

## Original Article

## How colorful are birds? Evolution of the avian plumage color gamut

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The avian plumage color gamut is the complete range of plumage colors, as seen by birds themselves. We used a tetrahedral avian color stimulus space to estimate the avian plumage color gamut from a taxonomically diverse sample of 965 plumage patches from 111 avian species. Our sample represented all known types of plumage coloration mechanisms. The diversity of avian plumage colors occupies only a portion (26–30%, using violet-sensitive and ultraviolet-sensitive models, respectively) of the total available avian color space, which represents all colors birds can theoretically see and discriminate. For comparison, we also analyzed 2350 plant colors, including an expansive set of flowers. Bird plumages have evolved away from brown bark and green leaf backgrounds and have achieved some striking colors unattainable by flowers. Feather colors form discrete hue “continents,” leaving vast regions of avian color space unoccupied. We explore several possibilities for these unoccupied hue regions. Some plumage colors may be difficult or impossible to make (constrained by physiological and physical mechanisms), whereas others may be disadvantageous or unattractive (constrained by natural and sexual selection). The plumage gamut of early lineages of living birds was probably small and dominated by melanin-based colors. Over evolutionary time, novel coloration mechanisms allowed plumages to colonize unexplored regions of color space. Pigmentary innovations evolved to broaden the gamut of possible communication signals. Furthermore, the independent origins of structural coloration in many lineages enabled evolutionary expansions into places unreachable by pigmentary mechanisms alone. *Key words:* bird vision, flower, gamut, morphospace, plumage, structural color, tetrahedral color space. [*Behav Ecol*]

## INTRODUCTION

Birds are the most colorful land vertebrates, with diverse plumages representing (to human eyes) almost every color imaginable (Figure 1). Vibrant bird names like Painted Bunting, Fire-maned Bowerbird, and Rainbow-bearded Thornbill attest to the stunning coloration of some feathers, whereas modest names like Drab Seedeater and Plain Wren disclose duller displays at the other extreme. Plumage colors serve many different signaling functions, ranging from crypsis and camouflage to social signaling and mate choice (Hill and McGraw 2006b). These diverse communication signals have likely evolved in response to the avian visual system rather than the other way around (Hart and Hunt 2007; Osorio and Vorobyev 2008), an idea supported by the fact that birds have relatively fixed receptor sensitivities despite marked diversity in their ecologies, lifestyles, and diets (Ödeen and Håstad 2003; Osorio and Vorobyev 2008). A key goal in sensory ecology is to understand the correspondence between visual signals and their relevant receivers. Osorio and Vorobyev (2008) demonstrated that some natural objects have evolved to be particularly discriminable to their corresponding animal receivers: Flowers are especially colorful to bees, primate fruit to primates, and plumages to birds. But just how colorful are plumages to birds, and how has this signal diversity evolved?

To date, the full range—or gamut—of avian plumage coloration has never been quantified, yet an estimate of signal breadth is critical to determining which factors constrain color diversity. To understand how bird colors evolved, it is essential to document and analyze the avian plumage color gamut.

In music, a “gamut” is the complete range of pitches available in a given musical scale. In graphics, a gamut includes all available colors in a display or printing technology. In biology, it refers to the diversity of signal phenotypes mapped to a receiver’s sensory space (Sumner and Mollon 2003; Endler et al. 2005). This gamut is a sensory morphospace. As with any morphospace (Raup 1966), a biological gamut is interesting for both what it includes and what it excludes. To explain the evolution of plumage signal color diversity, it is important to distinguish between different limits to the breadth of the avian plumage color gamut. In Aves, some plumage colors may be difficult or impossible to make: The gamut is constrained by physical, developmental, or physiological constraints on signal diversity. Other colors may be difficult to see and unfavorable as signals or too easy to see and subject to predation. Thus, the gamut is limited by natural and sexual selection on signal function and design. In primates, physical/mechanistic constraints impose limitations to the pelage color gamut. Fur colors are highly constrained because mammalian coloration is typically dominated by melanin pigments (Sumner and Mollon 2003). Cattanahine primates (Old World monkeys and apes) and some marsupials, which enjoy trichromatic vision, extend the mammalian gamut of signaling colors with vivid skin coloration (Sumner and Mollon 2003; Prum and Torres 2004): Notable examples include the mandrill’s

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**Figure 1**

Birds are renowned for their striking plumage colors, which are created by a diverse array of pigmentary and structural mechanisms. Shown here are 5 representatives of the 111 species studied. Left to right: *Passerina cyanea* (structural color from spongy medullary cells in feather barbules), *Aix galericulata* (melanin pigments, unpigmented white, and structural color from melanin arrays in feather barbules), *Tyto alba* (phaeomelanin and unpigmented white), *Xipholena punicea* (methoxy-ketocarotenoid pigments), and *Phoenicopterus ruber* (carotenoid pigments). Photo credits: A–C, David Kjaer; D, Tanguy Deville; and E, J. McKean/VIREO. A color version of this figure is available online.

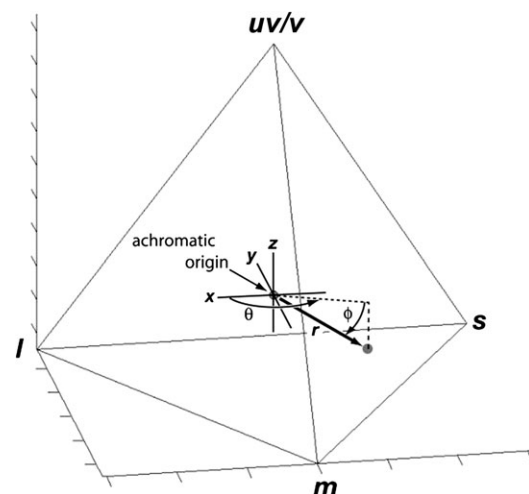
extraordinary blue, red, and purple coloring on its face, rump, and scrotum, and the bright blue scrotum skin of the vervet monkey and mouse opossum. It may seem obvious that understanding the evolution of animal coloration requires establishing the full sweep of possible colors in different taxonomic groups, yet the gamut concept has been employed sparingly. To our knowledge, the estimate of the primate pelage and skin gamut (Sumner and Mollon 2003) and detailed investigation of its evolution (Bradley and Mundy 2008) is the only such undertaking to date. The time is ripe to extend this idea to birds, whose superior color vision and remarkably colorful feathers make the venture all the more tantalizing.

Unlike human color vision, avian vision is tetrachromatic. Birds have 4 single cone-types that have peak sensitivities to longwave (*l*), mediumwave (*m*), shortwave (*s*), and ultraviolet (*uv*) or violet (*v*) light, cone oil droplets with carotenoid filters that refine spectral sensitivities of the *l*, *m*, and *s* cone-types, and one type of double cone thought to play a role in pattern and texture vision (Hart 2001; Jones and Osorio 2004; Cuthill 2006). Biologists have only begun to understand how the complexity of tetrachromatic avian color perception has influenced the evolution of plumage coloration (Vorobyev et al. 1998; Cuthill et al. 1999; Hart 2001; Eaton and Lanyon 2003; Eaton 2005; Endler and Mielke 2005; Stoddard and Prum 2008). One approach has been to investigate distributions of bird colors in a tetrahedral color space based on stimulation of the 4 avian receptor-types (reviewed in Vorobyev et al. 1998; Endler and Mielke 2005; Endler et al. 2005; Cuthill 2006; Osorio and Vorobyev 2008; Stoddard and Prum 2008). Analogous to the triangular spaces developed in human color science (Kuehni 2003), the avian tetrahedral color space is a chromaticity diagram in which the achromatic dimension is removed (Kelber et al. 2003; Cuthill 2006). These types of spaces have thus been popular for mapping signals used by animals with separate chromatic (i.e., hue and saturation) and achromatic (i.e., luminance or brightness) perception, which is thought to be true in birds (Vorobyev and Osorio 1998; Kelber et al. 2003; Jones and Osorio 2004; Endler and Mielke 2005).

