Widespread Cryptic Dichromatism and Ultraviolet Reflectance in the Largest Radiation of Neotropical Songbirds: Implications of Accounting for Avian Vision in the Study of Plumage Evolution

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WIDESPREAD CRYPTIC DICHROMATISM AND ULTRAVIOLET REFLECTANCE IN THE LARGEST RADIATION OF NEOTROPICAL SONGBIRDS: IMPLICATIONS OF ACCOUNTING FOR AVIAN VISION IN THE STUDY OF PLUMAGE EVOLUTION

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Abstract.—Avian coloration has played a central role in the study of sexual selection and other aspects of animal behavior. However, only recently have analyses of avian coloration been able to incorporate avian visual abilities. Although several studies have broadly sampled species for evidence of plumage coloration visible to birds but invisible to humans, few studies have quantified these data for all species in a single taxonomic group. We quantify ultraviolet (UV) plumage reflectance and document cryptic sexual dichromatism in the largest radiation of Neotropical songbirds, the cardinals and tanagers. Ultraviolet reflectance was common in the patches measured, with almost half of the species reflecting >20% of light in the UV range in at least one patch. High UV-reflecting patches, including 73 of the 91 patches that were found to be primarily UV colored, belonged to species in either *Passerina* or 2 of 13 major clades of tanagers. This indicates that high UV reflectance is not randomly distributed across the phylogeny. Sexual dichromatism was much more widespread in the group than previously thought. From a human visual perspective, about half the species in the group are sexually dichromatic; but from an avian visual perspective, 97% of species are dichromatic. We compared the implications of using human-perceived versus avian-perceived sexual dichromatism by mapping these traits onto tanager phylogenies. Quantifying dichromatism using an avian visual model provided a more accurate and detailed history of plumage coloration change across evolutionary history. *Received 19 August 2011, accepted 23 January 2012.*

Key words: avian vision, cardinal, coloration, sexual dimorphism, tanager, ultraviolet.

El Dicromatismo Críptico y la Reflectancia Ultravioleta están Ampliamente Difundidos en la Mayor Radiación Neotropical de Aves Canoras: Implicaciones de Considerar la Visión Aviar en el Estudio de la Evolución del Plumaje

Resumen.—La coloración de las aves ha jugado un papel central en el estudio de la selección sexual y otros aspectos del comportamiento animal. Sin embargo, sólo recientemente se ha logrado que en los análisis de coloración se incorporen las habilidades visuales de las aves. Aunque muchos estudios han muestreado especies ampliamente en busca de evidencia de coloración del plumaje visible para las aves pero no para los humanos, pocos estudios han cuantificado estos datos para todas las especies en un solo grupo taxonómico. Cuantificamos la reflectancia ultravioleta (UV) del plumaje y documentamos dicromatismo sexual críptico en la mayor radiación de aves canoras Neotropicales: los cardenales (Cardinalidae) y las tángaras (Thraupidae). La reflectancia ultravioleta fue común en los parches de plumaje medidos: casi la mitad de las especies reflejaron más del 20% de la luz en el espectro UV en al menos un parche. Se encontró que los parches con alta reflectancia de UV, incluyendo 73 de los 91 parches que fueron predominantemente de color UV, pertenecieron a especies del género *Passerina* o de 2 los 13 clados principales de tángaras. Esto indica que la reflectancia alta de UV no se encuentra distribuida aleatoriamente en la filogenia. El dicromatismo sexual está mucho más extendido en el grupo que los que se pensaba previamente. Desde un punto de visto humano cerca de la mitad de las especies en el grupo presentan dicromatismo sexual, pero desde el punto de vista de las aves el 97% de las especies son dicromáticas. Comparamos las implicaciones del uso del dicromatismo sexual percibido desde un punto de vista humano contra un punto de vista aviar mediante el mapeo de estos caracteres en la filogenia de las tángaras. La cuantificación del dicromatismo usando un modelo visual aviar condujo a una historia más exacta y detallada del cambio de la coloración del plumaje a lo largo de la historia evolutiva.

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For centuries, studies of coloration have been essential in furthering knowledge of avian behavior. Although scientists have known about ultraviolet (UV) vision in birds since the 1970s, only in the past decade or so have studies of plumage coloration incorporated this information (Cuthill 2006, Bennett and Théry 2007). In addition to UV vision, birds have oil droplets attached to each of their cone cells that act as long-pass cut-off filters, thus enhancing birds' discriminatory capabilities (Bowmaker 1977, 1980; Goldsmith et al. 1984; Vorobyev et al. 1998; Vorobyev 2003; Cuthill 2006). These two major visual differences, confirmed by behavioral tests, have shown the importance of taking the avian visual system into account when studying plumage coloration (Bennett et al. 1994, Cuthill et al. 1999, Håstad and Ödeen 2008), particularly sexual dichromatism.

As a result of a model of avian vision (Vorobyev et al. 1998), and the accessibility of spectrophotometers (Bennett and Théry 2007), studies of bird coloration that consider avian visual abilities are now common (e.g., Eaton and Lanyon 2003, Eaton 2005, Stoddard and Prum 2008). Despite this, few studies have surveyed each species in a single taxonomic group (but see Eaton 2006, Seddon et al. 2010). These types of studies are important for understanding variation among and within different groups of birds (e.g., Benites et al. 2010) and provide the data and foundation needed to look at the evolution of coloration in a phylogenetic context. Here, we report coloration data on two sister clades of birds, the Cardinalidae (cardinals and grosbeaks) and the Thraupidae (tanagers). These two groups are best known for their bright coloration, such as the striking red plumage of species in *Cardinalis*, and multicolored species in the genera *Passerina* and *Tangara*. However, many species of cardinals and tanagers are cryptically colored (e.g., species in the genus *Poospiza*, some species in *Saltator*, and females of many species). The two clades are sister taxa, and the species composition of each has recently been revised (Klicka et al. 2007, F. K. Barker et al. unpubl. data). Together, these two groups contain 417 species, or ~4.2% of all avian species and 8.0% of species in Passeriformes (perching birds). They are the largest radiation of songbirds in the Neotropics and are ecologically diverse, occurring in 27 of the 29 terrestrial habitats identified in the region (Parker et al. 1996). Given the size of the cardinal–tanager clade and the diversity of plumage colors and patterns within them, a study of their plumage provides a good opportunity to look at how accounting for avian vision might affect interpretations of plumage evolution and behavior. We focus our results on two aspects of avian coloration that escape human visual perception. First, we quantify the extent of UV reflectance in tanagers and cardinals. Second, we provide an assessment of sexual dichromatism for each species in the group, using a model that incorporates all aspects of avian visual abilities, not just UV vision.

