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RESEARCH ARTICLE

Concerted Shifts in Absorption Maxima of Yellow and Red Plumage Carotenoids Support Specialized Tuning of Chromatic Signals to Different Visual Systems in Near-Passerine Birds

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Abstract
Recent evidence that absorption maxima (λR_{min}) expressed by colorful plumage pigments align to diagnostic cone sensitivities of affiliated visual systems suggests that birds employ specialized signals in relation to their color vision. However, these studies compared different pigments and clades for the violet (porphyrins in non-passerines) and ultraviolet (carotenoids in passerines) sensitive system, which confounds chemistry and phylogeny with tuning patterns. To test whether signal alignments to violet (VS) and ultraviolet (UVS) systems transcend confounding factors, parallel analyses were conducted for a diversity of near-passerines, a group in which plumage carotenoids occur in taxa with either visual system. Conventional and phylogenetically informed analyses confirmed earlier findings: short wavelength absorbing (yellow carotenoid) pigments aligned λR_{min} with the violet-sensitive (V) cone of VS species but with the short wavelength-sensitive (S) cone of UVS species, whereas long wavelength-absorbing (red carotenoid) pigments aligned only with the S cone of VS species. More extensive variation among VS yellow carotenoids produced λR_{min} alignments to cone sensitivities that differed at shorter (peaks) versus longer (overlaps) wavelengths. Ancestral trait reconstructions indicated that signals evolved to match pre-existing VS systems, but did not resolve scenarios for UVS systems. Regardless of historical details, alignments expressed a higher-level pattern in which λR_{min} values were blue-shifted for yellow and red carotenoids in VS compared to UVS species, a pattern opposite that expressed by receptor sensitivities between systems. Thus, generalized functional designs attributed to avian color vision allow for specialized visual communication through the development of chromatic signals suited to each perceptual system.

Keywords Communication · Cone · Homoplasy · Pigment · Reflectance · Wavelength

Introduction

The distinction between specialized and generalized traits provides a useful conceptual framework for many ecological and evolutionary studies (Amadon 1943; Futuyma and Moreno 1988; Bleiweiss 1990; Kelley and Farrell 1998; Johnson and Steiner 2000; Poisot et al. 2011; Dapporto and Dennis 2012; Vamosi et al. 2014). As usually understood, these terms refer to organismal adaptations in relation to extrinsic factors (Litsios et al. 2014; Wilson and Hayek 2015) as described by physical (Hailman 1977; Endler 1993; Endler and Théry 1996; Heindl and Winkler 2003; Seehausen et al. 2008), ecological (Nosil 2002; Håstad et al. 2005; Jablónski et al. 2006), and social (Baker and Parker 1979; Götmark 1994; Senar 1999; Slagsvold et al. 1995; Hill 2002; Seehausen et al. 2008) environments. In principal, the same generalist–specialist paradigm also can be applied to communication systems, which involve the exchange of information mediated by intrinsic factors relating to the signaling system of "senders" and the sensory systems of "receivers" through one or more signaling and sensory modalities. Thus, generalist communication systems would be expected to operate with a wide variety of signals under a range of perceptual and social conditions whereas

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specialist communication systems would be expected to use only particular signals or to employ them only in certain contexts (Cariani 2001). It is easy to see from even these simple considerations that the distinction between generalist and specialist communication systems has obvious relevance to understanding fundamental evolutionary processes such as ecological and mate competition, speciation, and coevolution, especially as regards the relative importance of extrinsic vs intrinsic controls on these processes.

Consideration of functional and evolutionary properties of communication in a generalist–specialist context is especially useful for birds. In particular, the extent to which the two principal color vision systems documented among living diurnal birds are tied to generalist or specialist aspects of communication remains uncertain (Cuthill et al. 2000; Ödeen and Håstad 2003; Hart and Hunt 2007; Stevens and Cuthill 2007). Color perception by both the violet-sensitive (VS) and ultraviolet-sensitive (UVS) systems is based on the same four homologous single-cone classes, designated as violet wavelength-sensitive (V), short wavelength-sensitive (S), middle wavelength-sensitive (M), and long wavelength-sensitive (L). As indicated by their names, the cones of both systems are relatively evenly spaced across the ambient light spectrum, and behavioral experiments (Osorio et al. 1999) and visual modeling (Vorobyev et al. 1998) suggests that this shared property confers excellent general-purpose color vision on both systems. However, the potential for specialized communication by one or both systems is embodied by large differences between them in the sensitivities of their homologous cones, especially as regards the V and S classes, which peak at shorter wavelengths in the UVS relative to the VS system (Cuthill et al. 2000; Smith et al. 2002; Hart and Hunt 2007; Stevens and Cuthill 2007). These concerted shifts in receptor sensitivities appear to optimize the UVS system's perception of shorter, including ultraviolet (UV) wavelengths, and to expand this system's overall ability to discriminate physical stimuli as distinct colors (Vorobyev et al. 1998; Hart and Hunt 2007; Toomey et al. 2016).

The uncertainty surrounding generalized vs specialized attributes associated with the avian VS and UVS systems is especially germane to communication based on plumage signals, whose varied colors have served as models for many behavioral, ecological, and evolutionary processes. Some studies of specific avian groups suggest that the two systems are associated with differences in plumage reflectance at wavelengths that match the large differences in V and S cone sensitivities, especially as regards UV-based plumage reflectance (Mullen and Pohland 2008; Ödeen et al. 2011; Bleiweiss 2014). Moreover, modeling studies suggest that plumage colors of certain UVS birds are more conspicuous to UVS than to VS visual systems, and may therefore confer a private communication channel from predatory birds, which mainly have the VS system (Håstad et al. 2005). However, other evidence fails to support a strong match between visual system and plumage coloration (Coyle et al. 2012; Lind and Delhey 2015). Thus, both VS and UVS visual systems are widely distributed among diurnal birds across avian phylogeny, and each system occurs among species that differ greatly in their ecologies (Hart and Hunt 2007) and plumage colors (Hart et al. 2000; Coyle et al. 2012). Moreover, UVS color vision may not be all that superior to VS vision in the discrimination of plumage color of UVS birds (Lind and Delhey 2015), suggesting that UVS vision confers advantages that are non-specific and unrelated to visual signaling per se. These latter considerations have led to the alternative view that the relatively conserved systems of evenly spaced cones expressed by both color vision systems confer mainly more generalized functions that exploit the full range of wavelengths in avian signals and natural habitats (Vorobyev et al. 1998; Coyle et al. 2012; Lind and Delhey 2015).