Here, we use a well-described tetrahedral color space model based on avian cone-type sensitivities (Figure 2) (Goldsmith 1990; Endler and Mielke 2005; for details see Stoddard and Prum 2008) to estimate and analyze the avian plumage color gamut. We measured reflectance spectra of 965 plumage colors from a wide range of avian orders and families. Our sample included colors produced by all the known pigmentary and structural coloration mechanisms, including melanins, carotenoids, porphyrins, psittacofulvins, and structural colors derived from spongy medullary cells in the barb rami and from melanin arrays in barbules. Additionally, we analyzed 2350 natural plant spectra, including an extremely diverse set of flowers from the Floral Reflectance Database (FRd; Arnold et al. 2010). Mapping the plant gamut from the avian

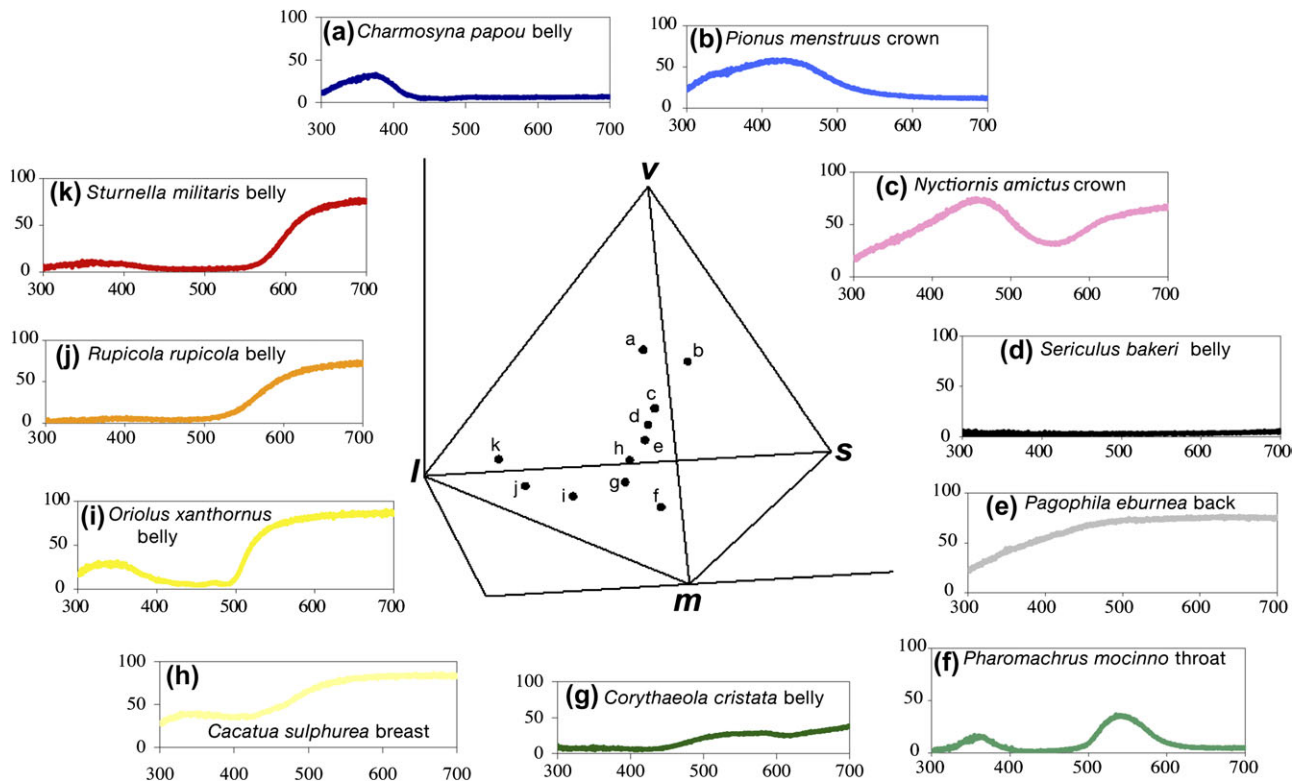
visual perspective is useful for 2 reasons. First, signals should be distinguishable from their backgrounds and distinct from other objects in the environment. Comparing plumage and plant distributions will reveal how feather colors have achieved this. Second, defining the plant gamut serves as a positive control. Plants, with the exception of fruits (purposefully excluded from this study) and relatively rare ornithophilous flowers (Cronk and Ojeda 2008; Ödeen and Håstad 2010), have not evolved in response to avian vision and therefore provide a reasonable estimate of the full range of nonsignaling natural colors a bird is likely to experience in its environment. Examining how the plumage gamut differs from an expansive range of nonsignaling plant colors will help to determine whether bird colors are particularly constrained relative to other natural objects.

The aims of this study were 4-fold: 1) to quantitatively describe the avian plumage color gamut relative to all colors birds can theoretically see (avian color space) and to other colors they practically experience (plant gamut); 2) to examine the contributions of different plumage coloration mechanisms to the overall gamut; 3) to determine whether limits to the gamut are imposed by physical constraints or by natural and sexual selection; and 4) to discover whether evolutionary novelties in plumage coloration expanded the avian color gamut.



**Figure 2**

A tetrahedral avian color space (from Stoddard and Prum 2008). The position of a color point is determined by the relative stimulation of the ultraviolet or violet (*uv/v*), blue (*s*), green (*m*), and red (*l*) retinal cones. The center of the tetrahedron is the achromatic point. Each color point is defined by the spherical coordinates  $\theta$ ,  $\phi$ , and  $r$ . The angles  $\theta$  and  $\phi$  define the hue, and the distance  $r$  defines the chroma, or saturation.



**Figure 3**

Examples of diverse avian plumage reflectance spectra produced by different physical mechanisms and the distribution of their representations in avian color space: Structural colors from spongy medullary keratin in feather barbs—(a) *Chamosyna papou* (Psittacidae), ultraviolet belly and (b) *Pionus menstruus* (Psittacidae), blue crown; Combined structural and pigmentary color—(c) *Nyctiornis amictus* (Meropidae), pink crown; Melanin pigment—(d) *Sericulus bakeri* (Ptilonorhynchidae), black belly; Unpigmented white—(e) *Pagophila eburnea* (Laridae), white back; Structural colored barbules—(f) *Pharomachrus mocinno* (Trogonidae), green throat; Porphyrin pigment—(g) *Corythaeola cristata* (Musophagidae), green turacoverdin belly; Psittacofulvin pigment—(h) *Cacatua sulphurea* (Psittacidae), yellow breast; Carotenoid pigments—(i) *Oriolus xanthornus* (Icteridae), yellow belly; (j) *Rupicola rupicola* (Cotingidae), orange belly; and (k) *Sturnella militaris* (Icteridae), red belly. A color version of this figure is available online.

## MATERIALS AND METHODS

### Plumage color measurement

We measured the reflectance spectra of 965 plumage patches on male specimens of 111 species from 55 families in 18 avian orders (species listed in Supplementary Material, Supplementary Table 1). The species were selected to provide a diverse set of colors produced by a variety of known and presumed coloration mechanisms (Figure 3; all 965 color patches listed in Supplementary Material, Supplementary Table 2). We measured color patches on one or more male representatives for each species using study skins from the Yale Peabody Museum (YPM) of Natural History, New Haven, CT. Reflectance spectra were measured from 6 standard plumage patches: crown, back, rump, throat, breast, and belly. Additional color patches were also measured for certain species if they had additional colors that were distinct to the human eye. Some species had no additional color patches, whereas others had as many as 7 additional patches. For most species, reflectance spectra were measured once per patch per individual; for others, multiple reflectance spectra were measured per patch in order to perform repeatability analyses.

The reflectance spectra of color patches were measured using an S2000 Ocean Optics spectrometer with an Ocean Optics DH-2000-BAL deuterium–halogen light source (Ocean Optics, Dunedin, FL). Reflectance was measured at normal incidence to the plumage using a bifurcated illumination/reflectance optical fiber. The optical fiber was held in an aluminum block that

eliminated other illumination. The fiber was approximately 6 mm above the plumage, illuminating a circular patch 3 mm in diameter. Each data point between 300 and 700 nm was recorded to obtain the reflectance spectra for the patch.

