

COHERENT SCATTERING OF ULTRAVIOLET LIGHT BY AVIAN FEATHER BARBS

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ABSTRACT.—Ultraviolet (UV) structural colors of avian feathers are produced by the spongy medullary keratin of feather barbs, but various physical mechanisms have been hypothesized to produce those colors, including Rayleigh scattering, Mie scattering, and coherent scattering (i.e. constructive interference). We used two-dimensional Fourier analysis of transmission electron micrographs of the medullary keratin of UV-colored feather barbs of the Blue Whistling Thrush (*Myiophonus caeruleus*) (Turdidae) to test the alternative hypotheses for production of those UV structural hues. The two-dimensional Fourier power spectra of the tissue reveal a ring-like distribution of peak periodicity at intermediate spatial frequencies ($\sim 0.078 \text{ nm}^{-1}$), which documents that *Myiophonus* medullary keratin is substantially nanostructured and equivalently ordered in all directions. This nanoscale spatial order falsifies a basic assumption of both the Rayleigh scattering and Mie scattering. A predicted reflectance spectrum based on the Fourier power spectra matches hue of the measured reflectance spectra of the feathers (345 nm). These results demonstrate that the *Myiophonus* medullary keratin is ordered at the appropriately nanoscale to produce the observed UV hues by coherent scattering. Received 19 March 2002, accepted 26 October 2002.

RESUMEN.—Los colores estructurales ultravioleta (UV) de las plumas de las aves son producidos por la queratina medular esponjosa de las barbas de las plumas. Varios mecanismos físicos se han propuesto para explicar la producción de estos colores, incluyendo difusión de Rayleigh, difusión de Mie y difusión coherente (i.e. interferencia constructiva). Para poner a prueba hipótesis alternativas para la producción de estos tonos estructurales, utilizamos análisis bi-dimensionales de Fourier de transmisión de micrografías electrónicas de la queratina de barbas con colores estructurales en *Myiophonus caeruleus* (Turdidae). El espectro de poder bi-dimensional de Fourier del tejido muestra una distribución tipo anillo de la periodicidad de los picos a frecuencias espaciales intermedias ($\sim 0.078 \text{ nm}^{-1}$), lo que documenta que la queratina medular de *Myiophonus* está sustancialmente nanoestructurada y ordenada de forma equivalente en todas las direcciones. Este orden espacial a nanoescala falsea una suposición básica de las hipótesis de difusión de Rayleigh y de Mie. Un espectro de reflectancia predicho con base en el espectro de poder de Fourier coincide con el tono de los espectros de reflectancia medidos en las plumas (345 nm). Estos resultados demuestran que la queratina medular de *Myiophonus* está ordenada a la nanoescala apropiada para producir los tonos de UV observados por difusión coherente.

THE AVIAN RETINA has four visual pigments that are maximally sensitive to red, green, blue or violet, and near ultraviolet (UV) light wavelengths (Burkhardt 1989, Burkhardt and Finger 1991, Burkhardt 1996, Hart et al. 1998, Das et al. 1999, Hart 2001). Recent investigations of behavior of a variety of species in both the field and the laboratory have further documented that near ultraviolet (300–400 nm) hues in avian plumage function in intersexual communication and mate choice (Andersson and Amundsen

1997; Hunt et al. 1997, 1998; Andersson et al. 1998; Johnsen et al. 1998). Given the role of UV hues in avian communication, it is important to have a detailed understanding of the physical mechanisms of UV color production by feathers.

The colors of avian plumage are produced by chemical pigments, or by nanometer-scale biological structures that differentially scatter, or reflect, wavelengths of light. No exclusively blue or UV-colored pigments are known in vertebrates (Fox 1976), but various carotenoid pigments in bird feathers produce UV wavelengths

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in combination with human-visible yellow, orange, or red colors (Burkhardt 1989, Burkhardt and Finger 1991). Ultraviolet structural colors of feathers can be produced by two types of structures (Prum 1999). Primarily iridescent colors are produced by arrays of melanin granules in feather barbules. Those structural colors are created by coherent scattering, or constructive interference, of light waves scattered from the layers of melanin granules in barbules (Durrer 1986; Dyck 1976, 1987). A few species of hummingbirds (Trochilidae; Bleiweiss 1994) and European Starling (*Sturnus vulgaris*, Sturnidae; Durrer 1986, Cuthill et al. 1999) are known to produce UV hues with coherently scattering melanin arrays in feather barbules.