A potential limitation shared by many of these studies, however, is their failure to distinguish among the physical mechanisms ultimately responsible for a colored appearance. The most distinct plumage color mechanisms arise through either wavelength-specific reinforcement due to photonic structures, or wavelength-specific absorption due to chemical pigmentation (Hill and McGraw 2006; Prum 2006). Different color mechanisms produce distinct kinds of spectra, so that combining them in an analysis may obscure mechanism-specific matches with visual systems. Notably, two recent studies found that each of the avian visual systems are associated with plumage pigments whose wavelengths of maximal absorbance (in plumage estimated as the wavelength of the reflectance minimum, hereafter λR_{min}) align specifically to diagnostic cones of their affiliated color vision system (Bleiweiss 2014, 2015). In particular, a broad survey of plumage carotenoids in UVS passerine birds indicated that λR_{min} of short wavelength (human-visible "yellow") plumage aligned strongly with the maximum sensitivity of this visual system's S cone, but that λR_{min} of long wavelength (human-visible "red") plumage did not align to the maximum sensitivity of this or any other cone class (Bleiweiss 2014). A parallel study of colorful plumage porphyrins in VS non-passerines indicated that λR_{min} of short wavelength ("green") plumage aligned strongly with the maximum sensitivity of this visual system's V cone, whereas λR_{min} of long wavelength ("red") plumage aligned with the maximum sensitivity of the corresponding S cone (Bleiweiss 2015). Ancestral character state reconstructions further suggested that at least in some cases, the aligned pigments were adopted to fit the visual system. Strong alignments of λR_{min} to visual systems bear directly on communicative functions because absorption encapsulates both the quantity (depth of maxima, as determined by a pigment's extinction coefficient and concentration)

and quality (spectral position of maxima, as determined by pigment molecular chemistry) of the signal's information content (Rodriguez-Amaya 2001). Thus, these preliminary studies suggest that the two avian visual systems adopt specialized signal (λR_{min}) characteristics.

However, more rigorous comparative tests are needed to separate the contributions by plumage pigment chemistry, phylogeny and visual system to alignment. For example, colorful porphyrins appear limited in their occurrence to certain VS non-passerine species, so chemistry and phylogeny are inextricable tied to alignment with the VS visual system alone (Bleiweiss 2015). Carotenoid plumage pigments on the other hand occur across avian phylogeny (Thomas et al. 2014) and visual systems (Ödeen and Håstad 2013), and their varied absorptive properties (Rodriguez-Amaya 2001) provide ample potential for specialization in relation to these factors even for specific clades and carotenoid pigment classes (yellow and red; Goodwin and Goad 1970; Fox 1976). One such comparative system is presented by so-called "near-passerine" birds, a diverse, cosmopolitan non-passerine lineage that contains some of the most characteristic and ecologically diverse land birds, including trogons and quetzals, woodpeckers, barbets, toucans, and bee-eaters (del Hoyo et al. 2001, 2002). A wide variety of yellow and red plumage carotenoids and both VS and UVS type visual systems occur among these birds (Ödeen et al. 2011; Ödeen and Håstad 2013), whose carotenoid-based plumage colors are physically and taxonomically widespread (Stradi et al. 1998; McGraw 2006; Thomas et al. 2014). Near-passerine carotenoids include pigments shared with other avian groups (e.g. yellow hydroxy-carotenoids, red β-keto-carotenoids), but also the more unusual "picofulvin" yellow carotenoids (Krukenberg 1882; Stradi et al. 1998; Brambilla et al. 1999; Prum et al. 2014) that absorb maximally at wavelengths well below (blue-shifted) more typical yellow carotenoids found in nature (Krukenberg 1882; Stradi et al. 1998; Brambilla et al. 1999; Prum et al. 2014). Thus, plumage absorption properties should vary enough among near-passerines to detect any associations with visual systems. Finally, the frequent expression of carotenoid-based plumage coloration in both sexes in near-passerines provides additional stratification for testing the robustness of the results.

This paper tests the alignment ("tuning") patterns suggested by past comparisons within this more rigorous comparative framework. The results suggest specialized alignments of carotenoid-based plumage absorption with VS and UVS visual system-specific receptor sensitivities, which is sensible given the importance of plumage carotenoids to avian communication, health, and fitness (Hill 1996, 2002; McGraw 2006).

Materials and Methods

Visual System Classification

Direct physiological measures (by microspectrophotometry, MSP) of color vision are laborious to obtain, and are available for relatively few birds and no near-passerines (Hart and Hunt 2007). However, visual pigment opsin sequence data are much easier to generate, more widely available, and are now routinely used to infer the avian color vision phenotype due to strong relationships between the opsin genotypes and the sensitivities of the affiliated single-cone classes (Ödeen et al. 2011; Ödeen and Håstad 2013). The SWS1 opsin of the V cone is most commonly used for this purpose based on several considerations. First, the transparency of the oil droplet associated with the V cone means the opsin directly determines the sensitivity of this cone class, which is most diagnostic of the VS and UVS systems (Ödeen and Håstad 2003). Second, the two distinct tunings of SWS1 correlate with properties of the other essential components that determine the color vision phenotype, including the absorptive properties of the other three cone class (S, M and L) opsins (respectively SWS2, MWS, LWS; Hart and Vorobyev 2005, their Fig. 5), of the pigmented oil droplets associated with each of these cone classes (Hart and Vorobyev 2005, their Fig. 5), and of the overarching ocular media (Lind et al. 2014, their Fig. 2). Thus, even SWS2 of the S cone can serve to infer visual system, although sequences for this opsin are less widely available.

Relevant opsin sequences (mainly SWS1 along with a few SWS2) were reported for a total of sixteen near-passerine species, including ten with plumage carotenoids (Table 1). Broader patterns strengthened inferences regarding variation in near-passerine color vision. Thus, interpretations of avian opsin sequences (see comprehensive surveys in Ödeen et al. 2011; Ödeen and Håstad 2013) and the more limited MSP data (Hart and Hunt 2007) data suggest that avian color vision systems are largely conserved up to the family level. The two exceptions are for circumscribed groups outside the near-passerines: a subset of Laridae in Charadriiformes, and Maluridae in Passeriformes (Ödeen and Håstad 2013; see also Moore et al. 2012; van Hazel et al. 2013; Porter et al. 2014; Borges et al. 2015; Wu et al. 2016). Similar conservatism in near-passerines was supported whenever replicate opsin sequences were available, for taxa both with (Table 1) and without (Ödeen and Håstad 2013) plumage carotenoids. Moreover, the single behavioral study of color vision in a near-passerine (for *Dryocopus pileatus*, O'Daniels et al. 2017) corroborated inferences from opsin data that woodpeckers are VS (Table 1).