We classified the 965 color patches according to their known or presumed mechanism (Supplementary Material, Supplementary Table 2). A large number of samples were chosen because their coloration mechanisms have been identified in that species or a close relative (e.g., Hill and McGraw 2006a, see chapters 5–8 on the mechanisms of carotenoid-based colors, melanin-based colors, structural colors, and uncommon colors, respectively). Coloration mechanisms of other plumage patches were inferred by comparison of visual appearance and microscopic color distribution (e.g., barb rami, barbules, or both) to feathers with known plumage coloration mechanisms. Color patches were classified into the following coloration mechanism groups and subgroups: melanins (eumelanin or pheomelanin), carotenoids (red, orange, yellow, or purple), porphyrins (turacin or turacoverdin), psittacofulvins, structural (spongy barb rami or barbule melanin arrays), white (normal unpigmented or spongy barb white), or a combination of structural and pigmentary mechanisms.

### Plant color analyses

We measured 192 plant leaf, stick, and bark reflectance spectra using wild samples from New Haven, CT, and a diversity of specimens from a tropical green house collection at the

Marsh Botanical Gardens, Yale University. We supplemented our modest sample with 2158 flower and leaf spectra from the FReD (Arnold et al. 2010), which includes thousands of natural spectral reflectance measurements sampled at wavelengths between 300 and 700 nm. We used all available records on the database, excluding only those spectra missing large amounts of data (i.e., with 25 or more reflectances equal = 0 across the 300–700 nm range). To our knowledge, our study is the first to analyze this tremendously rich collection of flower colors from the avian visual perspective. All together, our plant sample contained 2350 colors, including 48 bark and wood spectra, 589 leaf spectra, and a diverse array of flower and tree spectra. Because we wanted to compare plumage color signals to a range of nonsignaling plant colors, we excluded fruit colors from our sample. Fruit consumed by birds is under different selective pressure than background vegetation and may have evolved to be particularly conspicuous to frugivorous birds (Osorio and Vorobyev 2008). Ornithophilous flowers, or those pollinated by birds, may also have evolved to attract birds. However, we did not exclude these flowers from our sample because 1) they are relatively rare among flowering plants and represented only a fraction of our overall sample and 2) only 3 bird families have evolved as major flower specialists: hummingbirds (Trochilidae), sunbirds (Nectariniidae), and honeyeaters (Meliphagidae), so these flowers do not serve a signaling role for the majority of bird species (Cronk and Ojeda 2008).

### Color space analyses

In studies of communication and crypsis, signals should be analyzed with regard to the visual system of conspecific signal receivers or their predators. In this study, we model avian colors as they are seen by other birds. As in human color science (Kuehni 2003), tetrahedral avian color spaces have been developed to quantify how variation in reflectance corresponds to variation in avian visual stimuli (Burkhardt 1989; Goldsmith 1990; Endler and Mielke 2005; Endler et al. 2005; Stoddard and Prum 2008). The avian tetrahedral color space is a chromaticity diagram (Figure 2) in which the achromatic (or brightness) dimension has been removed and the chromatic signal (i.e., hue and saturation) is analyzed only (Kelber et al. 2003; Cuthill 2006). In birds, chromatic and achromatic information are thought to be processed independently, with the chromatic signal apparently stemming from the 4 color cones and the achromatic signal stemming from double cones (Vorobyev and Osorio 1998; Kelber et al. 2003; Jones and Osorio 2004; Endler and Mielke 2005). The edges of the tetrahedron represent the boundaries of all colors theoretically discriminable by birds. The presence of oil droplets in avian cones reduces spectral overlap, enabling birds to distinguish more colors than they would without droplets and thereby extending the boundaries of visible colors to the tetrahedron's edges (Goldsmith 1990; Vorobyev et al. 1998). Vorobyev (2003) modeled this explicitly, demonstrating that oil droplets expand the volume of discriminable avian object colors to the edges of cone space.

The tetrahedral color space is a straightforward quantitative representation of sensory stimulation and is not equivalent to sensory experience per se, which likely involves opponent mechanisms, color categorization, and a range of intricate psychophysical processes. Until we have a far better understanding of the complexity of bird vision, this pragmatic approach offers a convenient way to map and analyze bird colors with respect to avian perception. We apply the Goldsmith (1990) tetrahedral color space, which makes fewer assumptions than more detailed models (e.g., Endler and Mielke 2005). This tetrahedral color space is practical, quantitatively

precise, and yields measurements that are comparable across studies (Stoddard and Prum 2008).

To analyze avian plumage spectra in tetrahedral color space (Figure 2), we used the computer program TETRACOLORSPACE with MATLAB 7 software (Stoddard and Prum 2008). The idealized stimulus,  $Q_I$ , of each color cone-type was estimated by the reflectance spectrum of a plumage patch:

$$Q_I = \int_{300}^{700} R(\lambda)C_r(\lambda)d\lambda, \quad (1)$$

where  $R(\lambda)$  is the reflectance spectrum of the plumage patch and  $C_r(\lambda)$  is the spectral sensitivity function of each cone-type  $r$ .  $R(\lambda)$  and  $C_r(\lambda)$  functions were normalized to have integrals of 1. We assumed a standard constant illumination across all visible wavelengths. For each plumage color, the idealized stimulation values of the 4 color cones— $Q_I$ —were normalized to sum to one, yielding relative  $\{uv/v \ s \ m \ l\}$  values.

The  $\{uv/v \ s \ m \ l\}$  values of each reflectance spectrum were converted to a color point with spherical coordinates  $\theta$ ,  $\phi$ , and  $\tau$ , which define a color vector in the tetrahedral color space (Figure 2). This tetrahedral geometry places the achromatic point of equal cone stimulation—white, black, or gray—at the origin and the  $uv/v$  vertex along the vertical  $z$ -axis (Figure 2). Each color has a hue and saturation. Hue is defined as the direction of the color vector, given by the angles  $\theta$  and  $\phi$ , which are analogous to the longitude and latitude, respectively (Figure 2). Saturation, or chroma, is given by the magnitude of  $\tau$  or its distance from the achromatic origin. Because the color space is a tetrahedron and not a sphere, different hues vary in their potential maximum chroma, or  $\tau_{\max}$  (Stoddard and Prum 2008).

We estimated the achieved gamut of all plumage spectra combined ( $n = 965$ ) and the subgamuts of each distinct color mechanism (e.g., all carotenoid colors) by calculating the volume of color space occupied by the minimum convex polygon containing all relevant color points (Stoddard and Prum 2008). We express the color contribution of each mechanism as a proportion of both the total avian color space (volume = 0.2165) and total achieved plumage gamut (Table 1). We also calculated a range of color variables for each distribution, including measures of color span (Euclidean distances) and hue disparity (magnitude of the angle between color vectors). We used Robinson projections to view the distribution of hues independent of saturation (Endler et al. 2005; Stoddard and Prum 2008). The Robinson projection is a compromise between equal-area and conformal projections of the surface of a sphere in 2D, and it is a useful tool for visualizing the distribution of hue variation in color data. We repeated this entire procedure to estimate the gamut of natural plant spectra.

With the possible exception of penguins and owls, birds appear to be tetrachromatic (Hart 2001). Two classes of color vision prevail in birds, in which the fourth color cone uses ultraviolet-sensitive (UVS) or violet-sensitive (VS) opsin pigments. The phylogenetic distribution of color vision types in birds is complex, but recent analyses support VS as the ancestral state in birds and indicate that UVS has evolved at least 5 independent times (Ödeen and Håstad 2003; Carvalho et al. 2007). VS sensitivity curves were used in the comparative analyses of all color mechanisms because VS is the plesiomorphic, or ancestral, state in birds. For comparison, we reanalyzed the entire data set using the derived UVS sensitivity curves. Finally, we computed the color space occupied by the plumages of each species in this study. Following Ödeen and Håstad (2003), we noted the known or presumed class of color vision possessed by each species and used each species' own type of spectral sensitivity curves in the analysis of its plumage color

**Table 1**  
**Summary statistics describing the distribution of plumage colors in avian color space by color mechanism**