The most commonly distributed UV hues, however, are structural colors produced by light scattering from the spongy medullary layer of feather barbules. To date, primarily UV hues have been documented in the feather barbules of *Chalcopsitta* cockatoos (Psittacidae; Finger et al. 1992) and *Myiophonus* thrushes (Turdidae; Andersson 1996, 1999). Extensively UV hues with a peak reflectance in the human-visible blue range have been observed in feather barbules of Blue Tits (*Parus caeruleus*, Paridae; Andersson et al. 1998, Hunt et al. 1998), Bluethroats (*Luscinia svecica*, Turdidae; Andersson and Amundsen 1997, Johnsen et al. 1998), and Blue Grosbeak (*Guiraca caerulea*; Keyser and Hill 1999). In addition, we have found extensive UV reflectance from apparently blue feather barbules in many families and orders of birds including rollers (Coraciidae), motmots (Momotidae), manakins (Pipridae), cotingas (Cotingidae), leafbirds (Irenidae), fairy wrens (Maluridae), bluebirds (*Sialia*, Turdidae), buntings (*Passerina*, Cardinalidae), and others (R. O. Prum pers. obs.).

Finger et al. (1992) and Andersson (1996, 1999) have documented that the structural UV hues of feather barbules, like other barb structural colors, are produced by the keratin air matrix of the spongy medullary layer of the barb ramus. However, the precise physical mechanism by which the human-visible and UV barb colors are produced remains controversial (Dyck 1985; Finger 1995; Prum et al. 1998, 1999a; Andersson 1999; Cuthill et al. 1999). For most of the past century (Mason 1923a, b; Fox 1976), noniridescent structural colors of feather barbules were hypothesized to be produced by Rayleigh

scattering (also known erroneously as "Tyndall scattering"; see Young 1982). After showing that the blue medullary reflectance spectra contradict the predictions of Rayleigh's inverse fourth power law, Dyck (1971a, b) proposed the "hollow cylinder" model which hypothesized that the medullary matrix produces color by coherent scattering of (i.e. constructive interference among) light wavelengths from the multiple surfaces of the air-keratin matrix. Finger (1995) furthered the debate by proposing that the unimodal reflectance spectra of structurally colored feather barbules could be explained by a combination of incoherent Mie scattering by the medulla keratin and differential absorbance by the barb cortex. Subsequently, Andersson (1996, 1999) described and analyzed the coloration and ultrastructure of the medullary keratin of the strongly UV-colored feather barbules from the Blue Whistling Thrush (*Myiophonus caeruleus*, Turdidae), but he did not critically test the alternative coherent scattering, or interference (Dyck 1971a, b) and Mie scattering (Finger 1995) hypotheses.

Most recently, Prum et al. (1998, 1999a) analyzed the spatial distribution of air vacuoles and keratin bars in the medullary layers of four different avian species with different human-visible structural colors (440–540 nm) in an effort to critically test Dyck's coherent scattering hypothesis. Using two-dimensional discrete Fourier analysis of transmission electron micrographs (TEMs) of tissue, Prum et al. (1998, 1999a) demonstrated that the spongy medullary layer is sufficiently nanostructured at the appropriate spatial scale to produce the observed visible hues by coherent scattering, or constructive interference. Those analyses also demonstrated that a key assumption of the incoherent scattering mechanisms (including both Rayleigh and Mie scattering)—the spatial independence of scatterers—was not met by the medullary keratin of those feathers. Analyses by Prum et al. (1998, 1999a) included medullary tissues from psittaciform and passeriform species representing both major classes of medullary structure: uniform, circular air vacuoles with keratin bars of irregular widths (e.g. *Cotinga*, *Poephila*; type e, Dyck 1978), and channel-like air vacuoles and keratin bars of equivalent widths (e.g. *Agapornis*, *Melopsittacus*; type f, Dyck 1978).

Prum et al. (1998, 1999a) predicted that all structural colors of the medullary layer of

feather bars are created by coherent scattering. However, they did not examine any species with predominantly UV-colored feather barbs. Here, we present a two-dimensional Fourier analysis of the spongy medullary layer of the vividly UV-colored feathers of the Blue Whistling-Thrush. The following questions are addressed: (1) Is the keratin matrix appropriately structured to produce structural UV colors by incoherent (either Rayleigh or Mie) scattering? (2) Is the structurally colored spongy medullary keratin matrix sufficiently ordered to produce UV color by coherent scattering? (3) Is the medullary keratin matrix the appropriate size to produce the observed structural UV hues?