All birds are sensitive to light in the UV spectrum (300–400 nm). Some species have what is called the "UVS system," with maximal sensitivity between 355 and 370 nm, and others have the "VS system," with maximal sensitivity between 405 and 420 nm (Hart 2001, Cuthill 2006, Ödeen et al. 2011). Among Passeriformes, all members of the clade Passerida have the UVS system (Ödeen et al. 2011), including the only species of tanager studied, *Cyanerpes cyaneus* (Ödeen and Håstad 2010). Two studies have looked at the distribution of UV plumage coloration across all birds. Eaton and Lanyon (2003) randomly sampled 312 species from nearly all families of birds evenly and found that 99% of species examined had at least one patch reflecting >5% of light in the UV spectrum, and 91% reflected ≥10%. Contrary to these findings, Mullen and Pohland (2008) sampled 968 species distributed across all orders of birds and found that only 39% of species reflected 10% of light in the UV spectrum. This difference may be due to sampling differences of the two studies. By designing their study to survey avian orders, Mullen and Pohland (2008) had a greater concentration of sampling outside of the Passeriformes, where UV reflectance is less common (Mullen and Pohland 2008). We seek to compare UV reflectance in the tanager–cardinal clade with the distribution of UV reflectance in birds as a whole. In addition, although these studies (Eaton and Lanyon 2003, Mullen and Pohland 2008) have looked at the distribution of UV coloration across patch colors, none have looked for patches that are primarily UV colored. By thoroughly sampling two clades of birds, we will be able to examine the taxonomic distribution of UV colored patches and UV coloration in general.

Avian visual models have changed how studies address sexual dichromatism (Andersson et al. 1998, Cuthill et al. 1999, Eaton 2005). For example, Eaton (2005) indicated that sexual dichromatism might be much more widespread in birds than once thought. Randomly surveying 139 species of passerines thought to be monochromatic from the human visual perspective, Eaton (2005) found that 92.8% are dichromatic from the avian visual perspective. These results were confirmed in a geographically confined study in which 91.6% of 166 North American passerines that were thought to be monochromatic from the human visual perspective were found to be dichromatic from the avian visual perspective (Eaton 2007). Almost half (43%) of tanager and cardinal species are currently considered monochromatic from a human visual perspective (Ridgely and Gwynne 1989, Ridgely and Tudor 1989, Howell and Webb 1995, Castro and Phillips 1996, Raffaele et al. 1998, Isler and Isler 1999, Restall et al. 2007). However, at least one monochromatic species of tanager, *Stephanophorus diadematus*, is actually dichromatic from the avian visual perspective (Tubaro et al. 2005). Our study will examine the extent and taxonomic distribution of such cryptic sexual dichromatism in tanagers and cardinals. In addition, we look at the evolution of sexual dichromatism in detail by mapping dichromatism onto phylogenies for two clades of tanagers, comparing interpretations based on human-perceived vs. avian-perceived plumage dichromatism.

Methods

Taxonomic sampling.—To select species to include in our study, we followed recent phylogenies based on molecular sequence data (Burns 1997; Lougheed et al. 2000; Burns et al. 2002, 2003; Yuri and Mindell 2002; Burns and Naoki 2004; Klicka et al. 2007; Burns and Racicot 2009; Mauck and Burns 2009; Sedano and Burns 2010). All measurements were taken from museum specimens in the collections at the American Museum of Natural History. To avoid a potential effect of specimen age on the reflectance measures (Hausmann et al. 2003, McNett and Marchetti 2005, Armenta et al. 2008a, Doucet and Hill 2009), we chose the newest specimens with the freshest-looking plumage for each species (Eaton and Lanyon 2003, Armenta et al. 2008a, Doucet and Hill 2009). When possible, we also used males and females from the same locality and same season to avoid potential effects of geographic or seasonal variation (Tubaro et al. 2005). We were able

to quantify plumage of all but 16 of the 417 species of tanagers and cardinals (Table S1 in online supplemental materials; see Acknowledgments). Because only one sex was available for some species, we were unable to calculate the degree of sexual dichromatism for 25 additional species.

Ultraviolet reflectance.—To compare our data with those of previous studies, we followed the methods of Eaton and Lanyon (2003) and Eaton (2005) in collecting our reflectance data. We used an Ocean Optics (Dunedin, Florida) USB2000 spectrophotometer with the PX-2 pulsed xenon light source to record reflectance across the avian visual spectrum. We used an R200-7-UV/VIS reflection probe and fitted the probe with a modified rubber stopper to restrict incident light and to control the distance between the probe tip and feather surface. All measurements were taken at a 90° angle to the feather surface. We defined a color patch following the protocol of Eaton and Lanyon (2003). For each species and each sex, we measured all plumage patches that appeared to be differently colored to the human eye. We excluded patches that were less than ~4 mm^2 because they were too small to accurately measure with the probe. To facilitate analyses, measurements were later averaged into 10-nm bins across the avian visual range (300–700 nm) for analyses of UV using language written for the SAS statistical package. For analyses of sexual dichromatism, raw reflectance data were averaged into 1-nm bins.

To compare levels of UV reflectance among species, we quantified UV reflectance in three ways. First, we calculated the mean UV reflectance of a patch between 340 and 380 nm, following Eaton and Lanyon (2003). This was done by taking the average percent reflectance of the four 10-nm bins between 340 and 380 nm. We refer to this measure as "Aveg UV." In addition, to identify patches that reflected relatively more in the UV than in other parts of the spectrum, we calculated two measures, Max UV and Peak UV, initially described by Eaton (2006). A patch was considered to have Max UV if its maximum reflectance across the entire avian visual range (300–700 nm) was in the UV portion of the spectrum (300–400 nm). However, a patch might have its maximum reflectance in the UV portion of the spectrum, but this reflectance might be only slightly higher than at other wavelengths. Thus, we also calculated Peak UV, which is a measure of the contrast between the UV portion (320–400 nm) and the adjacent (blue) portion of the spectrum (401–480 nm). To calculate Peak UV, the reflectance of each 10-nm bin from 400–480 nm was summed and this number was subtracted from the total percent reflectance of each 10-nm bin from 320–400 nm. These ranges were chosen by Eaton (2006) because they represent equal portions of the light spectrum that roughly correspond with the UV-sensitive and violet-sensitive cones. Thus, patches with a high value for Peak UV have noticeably higher reflectance in the UV range than in the adjacent part of the spectrum. Patches with negative values of Peak UV have lower reflectance in the UV range than in the adjacent part of the spectrum. All these measures were used to consider the relative UV reflectance of a patch. For example, patches with Max UV, Peak UV, and high Aveg UV have high reflectance, and their largest percent reflectance values are in the UV portion of the spectrum. Because white patches reflect in all portions of the spectrum, including UV, we analyzed our data with white patches included as well as white patches excluded. Fewer UV-reflecting patches were identified with white patches excluded, but overall the results were qualitatively similar when we compared the sexes or across taxonomy. Thus, we report only the results that included all plumage patches, and we use the results reported for all plumage patches when we make comparisons to other studies.