Mechanism	Number of colors	Color volume	% Avian color space	% Avian plumage gamut	Color span	Max span	Average hue disparity	Maximum hue disparity	Average chroma
All (VS cone-type)	965	5.62E-02	26.0	100.0	2.10E-01	9.65E-01	1.31E+00	3.14E+00	1.39E-01
All (UVS cone-type)	965	6.50E-02	30.0	100.0	2.19E-01	9.50E-01	1.32E+00	3.14E+00	1.48E-01
Melanins	303	3.25E-03	1.5	5.8	9.97E-02	4.32E-01	9.26E-01	3.13E+00	5.30E-02
Eumelanin	225	1.87E-03	0.9	3.3	6.12E-02	3.75E-01	1.13E+00	3.13E+00	2.39E-02
Phaeomelanin	78	1.01E-03	0.5	1.8	1.03E-01	3.09E-01	3.15E-01	1.33E+00	1.37E-01
Carotenoids	145	7.65E-03	3.5	13.6	2.05E-01	6.18E-01	4.87E-01	2.82E+00	2.88E-01
Carotenoid orange	22	7.19E-04	0.3	1.3	1.48E-01	4.24E-01	2.23E-01	6.72E-01	3.99E-01
Carotenoid red	66	2.19E-03	1.0	3.9	1.62E-01	5.75E-01	1.97E-01	1.59E+00	3.21E-01
Carotenoid yellow	39	6.94E-04	0.3	1.2	1.10E-01	3.11E-01	2.05E-01	5.67E-01	2.28E-01
Carotenoid purple	18	5.55E-04	0.3	1.0	1.48E-01	3.76E-01	5.32E-01	1.86E+00	1.62E-01
Porphyryns	11	2.61E-04	0.1	0.5	1.18E-01	3.56E-01	9.54E-01	2.66E+00	1.19E-01
Turacin	1								
Turacoverdin	10	3.92E-05	0.0	0.1	7.34E-02	2.08E-01	7.91E-01	2.66E+00	1.03E-01
Psittacofulvins	28	5.94E-03	2.7	10.6	2.30E-01	5.28E-01	6.91E-01	2.94E+00	2.82E-01
Structural colors	244	3.88E-02	17.9	69.0	2.19E-01	7.96E-01	1.42E+00	3.11E+00	1.64E-01
Structural barbule	96	1.99E-02	9.2	35.4	1.88E-01	5.67E-01	1.30E+00	3.10E+00	1.39E-01
Structural barb rami	148	8.28E-03	3.8	14.7	1.65E-01	6.06E-01	8.23E-01	3.10E+00	1.80E-01
White	134	5.81E-05	0.03	0.1	3.03E-02	1.31E-01	3.09E-01	2.88E+00	5.10E-02
Combined mechanisms	100	2.04E-02	9.4	36.2	2.19E-01	7.83E-01	1.09E+00	3.13E+00	1.99E-01
Carotenoid orange + phaeomelanin	7	1.97E-05	0.0	0.0	8.64E-02	1.67E-01	9.42E-02	2.22E-01	3.04E-01
Carotenoid red + eumelanin	5	2.88E-05	0.0	0.1	2.15E-01	4.74E-01	1.69E-01	3.35E-01	2.46E-01
Carotenoid red + phaeomelanin	4	2.55E-07	0.0	0.0	4.08E-02	7.38E-02	2.72E-02	4.54E-02	2.57E-01
Carotenoid red + white	3	0.00E+00	0.0	0.0	6.06E-02	8.26E-02	1.49E-01	2.19E-01	1.33E-01
Carotenoid yellow + phaeomelanin	2	0.00E+00	0.0	0.0	1.01E-01	1.01E-01	2.21E-01	2.21E-01	2.53E-01
Eumelanin + phaeomelanin	2	0.00E+00	0.0	0.0	1.49E-01	1.49E-01	7.54E-01	7.54E-01	7.46E-02
Eumelanin + white	2	0.00E+00	0.0	0.0	5.54E-02	5.54E-02	2.04E+00	2.04E+00	2.98E-02
Phaeomelanin + turacin	1								
Phaeomelanin + white	3	0.00E+00	0.0	0.0	6.41E-02	9.30E-02	1.15E-01	1.56E-01	1.14E-01
Structural barbule + eumelanin	1								
Structural barbule + phaeomelanin	2	0.00E+00	0.0	0.0	3.54E-02	3.54E-02	2.02E-01	2.02E-01	1.66E-01
Structural barb rami + carotenoid	24	2.54E-03	1.2	4.5	2.00E-01	5.95E-01	7.61E-01	2.95E+00	2.33E-01
Structural barb rami + carotenoid purple	5	2.37E-06	0.0	0.0	3.71E-02	7.39E-02	1.03E-01	1.75E-01	1.90E-01
Structural barb rami + carotenoid red	6	2.49E-04	0.1	0.4	1.29E-01	2.48E-01	9.41E-01	1.94E+00	1.27E-01
Structural barb rami + carotenoid yellow	6	2.29E-05	0.0	0.0	8.42E-02	1.58E-01	1.72E-01	4.41E-01	2.17E-01
Structural barb rami + eumelanin	1								
Structural barb rami + phaeomelanin	4	1.27E-06	0.0	0.0	7.77E-02	1.21E-01	2.47E-01	4.22E-01	2.03E-01
Structural barb rami + psittacofulvin	17	2.76E-04	0.1	0.5	8.92E-02	2.32E-01	2.98E-01	1.07E+00	2.04E-01
Structural barb rami + white	1								
Structural white	3	0.00E+00	0.0	0.0	2.09E-02	2.84E-02	6.79E-01	1.02E+00	2.85E-02
Unknown	1								

Statistics were not calculated for mechanisms represented by a single color. Violet-sensitive (VS) cone-type sensitivity curves were used in the comparative analyses of all color mechanisms.

volume. Results for each species are reported in Supplementary Material, Supplementary Table 1. Subjectively colorful birds, such as Papuan Lorikeet (*Charmosyna papou*), Paradise Tanager (*Tangara chilensis*), White-fronted Amazon (*Amazona albifrons*), Red-collared Lorikeet (*Trichoglossus rubritorquis*), and Gouldian Finch (*Erythrura gouldiae*), achieved the highest color volumes. These 5 species have plumages that include colors produced by multiple chemical and physical mechanisms. Each has a plumage comprising colors produced by at least 4 different mechanisms, with Gouldian Finch boasting a plumage incorporating 6 mechanisms. Plumages with colors made by at least 4 different mechanisms tended to have high volumes, whereas those colored by a single mechanism had consistently low volumes.

## RESULTS

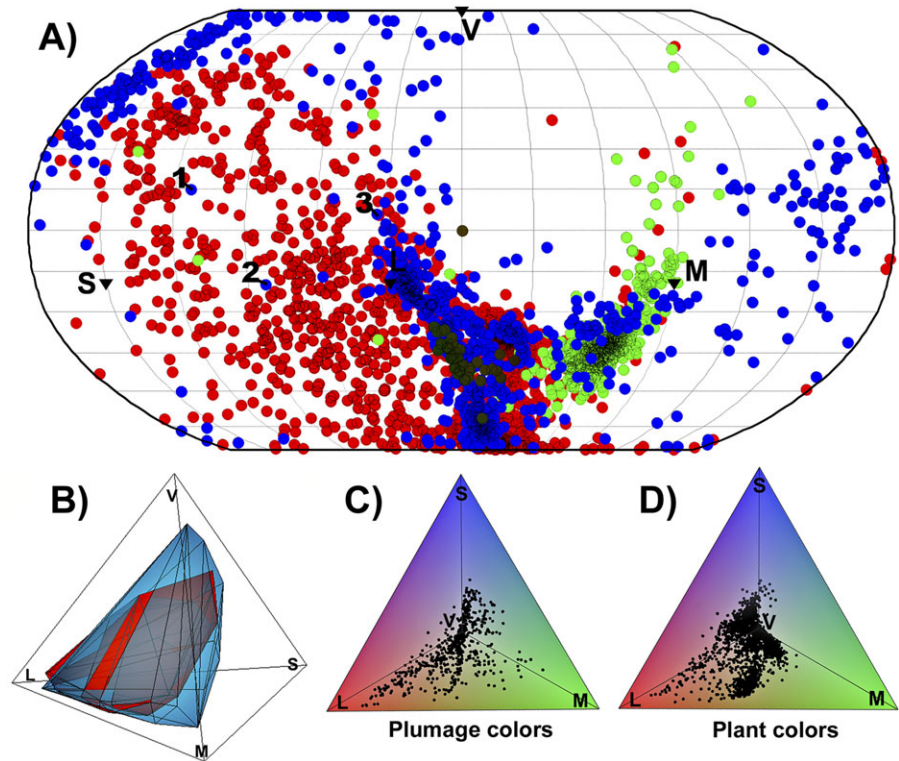
The 965 plumage colors measured occupied ~26% of the total available volume of the VS cone-type avian color space (Table 1, Figures 4B,C and 5A). The red, yellow, ultraviolet + blue, and ultraviolet regions of the color space are densely occupied

with plumage color points, whereas the green, blue, purple (blue + red), and ultraviolet + red regions of the color space lack highly saturated (i.e., chromatic) colors (Figures 4B,C and 5A). Plant colors occupy a smaller portion of the VS cone-type avian color space (~17%) than do bird plumage colors (Figure 4B). Bark colors are highly constrained and occupy <1% of avian color space, whereas mostly-green leaf colors occupy 2% (Figure 4A). Despite considerable overlap, plumage and plant colors have clearly colonized different regions of color space (Figure 4), with plumages particularly diverging from plant colors in the ultraviolet, ultraviolet + blue, blue + green, and green regions. By comparison, plants much more densely occupy the purple (blue + red) and ultraviolet + purple portions of color space (Figure 4).