However, several near-passerine groups were excluded from the present study due to the lack of visual system data

Table 1 Numbers of near-passerine taxa assayed for carotenoid-based plumage reflectance and the subset also assayed for visual system through opsin visual pigment (SWS1 or SWS2) sequence or behavioral (BEHAV) data

Sister clade Order Family[a]	Sampling			
	Plumage		Color vision system	
	Species[b]	Species	Criterion/system[c]	Genera/species[i]
UVS clade				
Trogoniformes				
Trogonidae	27	***Trogon curucui***	SWS1/UVS[d]	2/2
		Harpactes *erythrocephalus*	SWS1/UVS[e]	
VS clade				
Piciformes				
Picidae	23	***Dendrocopus major***	SWS1/VS[d]	4/5
		Picus viridis	SWS1/VS[e]	
		Picoides *pubescens*	SWS1/VS[f]	
		Picus *canus*	SWS2/VS[g]	
		Dryocopus pileatus	BEHAV/VS[h]	
Megalaimidae	7	***Psilopogon virens***	SWS1/VS[e]	1/1
Ramphastidae	14	***Ramphastos*** *tucanus*	SWS1/VS[e]	1/1
Coraciiformes				
Meropidae	10	***Merops apiaster***	SWS1/VS[e]	1/2
		Merops nubicus	SWS2/VS[g]	

[a]Trogons (Trogonidae), woodpeckers (Picidae), Asian barbets (Megalaimidae), toucans (Ramphastidae), bee-eaters (Meropidae)

[b]Reflectance spectra obtained for both sexes except for some females that lacked carotenoids. Trogon taxa include two distinctive allospecies that are restricted to southeastern Brazil

[c]Visual systems determined from DNA sequences of V (SWS1) cone ([d]Ödeen and Håstad 2003, [e]2013; [f]Borges et al. 2015) or S (SWS2) cone ([g]Wu et al. 2016) opsins, or from BEHAVioral tests ([h]O'Daniels et al. 2017). All bolded taxa (genera, species) included in plumage study

[i]Total numbers of ordinal members evaluated for visual system (adding the remaining ordinal opsin data from Ödeen and Håstad 2013) raises totals for Piciformes (to 8) and Coraciiformes (to 7)

(Capitonidae), or to the rarity (VS Alcedinidae, Coraciidae), ambiguity (VS Bucerotiformes, cosmetic application of carotenoids; Vevers 1964), or absence (UVS Momotidae) of plumage carotenoids (Thomas et al. 2014). The included families had either UVS [Trogonidae (trogons and quetzals)] or VS [Picidae (woodpeckers), Megalaimidae (Asian barbets), Ramphastidae (toucans), Meropidae (bee-eaters)] visual systems, and expressed a wide diversity of carotenoid-based plumages.

Selection of Species

Eighty-one putative near-passerine species from across the included families were studied. All genera and most species with plumage carotenoids and accompanying opsin or behavioral data on visual system were included in this sample (Table 1; Online Resource 1). For all taxa, one or more adults of each sex with carotenoids were examined for each species. Sampling intensity was constrained for the UVS trogons and quetzals (hereafter trogons, Trogonidae, Trogoniformes) due to their relatively low numbers of species (~45) and carotenoid-based plumage patches (typically on belly and vent, more rarely also head and back) compared to other near-passerines. However, geographically isolated (in southeastern Brazil) populations of *Trogon melanocephalus* and *T. viridis* also were retained as distinct due to their possible species status (del Hoyo et al. 2001). As constituted, the trogon sample included approximately 70% of all species with yellow plumage and 55% of species with red plumage, whereas the absolute numbers were generally higher but the percentages lower among the other sampled families.

Plumage Spectra Recordings

Data generation and classification followed earlier studies (Bleiweiss 2014, 2015; see also; Andersson and Prager 2006). In brief, the same set of plumage subdivisions was designated for all species, and spectra were recorded from all human-visible yellow, orange, or red patches (up to ten) with a WP230-1-XRS bifurcating fiber optic probe attached to a PX-2 pulsed xenon light source and to an Ocean Optics USB 2000+ spectrometer. The probe tip was fitted with a Delrin® black plastic sleeve to maintain a fixed (5 mm) distance between the probe and the plumage surfaces, and to exclude stray ambient light. For each specimen, reflectance was measured at 90°, first for a diffuse white standard

(Spectralon® WS-1-SL; Ocean Optics) and then for all carotenoid-based patches, repositioning the probe tip to obtain (typically two) replicate spectra from each patch in turn. Different sexes and species were measured in random order (subject to arrival of different loans), as were then the patches for each specimen. All spectra were generated over the avian visible range (320–700 nm), which includes the wavelengths visible to humans (400–700 nm).

Plumage Chemistry and Absorption

Earlier chemical, physical, and spectral analyses provided a strong basis for concluding that yellow, orange, and red plumages in near-passerines result from carotenoid pigments (Fox 1976; Goodwin and Goad 1970; Stradi et al. 1998; McGraw 2006; Thomas et al. 2014). For example, chemical analyses confirmed carotenoids as the principal basis for human-perceived yellow to red plumages in trogons (Fox 1976; Thomas et al. 2014; 14 species), woodpeckers (Stradi et al. 1998; Thomas et al. 2014; 19 species), Asian barbets (Thomas et al. 2014; 2 species), toucans (McGraw 2006; Thomas et al. 2014; 9 species), and bee-eaters (Thomas et al. 2014; 5 species). The rapid rise to a reflectance plateau at longer wavelengths present in all sampled spectra (Fig. 1) is typical of plumage carotenoids in vivo, further supporting inferences based on the more limited chemical data.

The chemistry of any carotenoid pigment is closely tied to its absorption maximum, which corresponds to λR_{min} in a quantitative plumage reflectance spectrum (Fig. 1). Thus, carotenoids distinguished as "yellow" or "red" based on human perceptions can be classified objectively based on their absorption patterns (Rodriguez-Amaya 2001; cf.; Toral et al. 2008). Yellow carotenoids (e.g. xanthophylls) have multiple absorption bands ("fine structure") surrounding the absorption maximum, whereas red carotenoids (e.g. β-keto-carotenoids) have only a single broad absorption maximum. In addition, the spectral location of the absorption maximum (e.g. λR_{min}) is located at shorter wavelengths for yellow compared to red carotenoids. A few species (the trogon *Harpactes oreskios*, various *Psilopogon* barbets) with human-visible orange plumage also were classified with yellow pigments based on their similar fine structure. Certain reflectance peaks of some carotenoid spectra may arise from interactions between pigments and nanostructure (Prum and Torres 2004), but these features were not considered in the present analysis.