METHODS

Feather barbs were collected from the distal ends of contour feathers from *Myiophonus caeruleus* specimens (NRM 87903) from three vividly UV-colored plumage patches: the primary wing coverts, lesser wing coverts, and a spangle from the tip of a mantle feather (i.e. back contour feather). Barbs were prepared and sectioned for transmission electron microscopy following Dyck (1978) (see Andersson 1996, 1999). Ultrathin transverse sections of the feather barbs were photographed in a Zeiss CEM 902A transmission electron microscope at 2,800 \times magnification.

Reflectance spectra were measured using a fiber optic spectrophotometer Ocean Optics S2000 with the PX-2 xenon light and a Labsphere Spectralon white standard. The measurements were made of 3 mm diameter plumage patches at 6 mm distance from *Myiophonus caeruleus* specimen KU 48889 (Thailand: Krabi, Khao-Khram; 22 August 1962). Those results were very similar to previous measurements reported by Andersson (1996, 1999).

According to previous theory (Benedek 1971; Prum et al. 1998, 1999a, b), significant reinforcement of the light waves scattered by a quasiordered array (i.e. a less than perfect lattice) is predicted only for those light waves that are twice the size of the largest components of the Fourier transform of the spatial variation in refractive index of the tissue. In previous papers, we have developed an application using the two-dimensional discrete Fourier transform to analyze the spatial periodicity of structurally colored tissues (for details see Prum et al. 1998, 1999a, b; programs available from the authors). The discrete Fourier transform is a basic mathematical tool used to decompose data into an equivalent sum of different periodic components (Briggs and Henson 1995). Discrete data are transformed into a sum of component sine waves of different amplitudes and frequencies (Briggs and Henson 1995). The relative squared amplitudes of those component waves, called the Fourier power spectrum, express the contributions of each frequency

of variation to the original data, and indicate which frequencies carry the most energy (Briggs and Henson 1995). The Fourier power spectrum of the spatial variation in refractive index of a tissue can predict which wavelengths will be constructively reflected by that tissue because the distribution of energy in the power spectrum is directly related to the spatial distribution of changes in refractive index experienced by light waves incident on the tissue.

Here, we use two-dimensional Fourier analysis to examine the relationship between the spatial variation in refractive index in the medullary keratin matrix of the UV barbs and their structural colors. Transmission electron micrographs were digitized at 900 dpi. The images were processed and analyzed using the computer program MATLAB (version 5.0; MATLAB 1992, Thompson and Shure 1995) on a Macintosh G4. Grayscale variation in the TEMs allowed us to distinguish between feather keratin and air vacuoles, and to estimate the spatial variation in refractive index in the spongy medullary keratin matrices. The scale of each digitized image (nanometers per pixel) was calculated by measuring the number of pixels in the original TEM scale bar in the micrograph. The largest available square portion of the keratin matrix (between 174–376 pixels²) from TEMs of feather barbs from a primary wing covert, a lesser wing covert, and a mantle feather tip were then selected for analysis. Large scale singularities in the images (e.g. cell boundaries, nuclear vacuoles, or melanin granules) were avoided because they disrupt the description of the nanoscale variation in the medullary keratin matrix.

The average of the refractive index (RI) of the material in tissue in each image was estimated by generating a two-bin histogram of image density from the processed images (Thompson and Shure 1995). The frequency distributions of the darker and lighter pixels in the block-processed images were used to estimate relative volume of keratin (RI = 1.54) and air (RI = 1.00) in the image, which was then used to calculate a weighted average refractive index for the tissue (Dyck 1971a).

The numerical computation of the Fourier transform was done with the well-established two-dimensional Fast Fourier Transform (FFT2) algorithm (Briggs and Henson 1995). The two-dimensional Fourier power spectra were expressed in spatial frequency (cycles per nanometer) by dividing the initial spatial frequency values by the length of the matrix (pixels in the matrix times nanometers per pixel). The four quadrants of each power spectrum matrix were shifted to place the four original corners of the matrix in the center so that the frequency origin is in the center of the image. We produced a predicted reflectance spectrum based on a combination of the two-dimensional Fourier power spectra of a sample of different feather barb images, and the sizes and average refractive indices of the images. First, we produced estimates of the percentage total Fourier power

