator of quality and is used in mate choice (Hill 1990, 1991). The range of variation in plumage coloration among male house

Table 2. *Three different methods for analysing the correlation between plumage variables and nutritional condition during moult as measured by non-ornamental feather growth rate per week*

	breast region						rump region					
method	% blue	peak	int	diff	slope	blueness score	% blue	peak	int	diff	slope	blueness score
I	0.22	−0.16	0.07	0.06	−0.20	—	0.47*	−0.35**	0.38**	0.37**	−0.11	—
II	0.35**	−0.32***	−0.02	−0.06	−0.20	—	0.48*	−0.37**	0.39**	0.37**	−0.10	—
III	—	—	—	—	—	0.28***	—	—	—	—	—	0.41**

Method I: analysis performed excluding all males with plumage maximally reflective above 525 nm (i.e. males not reflective in the blue region of the spectrum; $n=47$ for breast region and $n=53$ for rump region). Method II: analysis performed including all males ($n=55$ for breast and rump regions). Method III: analysis performed using combined blueness score (see § 3 for details; $n=55$ for breast and rump regions). Spearman's rank correlation coefficients are reported with significant correlations flagged ($^{*}p<0.001$; $^{**}p<0.01$; $^{***}p<0.05$).

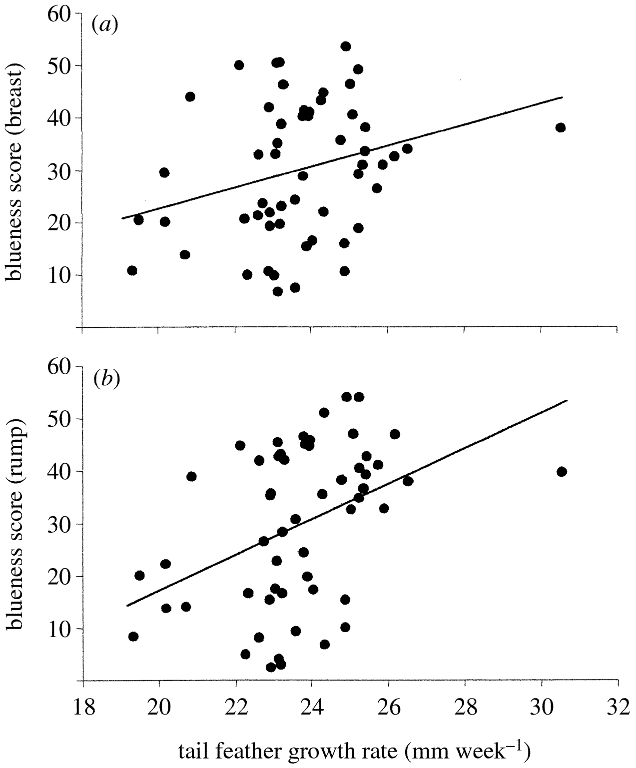

Figure 3. Correlation between plumage blueness on (*a*) the breast ($r^2=0.28, p=0.04$) and on (*b*) the rump ($r^2=0.41$, $p=0.002$) plotted against tail feather growth rate ($n=55$; mm week^{-1}). Removing the outlying data point does not change the results.

finches is clearly visible to a human observer and provides a benchmark to which the degree of variation outside the range of human visual perception might be judged (figure 2). The range of variation in peak wavelength and intensity of long-wavelength colours, as in house finches, is similar to that found in the short-wavelength colours of blue grosbeaks. We suggest that the variation in blueness of structurally based colours is sufficiently broad to act as an intraspecific signal. It is likely that grosbeaks can perceive this 'invisible' variation because several other passerine species, including northern cardinals (*Cardinalis cardinalis*), a species in the same subfamily as blue grosbeaks, can perceive ultraviolet light (Chen *et al.* 1984; Chen & Goldsmith 1986).

For male grosbeaks, ornamental plumage varies in coloration, peak wavelength, intensity, and difference in intensity between the peak and trough of the spectral curve. However, maximum slope of the spectral curve generated from blue feathers does not appear to be a particularly meaningful plumage descriptor. The maximum expression of plumage ornamentation entails an entirely blue body, the shortest wavelength of peak reflectance, the highest intensity of reflectance and the greatest contrast. This is a particularly interesting result when compared with data from a carotenoid-based signalling system. In house finches, plumage redness is positively correlated with increasing ornament size (Hill 1992). In addition, female house finches prefer males with the reddest, largest ornaments regardless of the size and colour of males in their own geographic region (Hill 1994). In both structural and carotenoid ornaments, ornament size is correlated with colour. However, these trends are the opposite of each other such that the carotenoid ornament is defined by the longest wavelengths ('red' range of the spectrum), and the structural ornament is defined by the shortest wavelengths of light ('blue' range).

Patterns of variation in the plumage of male grosbeaks are consistent with a signalling function. The honesty of the signal depends on whether blueness is costly to produce. Our second goal was to test this hypothesis. Blue grosbeaks undergo a complete moult in autumn that includes all ornamental and non-ornamental feathers. During this time, access to adequate resources is crucial. Male blue grosbeaks that display the most extreme plumage ornaments (greatest percentage of blue, shortest wavelengths, and highest intensity and contrast) also have the highest rate of tail feather growth (table 2; figure 3). This supports the hypothesis that blueness, which depends on the microstructure of the feathers, may require unrestricted access to nutrients for maximum expression. Any nutritional restriction could reduce plumage expression. These data suggest that ornamental plumage is condition dependent in this species and has the potential to function in reliable social signalling. Because the proportion of the variance in nutritional condition explained by plumage variables is not high, plumage blueness may not be a particularly accurate signal of quality. However, in conjunction with other male attributes, such as song, males may present a combined phenotype that is informative to females or other males.

Numerous studies have shown that pigment-based plumage coloration is condition dependent (Brawner 1997; Hill 1992; Hill & Montgomerie 1994; Thompson *et al.* 1997; Veiga 1995; Veiga & Puerta 1996) and that males displaying the most extreme expression of the ornament have higher reproductive success (Hill 1990; Møller 1987, 1988; Veiga 1993). Pigment-based ornament expression influences female choice such that by choosing a bright male, a female chooses a healthy male. However, to our knowledge, this study is the first to correlate nutritional condition during the moult with the expression of a structurally based ornamental trait. The data we present here also suggest that age might act in concert with condition to influence male ornamentation. Thus, if females assess blueness during mate choice or if other males focus on plumage during aggressive interactions, they may receive reliable information about both the age and the physical condition of the male.

This study demonstrates that a structurally based ornament has the potential to function in a manner similar to that of carotenoid-based ornaments. The similarity of function in two physiologically disparate mechanisms of colour production indicate that similar selective pressures, i.e. female choice or male competition, may have driven the evolution of these ornaments.

If structurally based ornamentation in other species is similar to that of blue grosbeaks, then an entire, expansive new suite of ornamental characters can be understood as reliable signals. These results suggest that 'invisible', ultraviolet variation in structural ornaments could be important for sexual selection. We suggest four directions for future research. First, more captive-based mate choice experiments should be conducted to test female choice for extreme ultraviolet ornamentation. Second, aviary experiments are needed to test the effect of environmental stress (poor nutrition or parasitic infection) on the expression of structurally based coloration. Third, a microscopic analysis of feather structure should be conducted to look for the structural basis of differences in feather colour. Finally, field studies should test the effect of male coloration on mate attraction, territory acquisition and paternal care.

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