Sexual dichromatism.—To quantify sexual dichromatism objectively, we used an avian visual model, following Eaton (2005). Sexual dichromatism was calculated using measurements taken from homologous patches between males and females. Dichromatism was scored as ΔS and calculated using the Vorobyev-Osorio color discrimination model (Vorobyev and Osorio 1998, Vorobyev et al. 1998). We calculated ΔS using the SPEC script (see Acknowledgments), implemented in the program R (R Core Development Team 2010). Avian cone sensitivities are highly conserved (Hart 2001), so spectral sensitivities for each cone type were used from another passerine, the Blue Tit (*Cyanistes caeruleus*), to calculate the quantum cone catch (Hart et al. 2000). Irradiance was disregarded because the effect of light environment was not of interest to our study (Eaton 2005) and has been shown to have little effect on the conclusions drawn from the scores, although the scores themselves might change slightly (Eaton 2005, Stoddard and Prum 2008). Blue Tit data were also used to approximate the abundance of different cone types (Hart et al. 2000). Although cone type abundance varies from species to species, there are very few data available. Eaton (2005) showed that using the densities from different species changed the exact values of the results, but not the conclusions drawn from them. The ΔS score was calculated for each pair of homologous male and female patches, where a separate patch could be detected in at least one sex. When the measurements were different for males and females, the measurements representing the same regions were compared. From these scores, the highest ΔS for each species was extracted for interspecific comparison as the dichromatism score. We chose to use the highest ΔS over the average ΔS because birds see each other on a patch-by-patch basis, and not as a patch average, and so that our results could be compared with previous work (e.g., Eaton 2005). The value of ΔS is measured in terms of just noticeable differences, or jnds. A jnd value >1.0 is the threshold for discrimination between two measurements, with the greater the jnd value, the greater the difference (Vorobyev and Osorio 1998, Vorobyev et al. 1998, Siddiqi et al. 2004, Eaton 2005). We consider species with at least one patch with $\Delta S > 1.0$ to be dichromatic. Because a jnd of 1.0 only indicates that discrimination is possible under ideal lighting conditions, we also summarized dichromatism under a more conservative threshold of 2.0.

We compared our quantitative measure of sexual dichromatism with published assessments of human-perceived sexual dichromatism. Human assessments of dichromatism were obtained from *The Tanagers* (Isler and Isler 1999) and other appropriate field guides (Ridgely and Gwynne 1989, Ridgely and Tudor 1989, Howell and Webb 1995, Castro and Phillips 1996, Raffaele et al. 1998, Restall et al. 2007, Ryan 2007). To provide a phylogenetic perspective to this comparison, we used the *Ramphocelus* clade (Burns and Racicot 2009), which contains species that appear primarily dichromatic to humans, and the *Tangara* clade (Sedano and Burns 2010), which contains species that are primarily monochromatic from the human perspective. For the *Ramphocelus* clade, we used a Bayesian consensus tree with all compatible groups (Burns and Racicot 2009: fig. 2). For the *Tangara* clade, we built a phylogeny using RAxML (Stamatakis 2006, Stamatakis et al. 2008) on the Cipres Science Gateway (Miller et al. 2010). We

used the data presented in Sedano and Burns (2010), with 1,000 bootstrap replicates. Both ΔS and the discrete human dichromatism designation were reconstructed onto the phylogenies using squared-change parsimony in the program MESQUITE (Maddison and Maddison 2010) and using maximum likelihood (Pagel 1994, Schluter et al. 1997) in the "ape" package (Paradis et al. 2004) in the R programming environment (R Core Development Team 2010). To assess the fit of the Brownian-motion model to our data, we compared Akaike's information criterion scores of the Brownian-motion model; the Ornstein-Uhlenbeck model (OU; Butler and King 2004); Pagel's (1999) lambda, kappa, and delta; and the white noise model, which disregards phylogenetic structure. We performed model fitting in the "geiger" package (Harmon et al. 2008) and obtained ancestral state estimates for the OU and Brownian-motion model in the OUCH (Butler and King 2004) package, implemented in the R programming environment (R Core Development Team 2010).

RESULTS

Ultraviolet Reflectance

Patches.—A total of 6,084 patches were measured from 805 individuals representing 401 species (Table S1). Ultraviolet reflectance was common in the patches measured; most patches (63%) had a reflectance of >5% in the ultraviolet range (Table 1). In addition, 9% of the patches showed an Aveg UV >20%. Although most patches reflected UV, only a few of these patches reflected more light in the UV portion of the spectrum than in other parts of the spectrum. Only 4% of patches showed their maximum reflectance (Max UV) in the UV portion of the range, and only 16% of patches showed a Peak UV >10%. Only 2.4% of patches showed both a large Peak UV (>10%) and Max UV, and only 1.5% of Peak and Max UV patches had an Aveg UV >20%. Although these patches (e.g., Fig. 1) are relatively rare compared with the number of patches measured, we identified a total of 91 of these primarily UV-colored patches.

Species.—The UV-reflecting patches were distributed across nearly all species measured. In fact, all species of cardinals and all

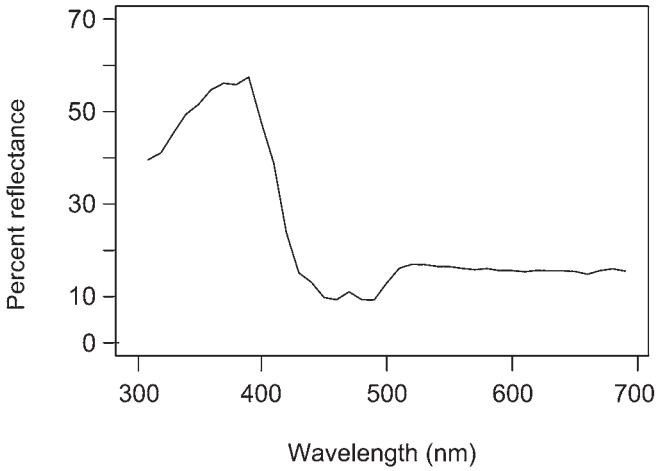

FIG. 1. A reflectance spectrum of the primarily UV-colored ear covert patch of *Chlorochrysa phoenicotis*.