Plumage Spectra Processing

Pseudo-replication of spectra was reduced by averaging each level of replication (replicate scans per patch × patches × individuals × sex) from the lowest to highest levels separately for yellow (plus orange) versus red colored patches for each species. Typical for spectral data (Lind and Delhey 2015), the distributional properties of λR_{min} for each visual system × pigment class × sex did not always meet the requirements of parametric statistical tests (for normality and equal variances), so data transforms or non-parametric approaches were applied as appropriate. Related to this issue, collection dates spanned more than 100 years, a time period over which plumage spectra can change significantly (McNett and Marchetti 2005; Armenta et al. 2008). The carotenoid-based colors of trogons in particular are sensitive to fading (Johnsgard 2000), and trogon specimens whose yellow to red plumage patches had visually whitened were avoided. In addition, outlier specimens were also identified and their influence on associations examined.

Plumage λR_{min} Values in Relation to Visual System

Conventional Analysis of Covariance (ANCOVA) was used to explore visual system differences in λR_{min} while controlling for collection date (as covariate). However, current evidence indicates that the basal sister clades within near-passerines also separate UVS (Trogoniformes) from VS (Bucerotiformes + Piciformes + Coraciiformes; see Table 1 for included families) taxa (Fig. 2), except for one family that lacks carotenoid-based plumage pigments (UVS Momotidae, nested deep within the otherwise VS Coraciiformes; see "Results"). The high degree of phylogenetic structuring of visual systems creates the potential for a corresponding degree of historical non-independence among observations when testing for associations between quantitative aspects of plumage reflectance and of visual systems. Therefore, data were analyzed in two additional ways to account for shared histories.

Analysis of Variances (ANOVAs) with Welch's corrections for unequal variances, with subsequent post-hoc tests were used to assess whether differences among sub-clades within visual system (VS woodpeckers, Asian barbets, toucans, bee-eaters) were less than between clades with different visual systems (the trogon-UVS clade vs each VS clade). In addition, the method of independent contrasts was used to test the significance of plumage differences between VS and UVS taxa in an explicit phylogenetic framework (Garland et al. 1993). The non-passerine system is ideal for this approach because VS and UVS taxa with plumage carotenoids are *de facto* sister clades, so the basal contrast between them embodies all the information on the history of their possible differences. Thus, one can compare the value of the basal contrast to the values of the test distribution of all other contrasts among subsidiary clade members to determine if the sister clade difference (plumage characteristics between visual systems) is significantly larger than among intra-clade differences (plumage characteristics within each

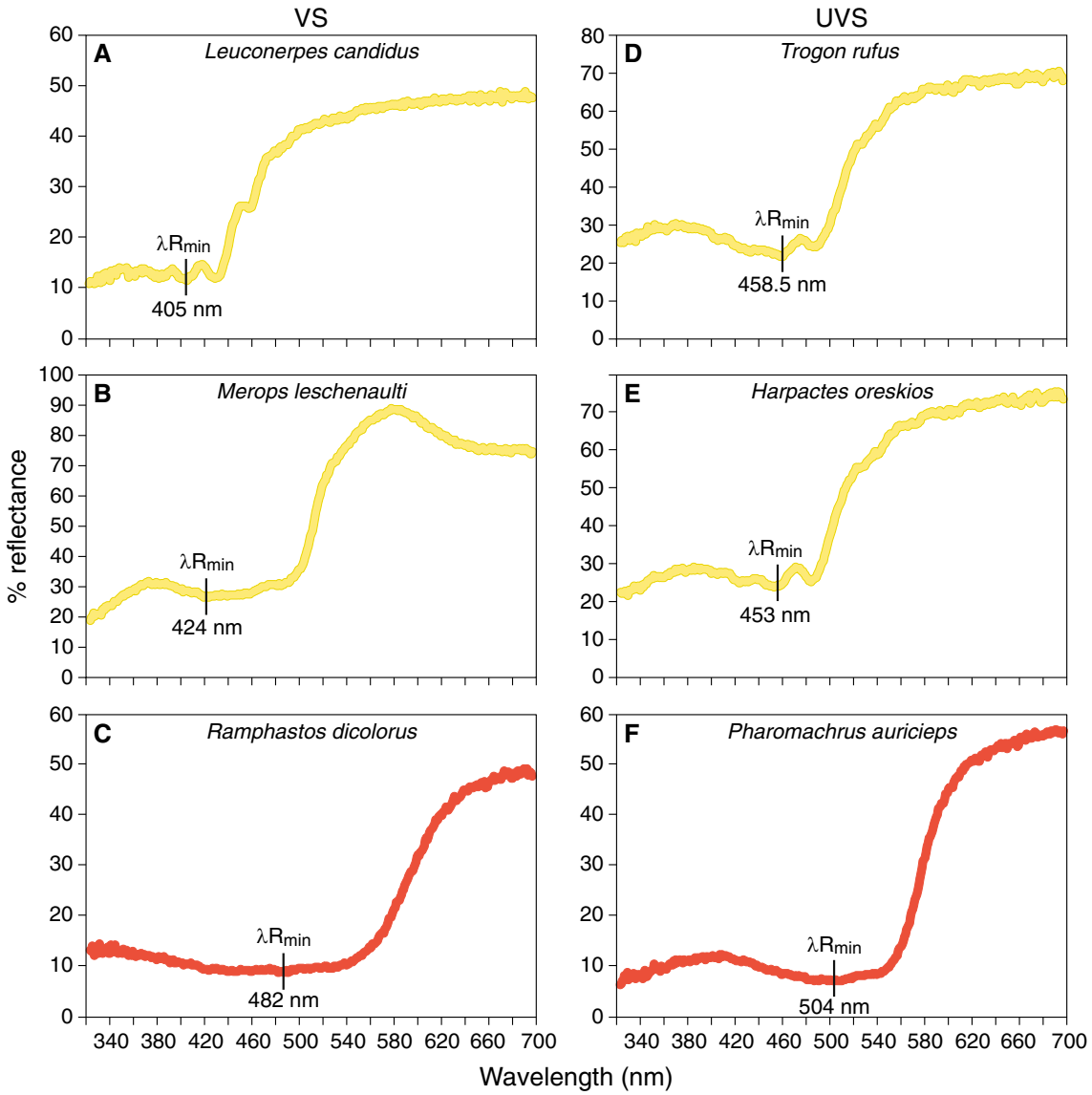

Fig. 1 Representative carotenoid-based plumage reflectance spectra recorded from near-passerine taxa examined in this study. VS taxa: **a** white woodpecker *Leuconerpes candidus* male, yellow belly; **b** chestnut-headed bee-eater *Merops leschenaulti* female, yellow throat; **c** red-breasted toucan *Ramphastos dicolorus* male, red rump. UVS taxa: **d** black-headed trogon *Trogon melanocephalus* female, yellow belly; **e** orange-breasted trogon *Harpactes oreskios* female, yellow–orange belly; **f** golden-headed quetzal *Pharomachrus auriceps* female, red belly. Vertical bars indicate the spectral location and value of each curve's wavelength of reflectance minimum (λR_{min}) for corresponding yellow and red carotenoids in the VS and UVS systems. (Color figure online)