of component waves of different sizes by taking a radial average of a series of 0.3 pixel radial intervals of spatial frequency (diameters) for a single quadrant of each power spectrum. The values of the radial average of each two-dimensional power spectrum were then rescaled so that the total volume and energy under the rotated radial average power function was equal to 1. Next, the relative percentage total power of Fourier components of different sizes (over all directions) was estimated by calculating volumes of radial segments, or shells, of the normalized, rotated, radial average of the power spectrum. The inverse of the spatial frequency values were then multiplied by twice the average refractive index of the medium and expressed in terms of wavelength (nanometers). Because the observed structural colors are the results of coherent scattering from multiple arrays, the data from multiple images were then combined to produce the best average estimate of the spatial variation in the UV-colored feather barbs. The result is a theoretical prediction of the relative magnitude of coherent scattering, or constructive interference, by the tissue that is based solely on the spatial variation in refractive index of the tissue.

RESULTS

The spongy medullary tissue of the UV-colored barbs of *Myiophonus caeruleus* show an organization typical of many structurally

colored avian feather barbs (Fig. 1). Specifically, the tissues can be characterized as having numerous keratin bars and air-filled vacuoles of approximately equivalent widths similar to psittaciforms (type f, Dyck 1976). As described by Andersson (1999), the widths of the keratin bars and air vacuoles are smaller on average than in the medullary keratin of feather barbs that produce visible colors (e.g. Dyck 1976). The reflectance spectrum of the UV-colored feather barbs displays a peak reflectance of 340 nm, as reported by Andersson (1996, 1999) (Fig. 2C).

The two-dimensional Fourier power spectra of the medullary keratin matrices of *Myiophonus caeruleus* exhibit a ring-like distribution of high magnitude values around the origin (Fig. 3). The combined, normalized, rotated radial average power spectra of four different medullary cells from different UV-colored feathers provides an estimate of the peak spatial frequency over all directions in the tissue (Fig. 2A). The power spectra and their combined radial average indicate that the predominant components of spatial periodicity in the tissue are localized at intermediate spatial frequencies. The ring-shaped concentration of energy in the power spectrum is quite distinct from the inverse logarithmic

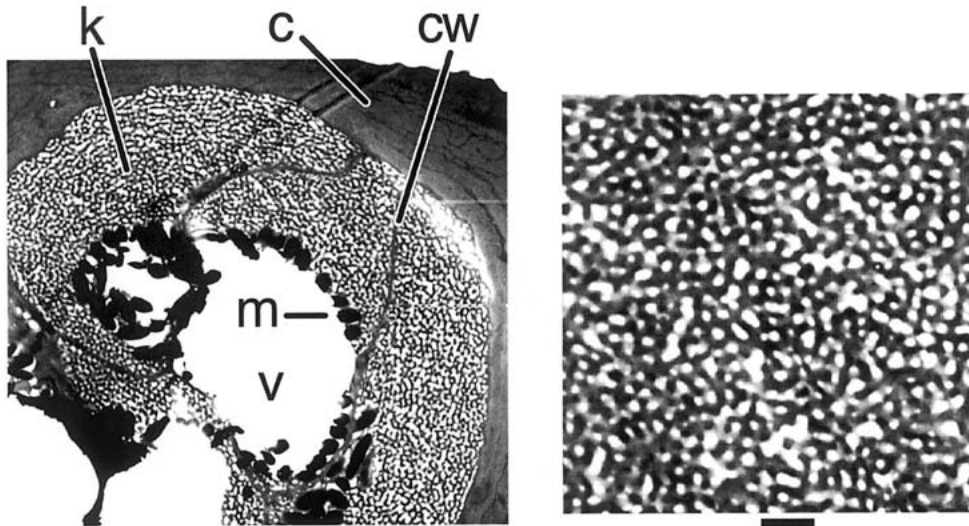


FIG. 1. Transmission electron micrographs of the spongy medullary keratin of the UV-colored feather barbs of *Myiophonus caeruleus* (NRM 87903). Left panel: cross-section of a UV-colored feather barb ramus showing the solid keratin of the barb cortex at the periphery, three adjacent medullary cells with spongy keratin matrix and cell walls, and melanosomes around the large vacuole at the center of the barb ramus. Right panel: close-up of the spongy medullary matrix of keratin bars and air vacuoles. Scale bar equals 500 nm. Abbreviations: c = barb cortex; cw = cell wall, k = spongy medullary keratin, m = melanosome, and v = air-filled vacuole.