TABLE 1. Values of ultraviolet reflectance for patches, species, and sexes of tanagers and cardinals. Values shown are percentages of species or patches with the ultraviolet reflectance characters defined in the text: Peak UV, Max UV, and Aveg UV.

	Number measured	Percent reflecting <5% Aveg UV	Percent reflecting 5–10% Aveg UV	Percent reflecting 10–20% Aveg UV	Percent reflecting >20% Aveg UV	Percent with Peak UV >%5	Percent with Peak UV >10%	Percent with Max UV reflectance
Patches of tanagers	5,240	37.82	37.18	16.16	8.83	22.88	14.10	4.14
Patches of cardinals	844	30.45	41.00	21.92	6.64	38.15	27.49	2.96
Total patches	6,084	36.71	37.71	16.96	8.53	25.00	15.96	3.98
Species of tanagers	354	0.85	12.71	38.14	48.31	72.88	45.48	21.75
Species of cardinals	47	0.00	12.77	44.68	42.55	89.36	89.36	19.15
Total species	401	0.75	12.72	38.90	47.63	74.81	50.62	21.45
Patches of female tanagers	2,523	35.47	40.15	17.80	6.58	20.33	12.52	2.58
Patches of female cardinals	395	31.90	47.09	19.49	1.52	27.34	17.47	0.25
Total female patches	2,918	34.99	41.09	18.03	5.89	21.28	13.19	2.26
Patches of male tanagers	2,688	40.10	34.49	14.69	10.75	25.00	15.36	5.58
Patches of male cardinals	449	29.18	35.63	24.05	11.14	47.66	36.30	5.35
Total male patches	3,137	38.54	34.66	16.03	10.81	28.24	18.36	5.55
Species of female tanagers	334	1.20	22.46	47.31	29.04	53.89	35.03	8.98
Species of female cardinals	47	4.26	27.66	57.45	10.64	59.57	48.94	2.13
Total females	381	1.57	23.10	48.56	26.77	54.59	36.75	8.14
Species of male tanagers	348	4.60	17.24	34.48	43.68	64.94	41.95	18.97
Species of male cardinals	47	0.00	17.02	44.68	38.30	89.36	89.36	19.15
Total males	395	4.05	17.22	35.70	43.04	67.85	47.59	18.99

but three species of tanagers (*Ramphocelus bresilius*, *R. dimidiatus*, and *R. melanogaster*) reflected ≥5% Aveg UV in at least one of their plumage patches (Table 1). Although only 9% of patches reflected >20% Aveg UV, these patches were distributed across nearly half (48%) of the species measured. Similarly, although relatively few patches showed Peak and Max UV, these patches were distributed across a number of different species. Fifty-one percent of species measured had Peak UV of >10%, and 21% of species measured had one of their patches showing a maximum reflectance in the UV portion of the spectrum. Fewer species (13.9%) had a patch with both Peak UV >10% and Max UV.

Taxonomic distribution.—Although UV-reflecting patches were found in a wide variety of species, those with the most UV-reflective patches were taxonomically restricted to a few clades. All patches with >50% Aveg UV were found in 2 of the 13 major clades of tanagers. One of these clades is the core tanager clade (Burns and Naoki 2004, Sedano and Burns 2010), which includes many colorful species, such as the species in the genus *Tangara* and mountain tanagers in the genera *Buthraupis*, *Anisognathus*, and *Bangsia*. The other clade with highly UV-reflective patches contains species of tanager-honeycreepers in the genera *Cyanerpes* and *Dacnis* (Burns 1998, Burns et al. 2003). Similarly, the patches showing the highest 1% of Peak UV were found in either species that are members of these two clades or in species that belong to the cardinal genus *Passerina*. In addition, roughly two-thirds of the Max UV species were found in these three clades, and 75% of the species that had both Max UV and Peak UV >10% were in these three clades. Of the 91 patches that showed high levels of UV reflectance in all three of our measures (Max UV, Peak UV >10%, and Aveg UV >20%), 73 of the patches belonged to species in one of these three clades.

Sexual Differences in the Ultraviolet Spectrum

Patches.—Overall, males had more patches than females (3,137 vs. 2,918), indicating the more diverse plumage patterning found in males than in females (Table 1). Ultraviolet-reflecting patches were widespread in both sexes. Somewhat unexpectedly, slightly more female patches than male patches reflected an average of >5% of light in the UV range. This was probably due to a greater number of darker melanin patches in males than in females. These dark patches likely increase the contrast with highly reflecting plumage patches found in adjacent body regions. Otherwise, male patches were more often found in categories defining the most reflective patches. For example, more male patches reflected >20% Aveg UV, and more male patches could be defined as having a Peak or Max UV (Table 1).

Species.—When summarized by species, these UV-reflecting patches were widespread in both sexes of each species. Thus, differences between sexes when summarized by species were similar to differences between sexes as summarized by patches described above. Only 1.6% of females and only 4% of males showed an Aveg UV >5% for all their patches. Although more females than males were UV reflective at the 5% and 10–20% levels, males were more likely than females to reflect the greatest amount of UV light. More males showed an Aveg UV >20%, and more males could be characterized as having Max and Peak UV. For example, 19% of species have males that have at least one patch with Max UV reflectance, whereas only 8% of species have females with a Max UV patch (Table 1).

Sexual Dichromatism Using an Avian Visual Model

Patches.—To measure sexual dichromatism, a total of 3,153 patch comparisons were made for 376 species using an avian visual model (Table S1). The ΔS values for these comparisons ranged from 0.014 (the breast and flank measurement of *Poospiza boliviana*) to 15.25 (the belly measurement of *Cyanerpes caeruleus*). Most of the patches (60%) had a ΔS score >1, and thus are dichromatic from an avian visual perspective (Fig. 2A). Using the more conservative threshold of $\Delta S > 2.0$, 56% of patches with a ΔS score >1 would still be considered dichromatic.