visual system). The appropriate formula for this test was given in Garland et al. (1993), simplified as:

$$t_s = (\text{basal contrast}) / \left[(\text{SD of all contrasts except the basal contrast}) \left[(n+1)/n \right]^{0.5} \right]$$

for all standardized contrasts, where n is the number of contrasts in the test distribution [the sample size minus 2 (the number of all contrasts except the basal contrast)] and t_s is the test statistic based on a t distribution and $n-1$ degrees of freedom (Garland et al. 1993).

The species-level working phylogeny used for these analyses (Fig. 2) was a composite based on genomic phylogenies for higher-level branches and multi-gene phylogenies for lower-level branches (Online Resource 2). As the working phylogeny was based on several different kinds of genetic data and tree building methods, branch lengths for the topology were specified according to two models with

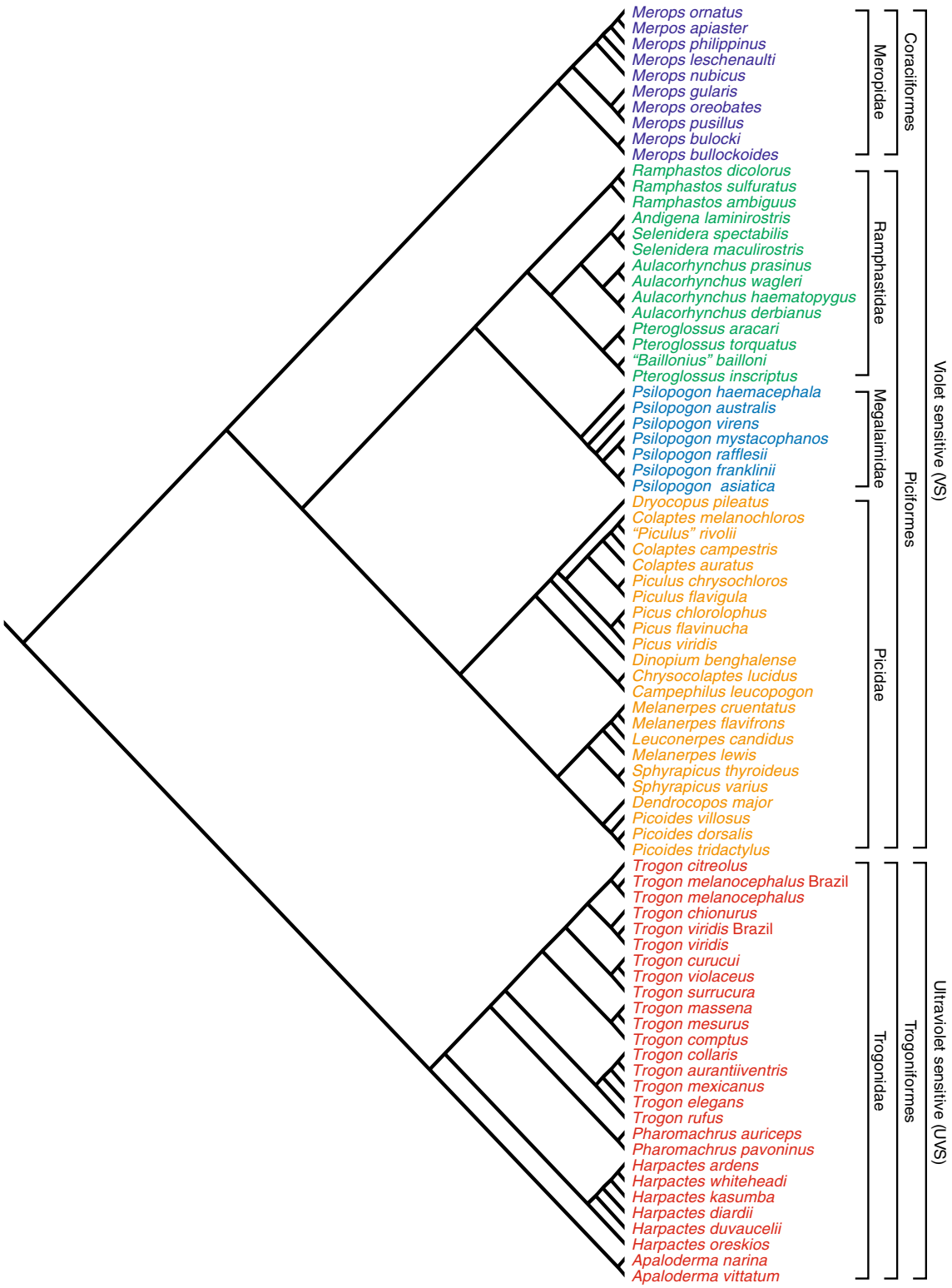

Fig. 2 Species level phylogeny of the eighty-one near-passerines with plumage carotenoids used in the study (see Online Resource 1 for specimen list, and Online Resource 2 for literature sources used for phylogeny construction). The basal split between Trogoniformes (UVS type vision) versus other near-passerines (VS type vision) coincides with a fundamental division between color vision systems. One derived clade nested deep within VS Coraciiformes (Momotidae, not shown) also has the UVS system but lacks plumage carotenoids. Subsidiary families within each order are color coded. Allopatric populations of *Trogon melanocephalus* and *T. viridis* in southeastern Brazil are retained as distinct. Quotes indicate distinctive taxa retained as separate branches even though molecular data indicate that they should be lumped with other genera ["*Baillonius bailloni*" (nested within *Pteroglossus*) and "*Piculus rivolii"* (nested within *Colaptes*)]; less distinctive taxa were lumped (*Leuconotopicus villosus* within *Picoides*). (Color figure online)

different assumptions. All branch lengths were set either equal to one (speciational model) or to arbitrary length (Grafen method). The arbitrary branch lengths were further transformed by setting Grafen's rho to 0.5, which lengthens branches towards the tips of the phylogeny (Grafen 1989; Garland et al. 1993). This manipulation was considered more appropriate than lengthening branches towards the root (rho > 1.0) because basal compression is typical for ancient divergences such as those incorporated in the near-passerine phylogeny. Phylogenies were assembled, and unitary branch lengths were assigned in Mesquite (v3.04, Maddison and Maddison 2015). Subsequent branch length transformations by Grafen's methods, as well as all independent contrasts analyses, were conducted in the PDTREE module of PDAP (Garland et al. 1993).