In total, pigments contribute only modestly to the total diversity of the avian plumage color gamut; pigments occupy 6.9% of avian color space or 26.7% of the avian plumage color gamut. Each separate class of feather pigments occupies a very small volume of the total avian color space (Table 1, Figure 5B,C)—carotenoids (3.5%), psittacofulvins (2.7%), melanins

**Figure 4**

A) The hue distributions of plumage and plant colors shown in a Robinson projection. Plumage colors are shown in blue, leaves are shown in green, bark and wood are shown in brown, and all other plant and flower colors are shown in red. Two “Easter Islands” of avian plumage color are shown. Point 1 represents the pink crown of the Red-bearded Bee-eater (*Nyctornis amictus*). Point 2 represents the iridescent magenta primaries of the Cuckoo-roller (*Leptosomus discolor*). The unique burgundy-purple colors of the Pompadour Cotinga (*Xipholena punicea*) are created by a mixture of methoxy-ketocarotenoid molecules; they cluster around Point 3, which represents the Cotinga’s crown. (B) The plumage (blue) and plant (red) gamuts in avian color space. (C, D) The distribution of plumage (C) and plant (D) colors in avian color space viewed as if looking down from the tetrahedron’s apex (representing the *v* cone-type). This illustrates variation in stimulation of the *s*, *m*, and *l* cone-types. A color version of this figure is available online.



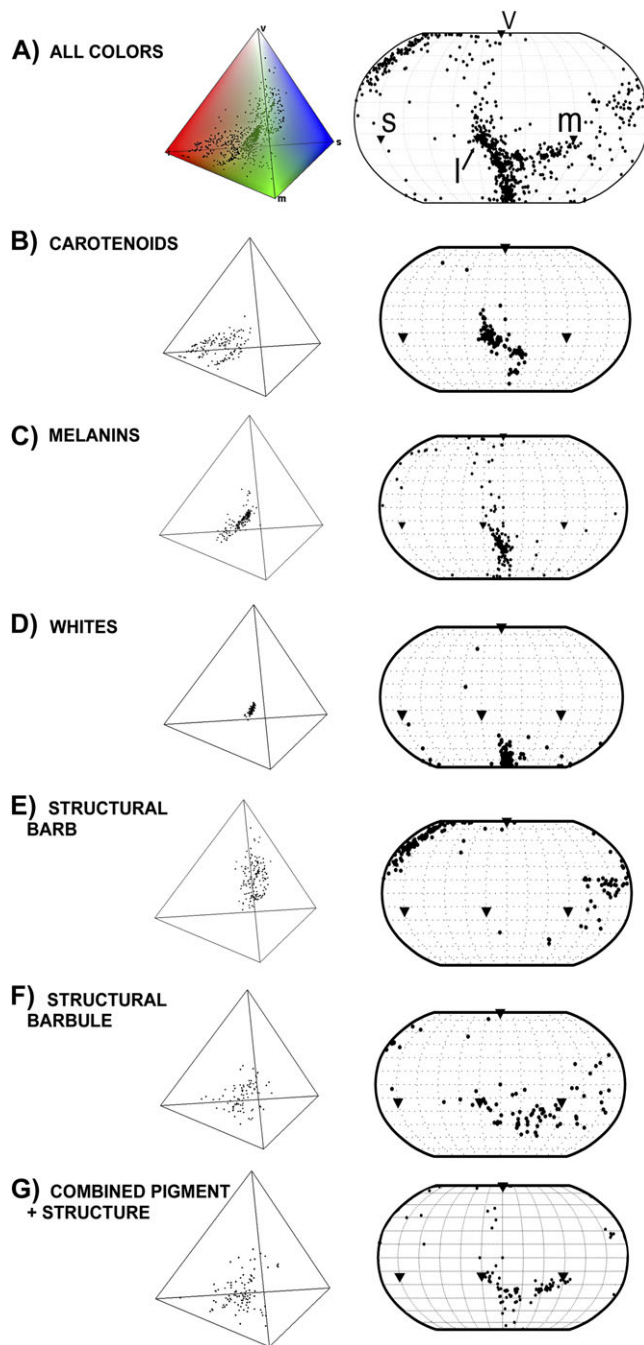
(1.5%), and porphyrins (0.1%), respectively. Among carotenoid pigments, red, and orange ketocarotenoid colors occupy 2.0% of the avian color space, whereas yellow xanthophylls occupy 0.3% (Table 1).

In contrast, structural colors occupy a relatively large volume (17.9%) of the avian color space (Table 1, Figure 5E,F). Among all structural colors, our sample of iridescent barbule colors occupies 9.2% of the avian color space (Figure 5F), whereas spongy barb structural colors occupy less than half that, or 3.8%, which is still greater than any single class of pigments (Figure 5E). Unpigmented white feathers occupy a tiny volume of color space (<0.03%) (Figure 5D). Clearly, the various coloration mechanisms contribute differently to the total achieved plumage color gamut of birds. Although structural colors consist of 25% of the plumage colors in the data set and a much smaller proportion of all bird plumage patches, they create nearly 70% of the achieved avian color gamut (Table 1). Intriguingly, the marked departures of the avian color gamut from the plant color gamut are achieved almost exclusively by structural colors (Figures 4A and 5E,F). This result may be less surprising when we recognize that the most diverse class of plumage pigments—the carotenoids—originate from plants. Furthermore, structural colors are thought to be rare in plants (but see Glover and Whitney 2010).

A Robinson projection of the hue angles ( $\theta$  and  $\phi$ ) of all colors analyzed demonstrates that plumage hues are not uniformly distributed but grouped into hue “continents” and “archipelagos” that are separated by largely unoccupied hue regions (Figures 4A and 5A). There are few purple hues (i.e., in the area between the *s*, *l*, and *v* vertices) and a near complete lack of saturated ultraviolet/green colors (i.e., in the area between the *m* and *v* vertices) (Figures 4A and 5A). The Robinson hue

projections of each class of coloration mechanism further document the specific constraints on the contributions of each coloration mechanism to avian hue diversity (Figure 5B–G). For example, the vast majority of unpigmented “white” plumage colors are notably lacking in ultraviolet, giving them conspicuously nonwhite hues when viewed by the birds themselves (Figure 5D; see also Stoddard and Prum 2008).

Reanalysis of the entire plumage data set using a UVS visual system showed an increase in the volume of the avian plumage gamut. The volume of the entire avian color gamut increases from ~26% of the total color space when perceived with the primitive (i.e., plesiomorphic) VS cone-type avian visual system to ~30.0% when perceived with the derived UVS cone-type visual system that has evolved in various avian lineages (Odeen and Håstad 2003). To test the hypothesis that the derived UVS visual system evolved specifically to expand the plumage color gamut, we reanalyzed the gamut of nonsignaling plant colors from the UVS perspective. The volume of the plant gamut increases from ~17% with the VS cone-type to ~32% with the UVS cone-type. UVS color vision thus appears to facilitate greater discrimination of all natural colors, not just those involved in social signaling. It appears that the derived UVS cone-type did not evolve specifically to broaden the stimulus diversity of plumage colors and thereby evade the mechanistic constraints on color production. These results agree with previous analyses showing that the UVS cone-type increases discriminability of natural objects (Schaefer et al. 2007; Osorio and Vorobyev 2008). Reduced overlap of all cone-types in the UVS visual system contributes to enhanced color separation at the cost of absolute sensitivity as well as increased noise in the UVS cone in dim light (Vorobyev et al.