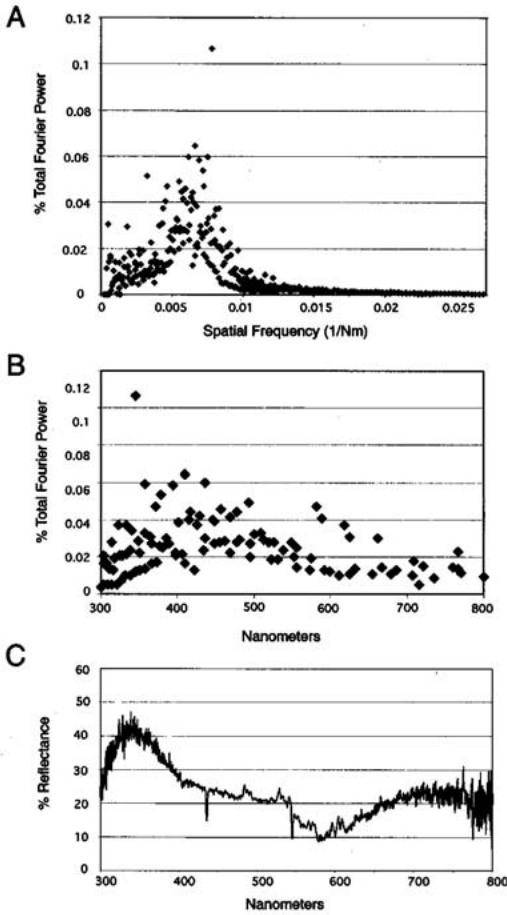


FIG. 2. (A) Combined, rotated, radial average of four power spectra of the medullary keratin matrix from lower wing covert, mantle spangle, and primary covert barb from *Myiophonus caeruleus* (NRM 87903). The distribution shows a peak at intermediate spatial frequencies. (B) Predicted reflectance spectrum based on the combined two-dimensional Fourier power spectra. The graph predicts the shape of the reflectance spectrum of the tissue based solely on transmission electron micrographs of the tissue (Fig. 1, right panel), and the refractive indices of keratin and air. (C) Reflectance spectra from a mantle spangle (tip of a back contour feather) of *Myiophonus caeruleus* (KU 48889). The reflectance spectrum shows a peak hue of 340 nm, substantially below the lower wavelength limit of normal human vision at 400 nm.

distribution that would be expected if variation in the data were the consequence of frequency-dependent noise, a good null model of spatial organization for a self-assembled matrix (Vaezy et al. 1995). Despite the lack of obvious laminar or crystalline spatial organization from inspec-

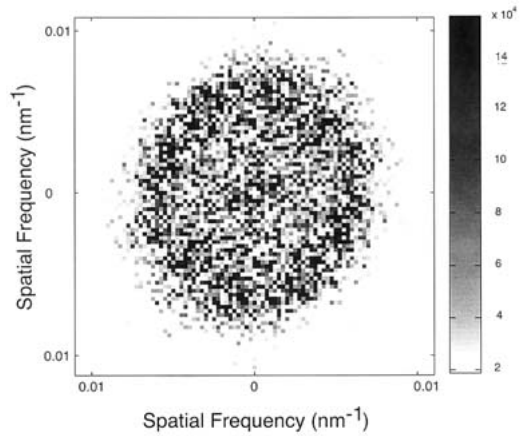


FIG. 3. The two-dimensional Fourier power spectrum of the medullary keratin matrix of a UV-colored feather barb from a lower wing covert of *Myiophonus caeruleus* (NRM 87903). The two-dimensional power spectrum shows the magnitude (darkness, dimensionless) of various component spatial frequencies (distance from the origin), in different directions within the tissue (direction from the origin). This power spectrum reveals a ring-like distribution of higher power values at intermediate spatial frequencies, and uniform spatial periodicity in all directions within the tissue.

tion of the electron micrographs, the medullary matrix of UV-colored *Myiophonus* feather barbs is substantially nanostructured at intermediate spatial frequencies.

Like the medullary matrix of other structurally colored feather barbs (Prum et al. 1998, 1999a), the ring-shaped power distribution of the *Myiophonus* feather barbs also documents that the spatial periodicity in the tissue is nearly equivalent in all directions. The predominant spatial frequency does not vary substantially with direction in the tissue (i.e. direction from the origin in the power spectrum; Fig. 3). That result means that light incident on medullary matrix from any direction will experience similar spatial periodicity in refractive index, and should produce similar optical results. Thus, like the structural colors of other feather barbs, the UV hues of *Myiophonus* are not iridescent, but generally uniform in hue with different angles of observation.