For the latter analyses, different sub-trees were used for each pigment (yellow, red) and sex (male, female), removing taxa that lacked yellow or red plumages respectively, for that sex. Further sub-trees that omitted extreme points (see "Results") were also used as the basis for analysis of contrasts. As a result, four different tests of basal contrasts were conducted for each sex (yellow or red pigment, with and without outliers). This approach is conservative, as the sub-trees do not take account of non-independence due to transitions between yellow and red pigments. Therefore, evidence for significant differences in basal contrasts should reflect robust plumage differences associated with the two visual systems.

Plumage λR_{min} Alignment in Relation to Visual System

Alignments of λR_{min} with visual system were tested for both wavelength of receptor peak (maximal absorption) and overlap (equal absorption, where sensitivity curves of adjacent cone classes cross) sensitivities. Peak sensitivity wavelengths were based on MSP measurements available in the literature for other birds, reported as cone effective sensitivities ($e\lambda_{max}$, the absorption by visual pigment multiplied by the transmittance of affiliated oil droplet + ocular medium) for a set of 10 VS and 12 UVS species (Hart and Hunt 2007; Coyle et al. 2012; Bleiweiss 2015). Corresponding overlap sensitivity wavelengths (ConeClass1oConeClass2) were calculated for the same species by first generating the visual pigment absorption curve of each receptor class, modifying each curve for affiliated oil droplet (both by standard formulae) and for ocular medium (based on published figures transcribed with GraphClick v3.0.2 and Microsoft®Excel® for Mac v14.5.9) transmittance (see Hart and Hunt 2007, and references therein), and then identifying wavelength of overlap to the nearest nanometer. Spearman's rank correlations were then generated between frequency distributions of plumage pigment and receptor absorption properties at 2 nm resolution across the avian visible spectrum. Peak (conspicuousness) and overlap (discrimination) sensitivity components of the cone array relate to somewhat different aspects of opponent perception (Hurvich 1981), thereby providing insight into tuning strategies based on visual system-specific plumage pigment alignment patterns.

Ancestral Character State Reconstructions

To examine the history of change in signal and receptor characteristics, ancestral character states were reconstructed over the same trees used to carry out the analyses of independent contrasts. The topologies were expanded to include Momotidae (a derived UVS family within the otherwise VS Coraciiformes) and the three nearest outgroups [owls (Strigiformes), eagles (Accipitriformes), New World vultures (Cathartidae)] to provide the most accurate estimates of ancestral character states. Motmots lack plumage carotenoids, thus defining a third plumage state. Similarly, the visual system of owls was scored as "trichromatic" based on their apparent lack of at least the V cone (associated SWS1 opsin visual pigment; Hart and Hunt 2007; Wu et al. 2016) diagnostic of the tetrachromatic (VS or UVS) arrays found amongst remaining taxa. Visual system-specific carotenoids were designated as those with non-overlapping λR_{min} values between visual systems. Ancestral character states were estimated by maximum likelihood as implemented in Mesquite (v3.04; Maddison and Maddison 2015). The likelihood analyses used a phylogeny with equal branch lengths, three discrete character states, and the default Mk1 model (one rate parameter, all character transitions considered equally probable; Maddison and Maddison 2015).

Significance of Associations

The importance of associations was assessed through significance levels and effect sizes. Reported significance levels are one-(e.g. predicted mean differences and alignment patterns) or two-tailed as appropriate. Correlation coefficient effect sizes were assessed directly from the test statistic, for which Cohen's (1988) convention for the interpretation of effect sizes as small (< 0.10), medium (< 0.30), and large (< 0.50) was applied. All analyses were conducted in SAS v9.4 (SAS Institute Inc. 2015). Significant ancestral character state designations were determined from a likelihood decision threshold of T = 2 (7.4 times more support for one character state) (Schluter et al. 1997).

Results

Mean Differences in Plumage λR_{min}

Conventional ANCOVA indicated that λR_{min} means were significantly shorter for yellow and red plumages of VS

compared to UVS taxa (Table 2; Figs. 3, 4). Appreciable effects of collection date were detected only for female red plumage (Table 2; caused by several older specimens of woodpeckers and toucans listed in Online Resource 3). In addition, inspection of box-and-whisker plots of raw data identified a few outliers among yellow (four trogoniforms) and red (one trogoniform, one piciform) plumages (Fig. 3; taxa listed in Online Resource 3). Older and outlier specimens were omitted from parallel analyses to explore analytical robustness (except for the trogon *Harpactes oreskios*, whose distinctness was due to its naturally orange plumage; Fig. 3).

Conventional ANOVA with post-hoc (Tukey's) tests indicated that λR_{min} means differed greatly between UVS trogons and each VS clade, but negligibly among VS clades (Table 3). These distinctions were accentuated when older and outlier specimens (see above) were omitted from the analyses. Within these overall patterns, differences in λR_{min} between VS and UVS taxa were less among females generally, and between UVS trogons vs VS Asian barbets or bee-eaters in particular (perhaps due to under-sampling or unusual spectral features such as the mid-wavelength reflectance peak in yellow bee-eater plumages; Fig. 1).

Analyses of independent contrasts with and without the older and outlier specimens indicated that sister clades/visual systems (UVS Trogoniformes vs VS Piciformes + Coraciiformes; see Fig. 2) differed significantly in λR_{min} of each pigment (yellow or red) class under assumptions of either unitary (Table 4, $P < 0.05$) or Grafen's (Table 5, $P < 0.0005$) branch length transforms. The one exceptional comparison was for female yellow plumages that included the two outlier specimens and assumed unitary branch lengths, which was only marginally non-significant. Thus, a variety of phylogenetically informed analyses of raw data and independent contrasts support a concerted shift in λR_{min} to shorter wavelengths for yellow and red plumage carotenoids in taxa of VS compared to UVS clades.

Alignments of Plumage λR_{min} with Diagnostic V and S Cone Peak Sensitivities

The aggregate distributions of λR_{min} values partitioned by visual system and sex were significantly correlated with $e\lambda_{max}$ for one or both diagnostic cones in both visual systems. Exclusion of older and outlier specimens improved these alignments. However, alignment patterns differed for UVS (Trogoniformes) and VS (Piciformes + Coraciiformes) taxa (Table 6; Fig. 4). Among VS taxa, λR_{min} for yellow to orange plumages were indexed to the corresponding V cone, while λR_{min} for red plumages were indexed to the S cone. The somewhat weaker correlation for yellow and orange than for red plumages paralleled a much greater variability of λR_{min} for yellow plumages, which ranged from approximately 405–460 nm. However, most λR_{min} values recorded for yellow to orange plumages in VS taxa occurred below 435 nm, a wavelength that lies near the upper end of the peak sensitivity range of V cones among VS taxa (Fig. 4).