**Figure 5**  
 (A) Complete gamut of all avian plumage color mechanisms shown in avian tetrahedral color space (left) with the corresponding Robinson projection showing variation in hue (right) (B–G) The separate gamuts of each major plumage coloration mechanism: (B) Carotenoid pigments, (C) Melanin pigments, (D) Nonpigmented whites, (E) Structural colors produced by barb rami, (F) Structural colors produced by barbules, and (G) Combined pigmentary and structural colors. All tetrahedra are depicted from the same perspective as Figure 2. In the Robinson projections, positions of the  $u$ ,  $s$ ,  $m$ , and  $l$  vertices of the color tetrahedron are depicted with triangles and labeled in (A). A color version of this figure is available online.

1998). We have previously hypothesized that the UVS cone-type evolved through selection on enhanced chromatic experience rather than for increased ultraviolet sensitivity itself (Stoddard and Prum 2008). Shifting the peak absorbance of

the UVS cone-type to shorter wavelengths reduces the range of overlap between the UVS and  $s$  (or blue) cone-types and increases the range of wavelengths which will produce saturated blue colors by exclusive stimulation of the  $s$  cone-type (Stoddard and Prum 2008).

## DISCUSSION

Contrary to our human notion of wildly diverse avian feather colors, bird plumage colors occupy only a small fraction (26–30%) of the possible colors birds can observe. Despite this, bird feathers produce an impressive range of colors that rivals or exceeds the diversity of plant bark, leaf, and flower coloration (Figure 4). Plumage colors are not uniformly distributed in color space, instead forming distinct hue “continents” that are separated by largely unoccupied hue regions (Figure 5). Feather pigments are highly constrained to occupy a small volume of the avian plumage gamut. Although they are relatively rare in bird plumages and in our sample, structural colors provide the vast majority of avian color diversity and allow bird plumages to evolve where no plant color has gone before. Even with the help of structural colors, bird plumages fall far short of filling avian color space and do not include many hues available to flowers. What constrains the avian plumage color gamut, creating unattained color regions?

### How colorful are birds?

Should we be surprised that bird plumage colors occupy between one-quarter and one-third of the avian color space? Although theoretically visible, only unnatural monochromatic spectra could actually reach the outer edges of color space other than the  $uv/v$  and  $l$  vertices (Vorobyev 2003). Our findings are congruent with previous work showing that plumages of Australasian parrots and passerines do not fill avian color space (Vorobyev et al. 1998). Our plumage sample was chosen to represent the breadth of plumage coloration mechanisms across a wide range of avian orders and families (Figure 3). Given that structural colors—particularly iridescent barbule colors—make a predominant contribution to the total avian plumage gamut, a more comprehensive sample of structural barbule colors would likely extend the gamut to saturated blue and green regions. Also, additional combined pigmentary + structural colors would likely further contribute to the avian plumage color gamut.

A more interesting biological question is: How colorful are bird plumages relative to other natural spectra? Comparison of the plumage gamut to an extensive set of plant colors reveals that bird feathers are at least as colorful as all plants, occupying 26% and 17% of the VS cone-type avian color space, respectively. We observe considerable overlap between the plumage and plant gamuts in the red and yellow portions of color space, where plant-derived avian carotenoid colors presumably coincide with those produced by floral pigments (Figure 4). Plumage colors especially diverge from plant colors in the ultraviolet, ultraviolet + blue, blue + green, and green regions, with some minor overlap between green feathers (resulting from porphyrin pigment, structural color, or combined pigment + structural color) and green chlorophyll-based leaves (Figure 4). Plumage colors falling outside the plant gamut are achieved almost entirely by avian structural colors, raising the intriguing possibility that structural mechanisms evolved not only to increase avian color diversity but also to create colors unlike others in the natural environment. Plumages and plants clearly possess different color-producing mechanisms that influence the diversity and expansion of their respective gamuts (Figure 4). Compared to

plumages, plants dominate purple (blue + red) and ultraviolet + purple hues, which are produced by endogenous anthocyanin pigments and their derivatives, such as pelargonidin (red), cyanidin (magenta and blue), and delphinidin (blue). Plant anthocyanin pigments facilitate expansion into the purple portion of color space, which is largely left vacant by plumage colors (Figures 4 and 5A).

### Constraints on plumage coloration

Why does the avian plumage gamut lack saturated green, blue, purple, uv-green, and uv-red colors (Figure 5A)? There are 2 possibilities: These colors may be very challenging or impossible to create (“blue rose” hypothesis), or simply undesirable or poorly functioning (“nosebleed section” hypothesis). Rose breeders have long considered blue roses to be the unattainable “Holy Grail” of the flower world. Because roses contain no natural blue anthocyanin pigments, blue roses have not been bred. (The creation of the first genetically engineered blue rose in Japan in 2004 demonstrates the unnatural mechanisms required to overcome this constraint). Like blue roses, some plumage colors may not be possible given the physical constraints on color-producing mechanisms. Or, organisms may possess a pigment but be unable to mobilize it to the appropriate tissues (see comment on parrot carotenoids below). Together, physical and physiological constraints on signal production may render certain colors unattainable. Alternatively, some colors may be unfavorable: Birds can physically evolve such colors, but natural and sexual selection dictate that they do so rarely. By comparison, we often avoid the nosebleed section, or those unfavorable seats high above the action at a stadium or too close for comfort at a theater.

First, we will consider the blue rose hypothesis. Examining the details of the avian color gamut (Figure 5) indicates that many of the unoccupied regions of color space require reflectance spectra that are challenging, if not impossible, to produce with existing plumage coloration mechanisms. Each class of feather pigments is highly constrained to a relatively tiny volume of the color space (Figure 5). Consequently, there are many regions in the avian color space that cannot be realized with the few classes of available pigments. For example, there are no blue pigments in bird feathers and green porphyrin pigments are very rare (Dyck 1992), providing only a very narrow range of colors (Table 1). Birds can absorb plant-derived dietary carotenoid pigments, and some birds have evolved the ability to deploy them in their feathers to create vivid plumage colors. By contrast, birds break down plant anthocyanin pigments during digestion and are unable to metabolically generate them. Thus, birds are restrained from producing many anthocyanin-based colors that plants can produce.

Structural colors provide a much broader range of colors than do pigments (Figure 5E,F). Coherent scattering, or constructive interference, by the nanostructures in the barb rami or barbules can produce saturated colors peaking at any point in the visible spectrum (Prum 2006). Combinations of structural and pigmentary colors provide additional breadth to the color gamut (Figure 5G). The overwhelming contribution of structural colors to the avian color gamut supports the hypothesis that structural colors have evolved to overcome the inherent physical constraints of primitive pigmentary mechanisms. Plants largely lack structural colors (but see Glover and Whitney 2010), providing further evidence that the different physical and chemical limitations in plumages and plants impose different constraints on their respective gamuts.

Yet none of the available plumage color mechanisms creates highly saturated colors in the green, blue, purple, uv-green, and uv-red regions of the color space (Figure 5A). Here, constraints on receptor physiology, combined with those on color-