Species.—We summarized these patch comparisons by species, determining the patch with the highest ΔS for each species. We found that these dichromatic patches are not restricted to a few species but are spread across almost all species of tanagers and cardinals (Fig. 2B). For the 376 species analyzed, 97.3% had a ΔS value >1.0 and, thus, can be designated as dichromatic from the avian visual perspective (Fig. 2B). Using a more conservative threshold of ΔS >2.0, 76% of species are dichromatic using an avian visual model. Dichromatism was more widespread in the cardinals than in the tanagers, with all cardinals and 97.0% of the tanagers identified as dichromatic, with at least one patch with a ΔS value >1.0. Using a threshold of $\Delta S > 2.0$, all cardinals are still dichromatic, but only 72% of tanagers were still identified as dichromatic.

Cryptic dichromatism.—Almost all species identified by humans as monochromatic were dichromatic from an avian visual perspective. Using published literature, 163 of the studied species were designated as monochromatic from a human visual perspective, and 213 species were designated as dichromatic (Table S1). We found that the vast majority (93.2%) of these 163 human monochromatic species are dichromatic from the avian visual perspective. However, these cryptically dichromatic species are more likely to have lower ΔS scores than species identified as dichromatic from a human visual perspective (t-test, $t = -12.19$, $df = 344.7$, $P < 0.001$).

Taxonomic distribution.—Sexual dichromatism, as defined by ΔS, was found to be ubiquitous across the tanagers and cardinals. However, the magnitude of that dichromatism varies across the different clades (Fig. 3). The cardinals as a whole are more dichromatic than the tanagers (Fig. 3). Within the tanagers, there are several clades that show higher measures of ΔS than the others. The most dichromatic species belong to the clade of tanager-honeycreepers from the genera *Cyanerpes* and *Dacnis* (Burns 1997, Burns et al. 2003), which typically consist of colorful, blue males and green females. Other clades with very high measures of ΔS are the clade containing members of *Hemithraupis*, *Chlorophanes*, *Chrysothlypis*, *Heterospingus*, and *Iridophanes* (Burns 1997); the clade containing *Compsothraupis*, *Cyanicterus*, *Nemosia*, and *Sericossypha* (Burns 1997, F. K. Barker et al. unpubl. data); and the lowland clade containing members of *Ramphocelus*, *Tachyphonus*, *Lanio*, *Eucometis*, *Trichothraupis*, *Rhodospingus*, and *Coryphospingus* (Burns and Racicot 2009).

The 10 sexually monochromatic species (*Camarhynchus heliobates*, *C. pallidus*, *Conirostrum margaritae*, *Diglossa brunneiventris*, *D. lafresnayii*, *D. mystacalis*, *Paroaria coronata*, *Phrygilus erythronotus*, and *Xenospingus concolor*) come from different clades within tanagers, although several are members of the genus *Diglossa*.

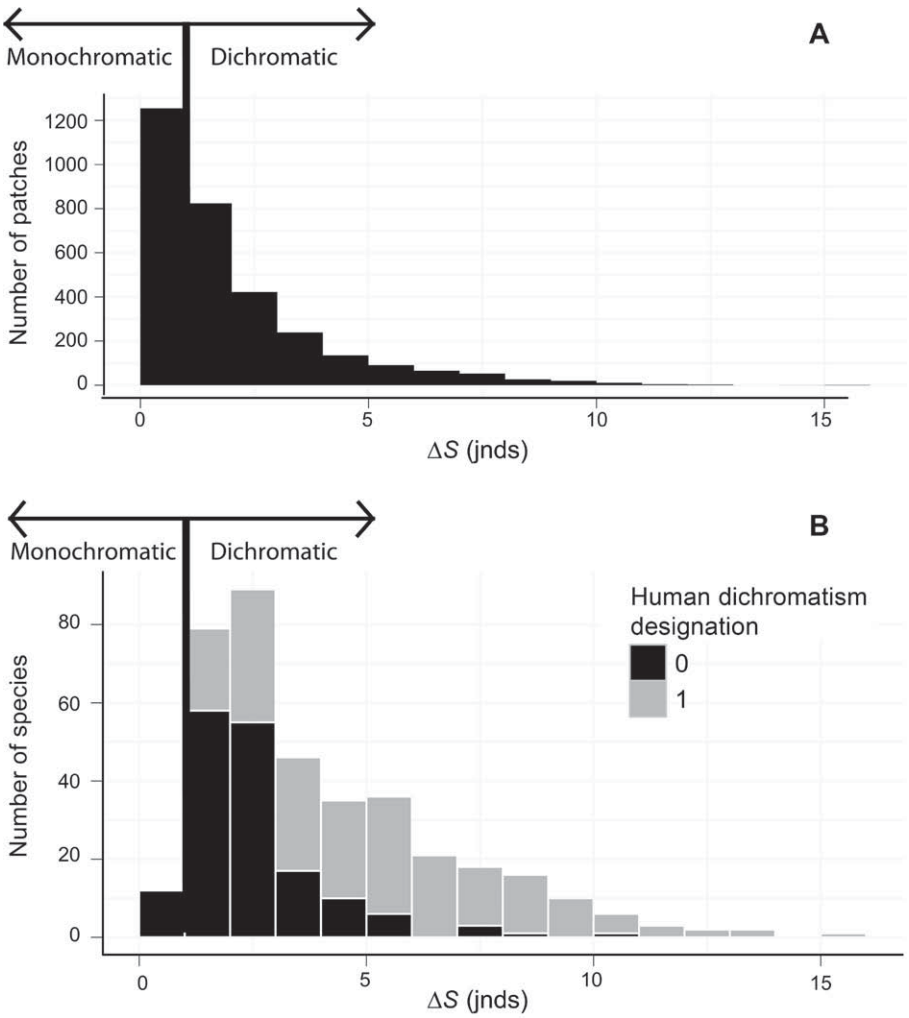

FIG. 2. (A) Distribution of Δ*S* values across all patches measured. (B) Distribution of the highest Δ*S* measured for each species. Δ*S* is measured in just noticeable differences (jnds), and a value greater than one indicates a perceivable difference.