Among UVS taxa (trogons), λR_{min} values for most yellow to orange plumages ranged from approximately 450–460 nm (Fig. 4), which produced a strong alignment with the corresponding S cone (Table 6; Fig. 4). Trogon λR_{min} values for red plumages occurred at the longest wavelengths of any pigment × visual system class combination, and failed to align with either the corresponding V or S cones (Table 6; Fig. 4).

Alignments of Plumage λR_{min} with Other Cone Sensitivities

The λR_{min} values of yellow and red plumage were uncorrelated with $e\lambda_{max}$ values of the M and L cones of their corresponding visual systems (Table 7). The similar patterns for both visual systems are unsurprising given that M and L cone sensitivities are quite similar between systems (Fig. 4). However, the mismatch is non-trivial because it demonstrates that correlations observed between plumage λR_{min} with cone $e\lambda_{max}$ of the V and S receptors are based on alignments specific to these shorter wavelength-sensitive receptors rather than to more general sensitivities that extend to longer wavelength-sensitive receptors.

Table 2 Differences in wavelength of reflectance minimum (λR_{min}) between visual systems (VS vs UVS) based on ANCOVA, with collection date treated as covariate. Data partitioned by sex and carotenoid pigment type (yellow vs red)

Sex	Male				Female			
Pigment	Yellow		Red		Yellow		Red	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Variates[a]								
Collection date	0.56	0.4596	0.16	0.6902	0.02	0.8858	3.49	0.0692
Visual system	19.60	< 0.0001	61.54	< 0.0001	12.15	0.0011	38.57	< 0.0001

[a]ANCOVA performed in PROC GLM (SAS v9.4); *P* values are based on two-tailed tests

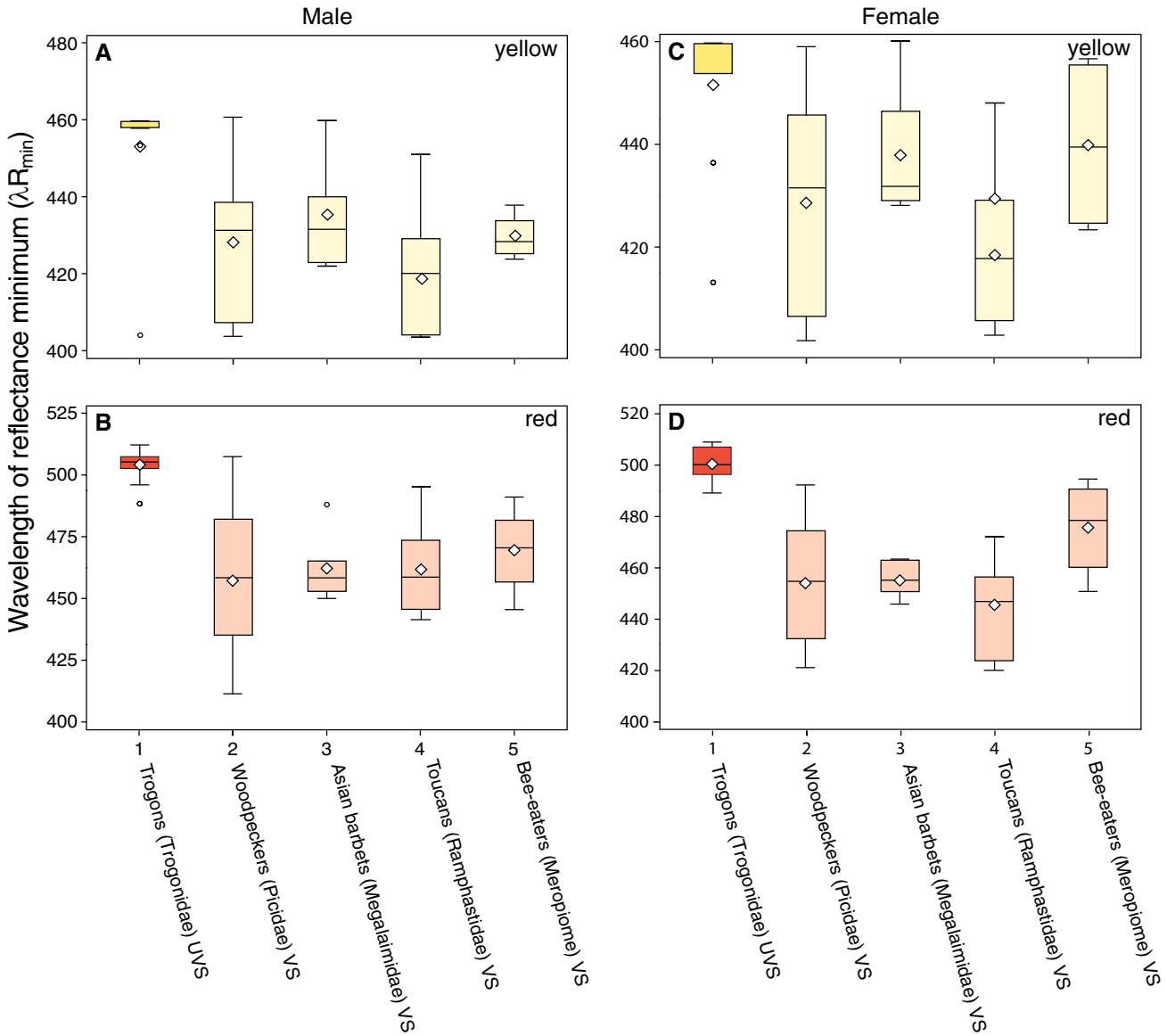

Fig. 3 Box-and-whisker plots of variation in wavelength of reflectance minimum (λR_{min}) as a function of visual system and clade (as indicated). Box length is the 25th to 75th quartiles; diamond is the group mean; horizontal line is the group median; vertical lines issuing from box are group maximum and minimum values within upper and lower fence (default, which is upper and lower limit of third interquartile range). Open circles indicate outlier values (complete list of faded and outlier specimens provided in Online Resource 3); distinctness of the trogon *Harpactes oreskios* was due to its naturally orange plumage (coincident with group mean in plot of yellow male plumage). Plots generated in SAS PROC BOXPLOT (SAS v9.4). (Color figure online)

Consistent with these broader patterns, yellow and red plumage λR_{min} values in the VS system also aligned with their V-S cone overlaps (Table 8). The VS alignments of λR_{min} to VoS were somewhat weaker than to $e\lambda_{max}$ of the component cone classes. However, any alignment in the region of cone overlap should enhance discrimination among the broader range of λR_{min} values among VS compared to UVS affiliated carotenoids (Fig. 4).