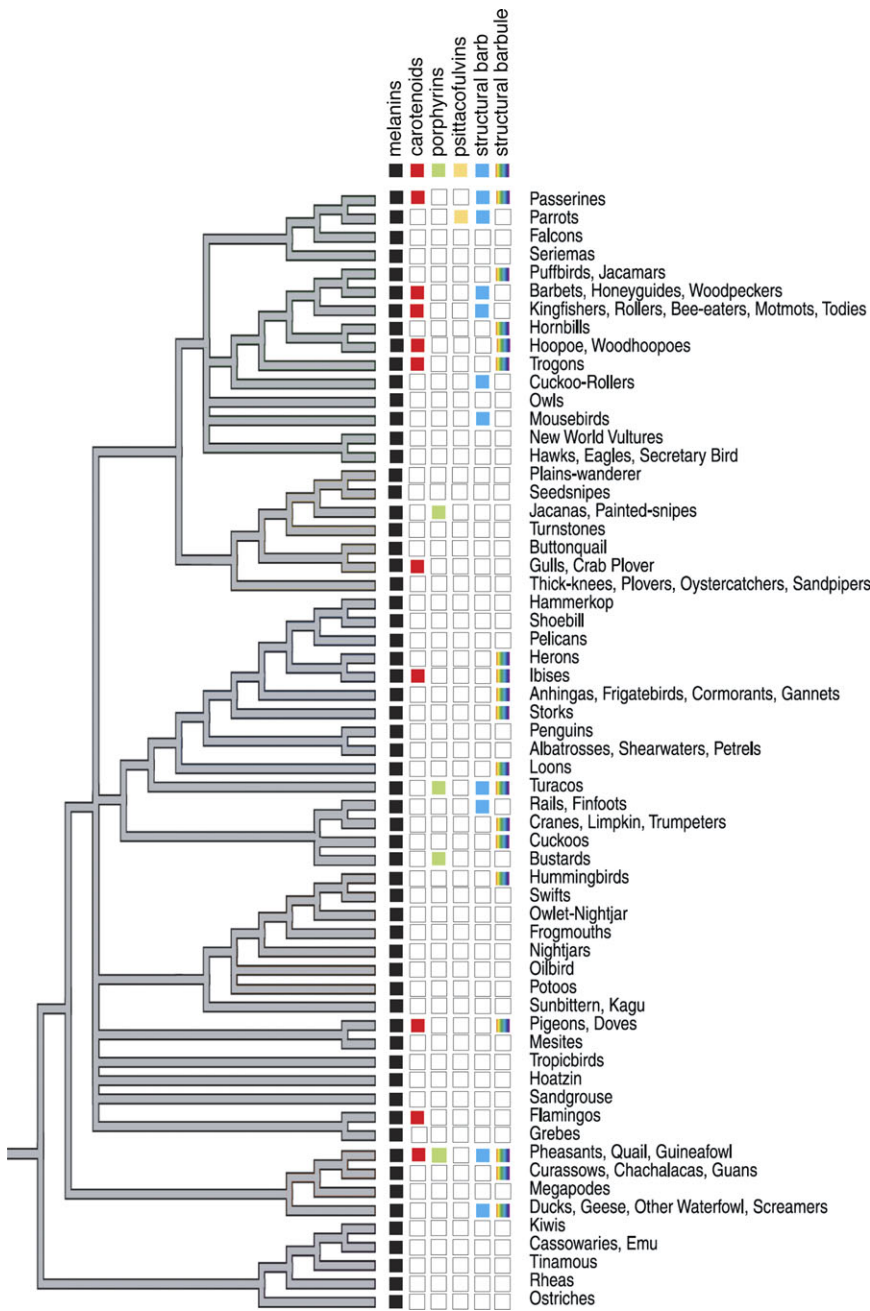
producing mechanisms, contribute to these unoccupied color regions. For example, it is easier to produce highly saturated colors at either extreme of the visible spectrum, where the  $uv/v$  and  $l$  cone pigments do not overlap in absorbance with any others. Few colors stimulate the very narrow band of wavelengths in the  $s$  and  $m$  cone sensitivities that have no overlap with each other or the  $uv/v$  and  $l$  sensitivities (Hart 2001; Cuthill 2006). As a result, it is easier to achieve highly saturated ultraviolet and red colors than blue and green colors just as a function of avian cone-type physiology. It is also important to consider that saturated colors in the unoccupied uv-green or uv-red regions of the color space would require strong simultaneous reflectance of nonadjacent portions of the visible spectrum. Although there are examples of primarily green and red colors with some ultraviolet reflectance (Stoddard and Prum 2008), the relatively small ultraviolet component in these colors would prevent them from extending into the unoccupied regions of the color space. Reflectance spectra that strongly stimulate only nonadjacent cones are difficult to produce with pigments and structural coloration mechanisms available in avian plumages. Given this, we might wonder why birds have the ability to see colors that are very challenging to make by plumages and plants alike. In birds, color vision serves many purposes, not just those related to communication, signaling, or foraging (Osorio and Vorobyev 2008). At least to some extent, the distribution of avian plumage colors is an epiphenomenon of a tetrachromatic visual system that evolved early in vertebrates and has been maintained in birds for capabilities beyond those required just for signal processing.

The blue rose hypothesis clearly explains why some regions of color space are physically unreachable by bird plumage colors, but what have been the effects of natural and sexual selection (the nosebleed section hypothesis)? Adaptation has likely restricted the achieved color gamut of specific subclades. Nocturnal owls and nightjars, for example, stay hidden during the day and have no need for flashy color signals, so their dull cryptic coloration likely results from natural selection on signal function rather than mechanistic constraint. But whether these events have had a noticeable effect on the overall plumage gamut is challenging to determine. Consider the dearth of plumage colors in the purple region densely occupied by plants. Very few plumage colors pioneer this color region. However, the vibrant pink crown (Figure 3c and 4A, color point 1) of the Red-bearded Bee-eater (*Nyctinoris amictus*) and the iridescent magenta primaries (Figure 4A, color point 2) of the Cuckoo-roller (*Leptosomus discolor*) are notable exceptions. These are the “Easter Islands” of bird colors—those furthest away from all other bird colors (Figure 4A). Are these examples of mechanistic innovations (i.e., genuine blue roses) or special cases of extraordinary natural or sexual selection for these colors in special environments? The former seems more likely. Both colors arise from special color-producing mechanisms that have permitted rare colonization of otherwise unoccupied color space. The Red-bearded Bee-eater’s pink crown is a combined carotenoid + structural color, whereas the Cuckoo-roller’s vibrant magenta primaries result from iridescent coloration created by structural barbules. Clearly, identifying constraints on signal diversity is not always straightforward, and further work on plumage evolution in different avian groups will help to clarify which explanations apply. Additionally, many bird plumages have intricate patterning (e.g., streaks, barring, and countershading), and exploring the morphological possibilities of color and pattern in concert is an exciting prospect for the future (Riegner 2008).

### Evolutionary novelties in plumage coloration mechanisms

Have evolutionary novelties in plumage coloration mechanisms contributed to expansion of the plumage color gamut? Or have new coloration mechanisms redundantly replaced





**Figure 6** Phylogenetic distribution of 6 major feather pigment and structural coloration mechanisms on a phylogenetic hypothesis for the major lineages of birds from Hackett et al. (2008). The use of melanin plumage pigments is primitive to all extant birds. Other pigimentary and structural coloration mechanisms have had multiple independent origins in different lineages of birds, resulting in phylogenetically parallel expansions in the plumage color gamuts of different clades. A color version of this figure is available online.

more primitive ones, perhaps at lower physiological cost? A recent higher-level phylogenetic hypothesis of birds by Hackett et al. (2008) provides an opportunity for an initial estimate of the phylogenetic history of plumage coloration mechanism and color gamut evolution at the broadest phylogenetic level (Figure 6). The primitive plumage coloration mechanisms of extant birds are melanin pigmentation and its absence, unpigmented white (Figure 6). Carotenoid pigments are absent from most plumages of the phylogenetically basal lineages of birds (i.e., Paleognathes, Anseriformes, and most Galliformes) but have evolved independently in many (but not all) higher avian lineages. Indeed, one of the major contributors to plumage diversity has been birds' evolution of the capacity to deploy diet-derived plant pigment molecules in their feathers. Despite using dietary carotenoids in various metabolic processes, mammals have never achieved the evolutionary innovation of coloring their hair with carotenoids.

Furthermore, the independent origins of structural colors have permitted plumage colors to reach places unreachable by feather and plant pigments alike.

Evolutionary novelties in exogenous pigment metabolism have clearly permitted phylogenetic expansions of the color gamut. Social and sexual selection for new plumage colors have likely contributed to the evolution of metabolic innovations in carotenoid pigment structure. For example, the physiological alteration of yellow xanthophylls (which are acquired from the diet) into red/orange ketocarotenoids for deposition in the plumage has evolved independently in many different lineages of birds (McGraw and Nogare 2004). Compared with primitive, metabolically unaltered xanthophylls, derived red/orange ketocarotenoids provide a much larger contribution to the color gamut (Table 1). Metabolic evolutionary innovation has continued in many lineages of birds. The polygynous male Pompadour Cotinga

(*Xipholena punicea*) has a deep burgundy–purple plumage color, which is produced by a mixture of 6 unique, metabolically transformed methoxy-ketocarotenoid molecules (LaFountain et al. 2010). In avian color space, these burgundy–purple hues (Figure 4A, color point 3) share regions occupied otherwise only by parrot-unique psittacofulvin-based colors, reinforcing the idea that mechanistic novelties in different lineages have evolved—sometimes convergently—to expand the gamut (see below).