Phylogenetic perspective.—Using our model-fitting technique, we determined that for the *Ramphocelus* clade, the best-fit models were white noise, OU, and lambda. For the *Tangara* clade, the best-fit models were OU and lambda. In both cases, the chosen OU models had high alpha values and lambda values close to zero, indicating a small contribution of phylogeny. We also reconstructed degree of sexual dichromatism as defined by Δ*S* scores and by the human visual perspective onto the phylogenies of two clades of tanagers (Figs. 4 and 5). The reconstruction methods currently available assume a Brownian-motion model, which was not the best-fit model to our data. However, root values can be calculated for the OU model, the model that provided a better fit in both clades. Therefore, we compared these root estimates (calculated for the OU model using the OUCH package) to those obtained under Brownian motion using maximum likelihood as a way of verifying the general accuracy of our ancestral character-state reconstructions. Root estimates using either model were very similar for both clades. The root value for the *Ramphocelus* clade was 5.95 (95% CI: 4.32–7.57) using the Brownian-motion model, and 5.90 (95% CI: 5.88–5.95) using the OU model. The root value for the *Tangara* clade was 4.09 (95% CI: 2.80–5.39) using the Brownian-motion model, and 3.65 (95% CI: 3.64–3.67) using the OU model. The similarity of these values indicates that the ancestral state reconstructions can demonstrate, at least in a general sense, how using different methods of categorizing sexual dichromatism can result in different conclusions across the tree. The human characterization contradicts the avian perception at many nodes, provides less detail, and fails to detect some transitions between dichromatism states as well as changes in the degree of dichromatism (Figs. 4 and 5).

DISCUSSION

Ultraviolet reflectance.—The results of our survey of UV reflectance in cardinal and tanager plumage patches mirror those of Eaton and Lanyon (2003), which randomly sampled patches across avian families. For example, both studies found that 63%

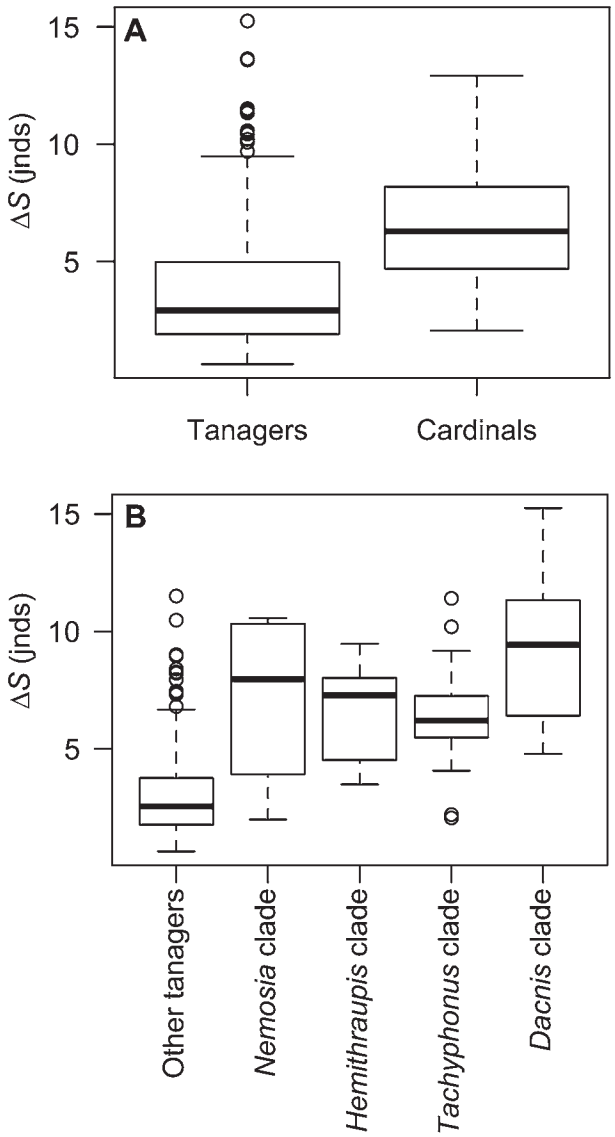

Fig. 3. Box-and-whiskers plots summarizing (A) the range of Δ*S* values of tanagers and cardinals and (B) four clades of tanagers compared with the rest of the species in the tanager clade. *Nemosia* clade = *Nemosia, Compsothraupis, Cyanicterus, Sericossypha; Hemithraupis* clade = *Hemithraupis, Chlorophanes, Chrysothlypis, Heterospingus, Iridophanes; Tachyphonus* clade = *Ramphocelus, Tachyphonus, Lanio, Eucometis, Trichothraupis, Rhodospingus, Coryphospingus; Dacnis* clade = *Cyanerpes, Dacnis, Tersina*.

of patches had an average reflectance >5%. Furthermore, both the present study and Eaton and Lanyon (2003) show that virtually all species have a patch on their body that reflects a substantial amount of UV. Similarities between the broader survey of Eaton and Lanyon (2003) and analyses of this clade show that the clade containing cardinals and tanagers display the full diversity of UV reflectance seen in all birds. This diversity may reflect the fact that cardinals and tanagers vary greatly in their ecology, morphology, and behavior. This is not necessarily true of other clades of birds. For example, assessment of UV reflectance in the grackles and allies showed that this group has lower levels of UV reflectance than birds as a whole (Eaton 2006), and Seddon et al. (2010) found that only 25% of plumage patches in antbirds have an average reflectance >5%. Mullen and Pohland (2008) found that no species in Struthioniformes, Tinamiformes, Craciformes, Turniciformes, Apodiformes, Strigiformes, and Bucerotiformes reflected 10% of light in the UV spectrum. Of the remaining orders surveyed by Mullen and Pohland (2008), only the Psittaciformes exhibited levels similar to those of the tanagers and the cardinals, with 140 of 143 species reflecting 10% of light in the UV spectrum.

Although UV reflectance was prevalent throughout the clade we studied, some groups were more reflective of UV light than others. Previous studies have shown correlations between UV reflectance and aspects of natural history such as diet, habitat, and mating systems (Bleiwess 2004, Eaton 2006). Although we are currently unable to complete a rigorous analysis of ecological correlates to UV reflectance, we hypothesize a relationship between UV reflectance and forested habitats. The two clades that had the most UV-reflecting plumage (the core tanagers and the tanager honeycreepers) are mostly forest-dwelling species. Many also occur in dense-forest canopy, where close signaling distance is a necessity and UV light is abundant. Tanagers and cardinals are an ideal group for future studies of a potential correlation between UV reflectance and habitat, given the extent of variation in both plumage and habitat preference in the group.