In a quasiordered array, the inverse of the peak spatial frequency corresponds to the average distance between centers of neighboring light scatterers (Vaezy et al. 1995; Prum et al. 1998, 1999a, b). The peak spatial frequency is

0.007803 nm⁻¹ (Fig. 2A), and the corresponding estimated average distance between scatterers is 128.16 nm. That value is smaller than the sum of the average keratin-bar and air-channel widths for the three UV feather barb types from Andersson (1999): primary coverts, 145 nm ± 33; lesser wing coverts, 149 nm ± 29; and mantle spangles 142 nm ± 32, but only by 0.4–0.7 standard deviations

This substantial nanostructure observed at intermediate spatial frequencies also falsifies a fundamental assumption of the incoherent scattering models. Both Rayleigh and Mie scattering models assume that light-scattering objects are spatially independent, or randomly distributed over distances of the same order of magnitude as wavelengths of visible light (Bohren and Huffman 1983). Because the *Myiophonus* medullary keratin shows significant nanostructure with a maximum periodicity near 128 nm, that assumption is clearly violated by the tissue. Thus, Rayleigh and Mie scattering cannot be considered as appropriate explanations of the light-scattering behavior of those UV-colored feather barbs.

The predicted reflectance spectrum based on the combined rotated radial average Fourier power spectra exhibits a discrete peak at 345 nm (Fig. 2B). The peak hue of the Fourier predicted reflectance spectrum of the *Myiophonus* feather barbs is congruent with the peak and the shape of the observed reflectance spectrum of these feather barbs (Fig. 2C). This result demonstrates that the spatial periodicity observed in the medullary tissue of the *Myiophonus* feather barbs is appropriately sized to produce the measured UV color by coherent scattering.

DISCUSSION

The two-dimensional Fourier analysis of the spongy medullary keratin of UV-colored feather barbs of *Myiophonus caerulea* demonstrates that this color-producing tissue is substantially nanostructured at the appropriate spatial scale to produce the observed ultraviolet hues by coherent scattering, or constructive interference. Like the medullary keratin of other feathers producing human-visible structural colors (Prum et al. 1998, 1999a), this nanostructure falsifies the spatial independence assumption that is required by the Rayleigh (Fox 1976) and Mie scattering (Finger 1995) hypotheses. The similarity in nanostructure between *Myiophonus*

keratin and other structurally colored feather barbs with both UV (Finger 1995) and visible (Dyck 1976) hues supports the prediction that all feather barb structural colors are produced by coherent scattering. The uniform spatial periodicity in all directions explains why those structural colors are not iridescent, and therefore physically convergent with the predictions of Rayleigh scattering theory.

Ultimately, understanding the evolution of UV structural colors in avian plumages will require detailed comparative information on many subjects including avian visual perception, the development of medullary keratin, the heritability and plasticity of UV hues, and the function of UV colors in communication in various behavioral contexts. A physical understanding of the mechanism by which structural UV colors of feather barbs are produced and developed will be critical to testing several prominent hypotheses in social and sexual selection theory. For example, several popular mechanisms of sexual selection predict that sexually selected traits should evolve to be honest indicators of quality (Andersson 1994). Such traits require low genetic variation and high, quality-correlated phenotypic plasticity. Variation in structural blue-UV colors of the male Blue Grosbeak (*Guiraca caerulea*) have been correlated with male territorial quality in the field (Keyser and Hill 1999). In contrast, there is no well-established relationship between variation in structural colors and diet quality in the many species of domesticated and captive birds.

Structural feather-barb colors require developing nanoscale keratin bars and air vacuoles in the medullary layer. Differences in the average spatial periodicity as small as 5 nm will produce distinct hues that differ in wavelength by approximately 12–15 nm. Such differences in hue would easily be distinguishable by avian visual systems. It is tempting to conclude that the small sizes of those color producing arrays should make them easily perturbed by dietary or other environmental factors (Andersson 1996). However, like many structurally colored biological tissues, feather keratin is a self-assembled material. In nanoscale self-assembly, precise order often results deterministically from the details of the molecular structure of the components (e.g. Hemsley et al. 1994, 1996). Little is known about the molecular details of the development of the medullary keratin in

structurally colored feathers (e.g. Auber 1971–1972). It is likely, however, that the size, shape, and spatial periodicity of the color-producing medullary matrix is partly determined by the molecular details of keratin filament self assembly, and may be subject to little environmental or condition-dependent perturbation. These data will be critical to understanding whether structural colors of avian feather barbs may have evolved as indicators of quality.

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