Interestingly, the unique psittacofulvin pigments of parrots (Stradi et al. 2001; McGraw and Nogare 2004; McGraw 2006) occupy an essentially identical red/orange/yellow region of color space as the carotenoid pigments found in their apparent sister group, the passerines (Passeriformes) (Supplementary Material, Supplementary Figure 1). However, carotenoid expression in plumage was not present in the immediate common ancestor of parrots and passerines (Figure 6). Although parrots have ample concentrations of carotenoids in their blood to color their feathers (McGraw and Nogare 2004), they convergently evolved a distinct alternative pigmentary mechanism for expanding their color gamut into the long wavelength regions of color space (Supplementary Material, Supplementary Figure 1). Thus, parrots are developmentally constrained from deploying carotenoids into their feathers and did not evolve psittacofulvin feather pigments to avoid the cost of obtaining carotenoids.

Over evolutionary time, structural colors have greatly expanded the gamut of avian plumage colors (Figure 5E,F) and also created colors unachievable by plants (Figure 4A). By analogy, the fortuitous advent in 1856 of a new purple dye called mauveine revolutionized the textile industry; this synthetic dye created a dazzling fadeproof color unlike any other previously made from natural dyes. Both barb rami and barbule structural colors have evolved independently in many different lineages of birds (Figure 6). Detailed examination of the few cases in which color mechanism novelties appear to be shared by closely related lineages in this phylogeny indicates that these novelties evolved within separate lineages of these clades and not in their shared common ancestors. For example, the derived structural barb and carotenoid colors of the Piciformes and Coraciiformes evolved in separate lineages within each order and not in the shared common ancestor of these orders (Figure 6). Thus, the current phylogenetic pattern indicates that the avian plumage color gamut has increased substantially, and its expansion resulted from the independent evolution of new pigmentary and structural mechanisms in many bird groups.

Unraveling the details of the avian plumage gamut paints an intricate picture of color evolution in birds. Sensory-morphospace analyses offer a promising framework for identifying mechanistic constraints and addressing macroevolutionary questions in the future. Whether any animal group on the planet comes close to rivaling avian color diversity remains to be seen.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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## REFERENCES

- Arnold SEJ, Faruq S, Savolainen V, McOwan PW, Chittka L, Giurfa M. 2010. FRcD: the floral reflectance database—a web portal for analyses of flower colour. *PLoS One*. 5:115–127.
- Bradley BJ, Mundy NI. 2008. The primate palette: the evolution of primate coloration. *Evol Anthropol*. 17:97–111.
- Burkhardt D. 1989. UV vision: a bird's eye view of feathers. *J Comp Physiol A*. 164:787–796.
- Carvalho LS, Cowing JA, Wilkie SE, Bowmaker JK, Hunt DM. 2007. The molecular evolution of avian ultraviolet-and violet-sensitive visual pigments. *Mol Biol Evol*. 24:1843–1852.
- Cronk Q, Ojeda I. 2008. Bird-pollinated flowers in an evolutionary and molecular context. *J Exp Bot*. 59:715–727.
- Cuthill IC. 2006. Color perception. In: Hill GE, McGraw KJ, editors. *Bird coloration, Vol 1, mechanisms and measurements*. Cambridge (MA): Harvard University Press. p. 3–40.
- Cuthill IC, Bennett ATD, Patridge JC, Maier EJ. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am Nat*. 160:183–200.
- Dyck J. 1992. Reflectance spectra of plumage areas colored by green feather pigments. *Auk*. 109:293–301.
- Eaton MD. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually “monogamous” birds. *Proc Natl Acad Sci U S A*. 102:10942–10946.
- Eaton MD, Lanyon SM. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proc R Soc B Biol Sci*. 270:1721–1726.
- Endler JA, Mielke PWJ. 2005. Comparing entire colour patterns as birds see them. *Biol J Linn Soc*. 86:405–431.
- Endler JA, Wescott DA, Madden JR, Tobson T. 2005. Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution*. 59:1795–1818.
- Glover BJ, Whitney HM. 2010. Structural colour and iridescence in plants: the poorly studied relations of pigment colour. *Ann Bot (Lond)*. 105:505–511.
- Goldsmith TH. 1990. Optimization, constraint, and history in the evolution of eyes. *Q Rev Biol*. 65:281–322.
- Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han K-L, Harshman J, et al. 2008. A phylogenomic study of birds reveals their evolutionary history. *Science*. 320:1763–1768.
- Hart NS. 2001. The visual ecology of avian photoreceptors. *Prog Retin Eye Res*. 20:675–703.
- Hart NS, Hunt D. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *Am Nat*. 169:7–26.
- Hill GE, McGraw KJ, editors. 2006a. *Bird coloration, Vol. 1, mechanisms and measurements*. Cambridge (MA): Harvard University Press.
- Hill GE, McGraw KJ, editors. 2006b. *Bird coloration, Vol. 2, function and evolution*. Cambridge (MA): Harvard University Press.
- Jones C, Osorio D. 2004. Discrimination of oriented visual textures by poultry chicks. *Vision Res*. 44:83–89.
- Kelber A, Vorobyev M, Osorio D. 2003. Animal colour vision—behavioural tests and physiological concepts. *Biol Rev*. 78:81–118.
- Kuehni RG. 2003. *Color space and its divisions*. Hoboken (NJ): John Wiley & Sons.
- LaFountain A, Kaligotla S, Cawley S, Riedl K, Schwartz S, Frank HA, Prum R. 2010. Novel methoxy-carotenoids from the burgundy colored plumage of the Pompadour Cotinga *Xipholena punicea*. *Arch Biochem Biophys*. 504:142–153.
- McGraw KJ. 2006. Mechanics of uncommon colors in birds: pterins, porphyrins, and psittacofulvins. In: Hill GE, McGraw KJ, editors.

- Bird coloration, Vol I, mechanisms and measurements. Cambridge (MA): Harvard University Press. p. 354–398.
- McGraw KJ, Nogueira MC. 2004. Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots. *Comp Biochem Physiol Biochem Mol Biol.* 138:229–233.
- Ödeen A, Håstad O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol Biol Evol.* 20:855–861.
- Ödeen A, Håstad O. 2010. Pollinating birds differ in spectral sensitivity. *J Comp Physiol A.* 196:91–96.
- Osorio D, Vorobyev M. 2008. A review of the evolution of animal color vision and visual communication signals. *Vision Res.* 48:2042–2051.
- Prum RO. 2006. Anatomy, physics, and evolution of avian structural colors. In: Hill GE, McGraw KJ, editors. *Bird coloration, Volume 1 mechanisms and measurements.* Cambridge (MA): Harvard University Press. p. 295–353.
- Prum RO, Torres RH. 2004. Structural coloration of mammalian skin: convergent evolution of coherently scattering dermal collagen arrays. *J Exp Biol.* 207:2157–2172.
- Raup D. 1966. Geometric analysis of shell coiling: general problems. *J Paleontol.* 40:1178–1190.
- Riegner MF. 2008. Parallel evolution of plumage pattern and coloration in birds: implications for defining avian morphospace. *Condor.* 110:599–614.
- Schaefer HM, Shaefer V, Vorobyev M. 2007. Are fruit colors adapted to consumer vision and birds equally efficient in detecting colorful signals? *Am Nat.* 169:159–169.
- Stoddard MC, Prum RO. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *Am Nat.* 171:755–776.
- Stradi R, Pini E, Celetano G. 2001. The chemical structure of the pigments in *Ara macao* plumage. *Comp Biochem Physiol B Biochem Mol Biol.* 130:57–63.
- Sumner P, Mollon JD. 2003. Colors of primate pelage and skin: objective assessment of conspicuousness. *Am J Primatol.* 59:67–91.
- Vorobyev M. 2003. Coloured oil droplets enhance colour discrimination. *Proc R Soc B Biol Sci.* 270:1255–1261.
- Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. *Proc R Soc B Biol Sci.* 265:351–358.
- Vorobyev M, Osorio D, Bennet ATD, Marshall NJ, Cuthill IC. 1998. Tetrachromacy, oil droplets and bird plumage colours. *J Comp Physiol A.* 183:621–633.