Sexual dichromatism.—In terms of the degree of sexual dichromatism, tanagers and cardinals reflect the pattern seen within passerine birds as a whole. We found that only 7% of human-perceived monochromatic species are also monochromatic from an avian perspective, and Eaton (2005) estimated this value as 10% in passerines. In fact, the distribution of Δ*S* values in Eaton's (2005) study are not significantly different from those we found for monochromatic tanagers and cardinals (*t*-test, $t = -1.41$, df = 256.45, $P = 0.16$). However, tanagers–cardinals are not representative of birds as a whole in terms of sexual dichromatism, because nonpasserine birds are less sexually dichromatic. Armenta et al. (2008b) surveyed >1,000 species of birds across all avian groups (including passerines and nonpasserines) and found that 62% of birds were identified as monochromatic both by humans and by having a Δ*S* value <1.0. Armenta et al. (2008b) attributed the difference between their results and those of Eaton (2005) to their inclusion of nonpasserine birds. Overall, our results indicate that tanagers and cardinals reflect the general pattern of sexual plumage dichromatism of passerine birds and the UV reflectance patterns of birds as a whole.

Evolution of sexual dichromatism (human-perceived vs. avian-perceived).—Seddon et al. (2010) compared a human-perceived measure of sexual dichromatism with avian-perceived sexual dichromatism and found that human scores explained 34% of the variation in avian-perceived dichromatism in antbirds, a largely dichromatic clade with VS spectral sensitivity. Such a correlation is also suggested in our data because birds that humans perceive to be monochromatic tend to have lower Δ*S* values (Fig. 2). However, human scores are a poor predictor of sexual dichromatism in many individual species, as indicated

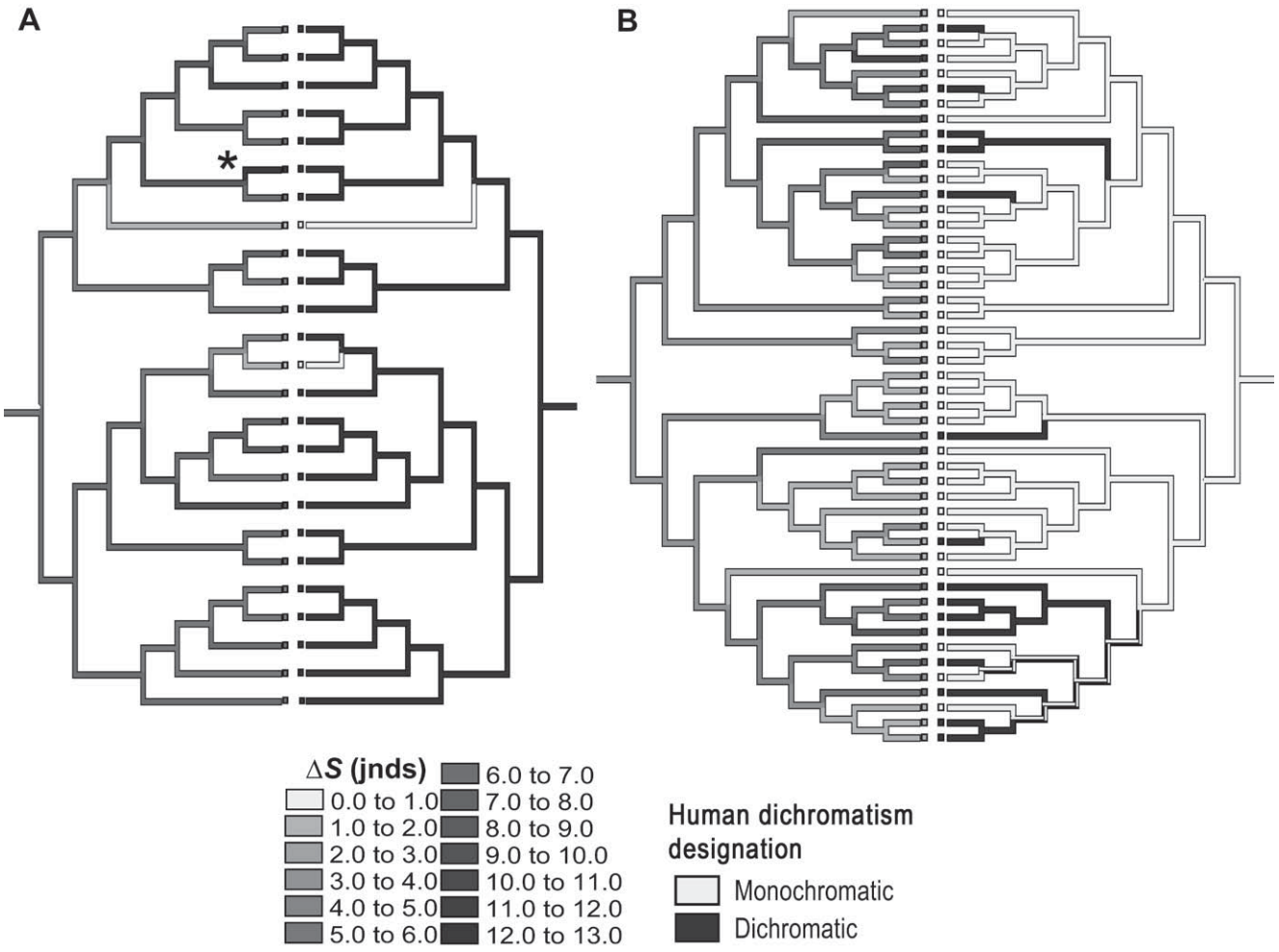

FIG. 4. Ancestral state reconstruction of dichromatism using squared-change parsimony for (A) the *Ramphocelus* and allies clade and (B) the *Tangara* clade. In both clades, avian perception is shown on the left and human perception on the right. The position of *Ramphocelus passerinii* (indicated by asterisk) demonstrates one example in which there is much more information in the Δ*S* reconstruction than in the human-designation reconstruction.

by the scatter present in figure 3 of Seddon et al. (2010) and the large number of human-perceived monochromatic species with high Δ*S* values in the present study (Fig. 2). For example, in our study, 153 species are considered monomorphic to humans but dichromatic to birds (Δ*S* threshold of 1.0; 92 species using Δ*S* threshold of 2.0). Thus, it is impossible to study the evolution of sexual dichromatism in these 153 species using only a human scoring system. Furthermore, studying correlations between sexual dichromatism and other traits across the group would be compromised by improperly scoring ~41% of the species in the study.

Scoring human-perceived dichromatism on a scale of 0–10 as in Seddon et al. (2010) allows a means to capture some of the variation in degree of sexual dichromatism, especially in groups with colors like brown and black that are generally perceived similarly between birds and humans. Unfortunately, many evolutionary and comparative studies (e.g., Barraclough et al. 1995, Figuerola and Green 2000, Friedman et al. 2009) have used a discrete, two-state character for sexual dichromatism as scored by humans. Our results show contrasting evolutionary interpretations when dichromatism is instead quantified and considered in the context of the visual capabilities of birds. Within a clade of lowland tanagers (Burns and Racicot 2009; Figs. 4A and 5A), most species have traditionally been identified as dichromatic, with two species identified as monochromatic. Thus, the ancestor to these species is inferred to be dichromatic, regardless of the underlying model, with two instances in which dichromatism was lost, likely through an increase in female colorfulness (Burns and Racicot 2009). However, using Δ*S*, we infer a more detailed interpretation. Dichromatism is seen as a continuum, with each species showing varying degrees of dichromatism in their most dichromatic patch. The ancestral species is inferred as intermediately dichromatic, with two instances of a decrease in dichromatism. In addition, one lineage (*Ramphocelus passerinii*; Fig. 4A) shows a dramatic increase in dichromatism (Δ*S* increased from 8.2 to 11.4), a pattern not revealed when mapping dichromatism from a human visual perspective.

Similarly, the evolution of dichromatism in the genera *Tangara* and *Thraupis* (Figs. 4B and 5B) shows more detail when the avian visual perspective is considered. Most species in this clade

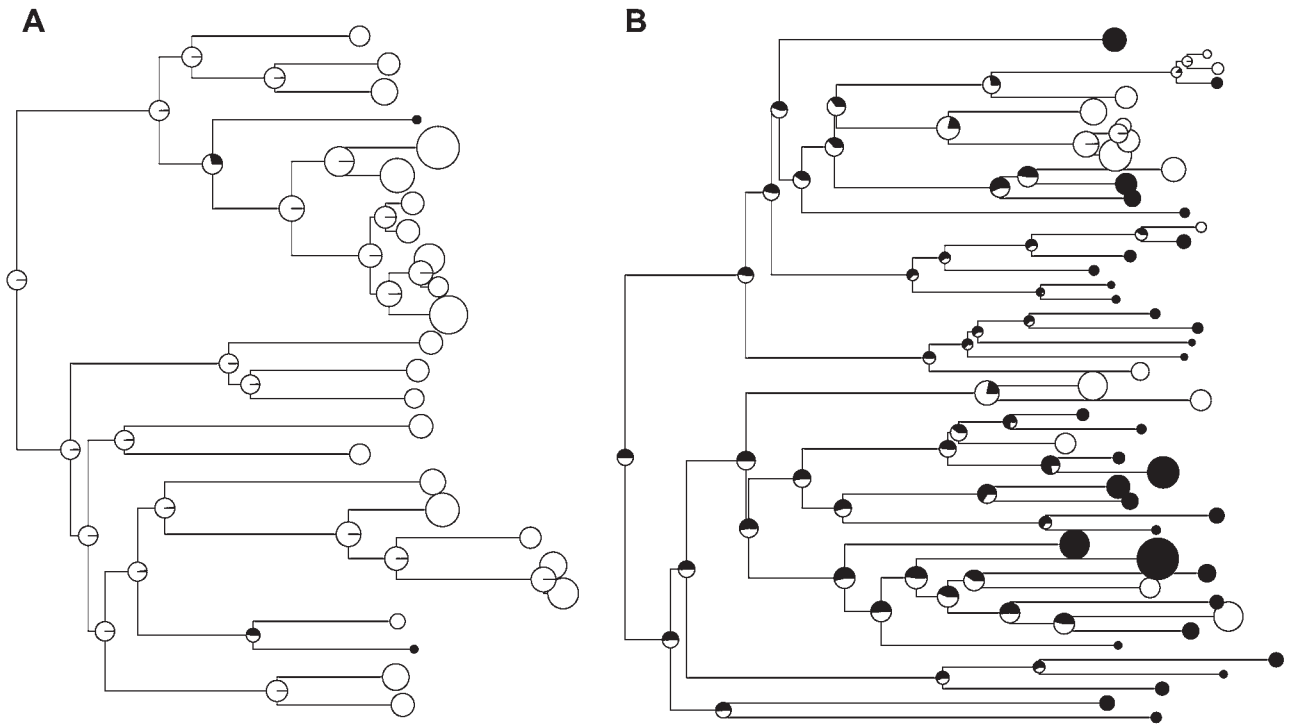

Fig. 5. Ancestral state reconstruction of dichromatism using maximum likelihood for (A) the *Ramphocelus* and allies clade and (B) the *Tangara* clade. The size of each circle represents the Δ*S* value at that tip or each node (i.e., small Δ*S* values are less dichromatic and have small circles, and large Δ*S* values are more dichromatic and have large circles). For uncertainty in the continuous Δ*S* reconstruction, see Figure S1 in online supplemental materials. Dark vs. white circles indicate human-perceived dichromatism, with dark circles representing monochromatic taxa and white circles representing dichromatic taxa. The proportion of dark vs. white in a given circle indicates relative uncertainty in the ancestral reconstruction, with the proportion of white indicating the likelihood of a human-designated dichromatic taxon at that node. Small white circles and large dark circles indicate disparity between human and avian perceived dichromatism.

were considered monochromatic, but Δ*S* values show that all species are at least moderately dichromatic. Thus, mapping dichromatism from a human perspective would indicate that there were numerous transitions from monochromatism to dichromatism. However, the pattern of Δ*S* evolution reveals that the degree of dichromatism has increased in many lineages but has decreased in others. Thus, instead of explaining why dichromatism has evolved in so many lineages, the more informed approach would look for correlations with changes in degree of dichromatism across the phylogeny. As has been noted elsewhere (Burns 1998, Wiens 2001, Badyaev and Hill 2003, Hofmann et al. 2008), these changes in dichromatism could be due to gains or losses in either male or female plumage. Thus, sexual dichromatism itself is a composite trait (McLennan and Brooks 1993), and a detailed study of plumage colors and mechanisms of each species and sex would be needed to make such interpretations. Finally, our results show that the greater difference between human and Δ*S* reconstructions in the *Tangara* clade than the *Ramphocelus* clade (Figs. 4 and 5) indicates that there may be more conflict in clades with species that humans perceive as monochromatic.

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