Ancestral Character State Reconstructions

Reconstructions for all sex × pigment class combinations indicate that the VS visual system was ancestral for near-passerines (Fig. 5; genus-level reconstructions simplified from species level reconstructions provided in Online Resource 4), and that plumage carotenoids were absent from the common ancestor(s) to near-passerines and their most closely

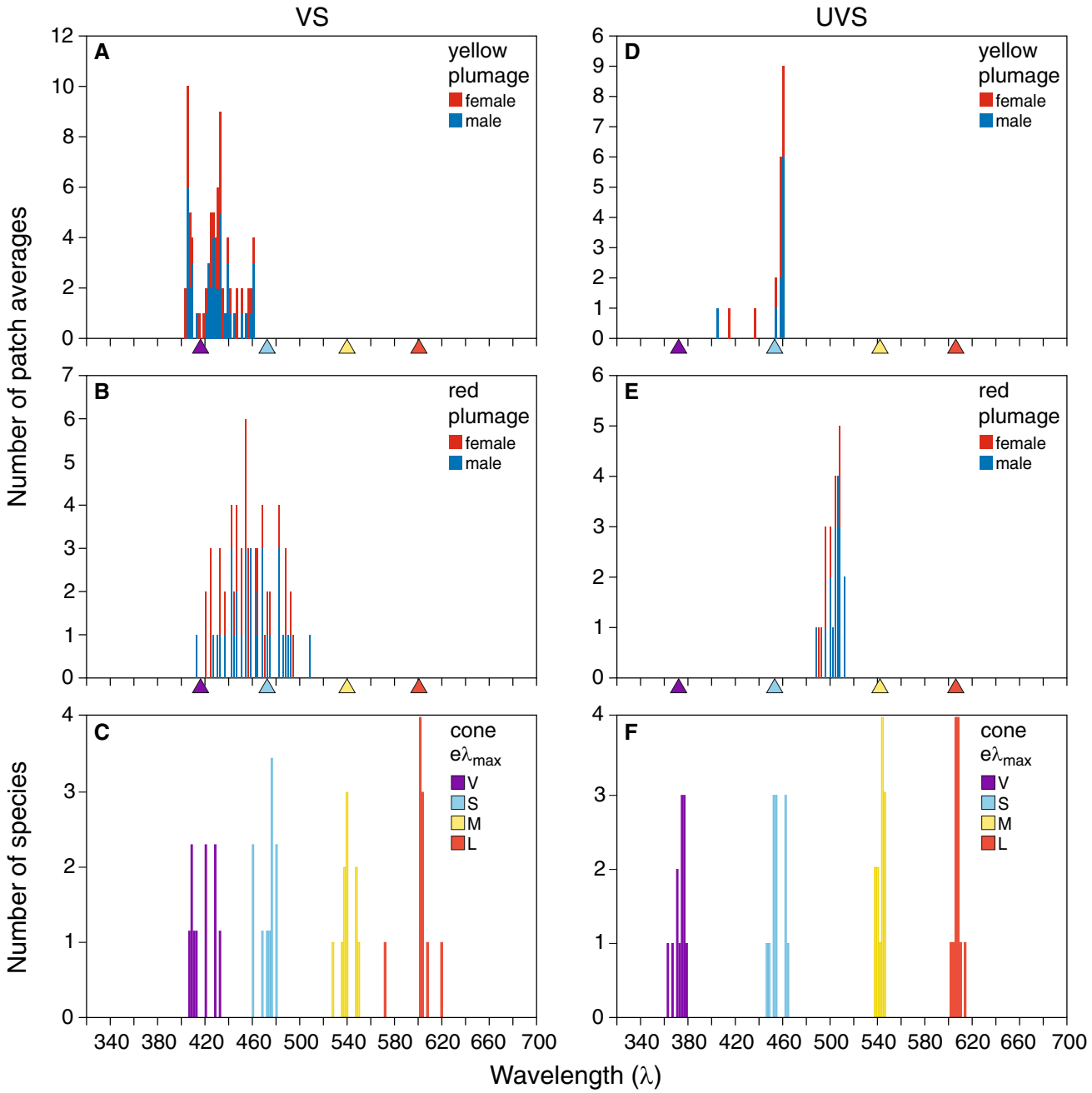

Fig. 4 Spectral distribution for wavelength of reflectance minimum (λR_{min}) among VS (left column) and UVS (right column) near-passerines for yellow (top row) and red (middle row) plumage in relation to receptor maximum effective sensitivity ($e\lambda_{max}$) of all four avian single cones (bottom row). Each observation for λR_{min} is the average of all levels of replication (within and among patches) for that pigment type (yellow or red) of that species, with sexes stacked within panels. Orange pigments (rare) were combined with yellow pigments based on similar fine structures (local absorption bands). Outliers were due to apparent fading of plumage in older specimens (see text); exclusion of outliers further strengthened associations between λR_{min} and $e\lambda_{max}$ for each visual system (see Tables). Color-coded arrowheads along wavelength axis in upper four panels indicate mean sensitivities ($e\lambda_{max}$) for each of the four single cone classes shown in panels c (for VS) and f (for UVS). Cone overlap values are located roughly midway between corresponding pairs of receptor $e\lambda_{max}$ values. (Color figure online)

related outgroup clades (Fig. 5). Thus, VS species apparently matched their signals to their visual system (Fig. 5, a pattern akin to sensory exploitation; Shaw 1995). Current resolution suggests that the UVS visual system evolved in the common ancestor to trogons. However, reconstruction of the steps leading to the UVS tuning pattern was ambiguous

Table 3 Differences in wavelength of reflectance minimum (λR_{min}) between (UVS vs VS) and within (VS) visual systems based on ANOVA. Data partitioned by sex and carotenoid pigment type (yellow vs red)

Sex	Male				Female			
Pigment	Yellow		Red		Yellow		Red	
Sample								
ANOVA[a]	F[f]	P	F	P	F[f]	P	F	P
Clade ID[b]	$\Delta\overline{X}$[f]	P	$\Delta\overline{X}$	P	$\Delta\overline{X}$[f]	P	$\Delta\overline{X}$	P
Complete[c]								
ANOVA 1–5[b]	5.850	0.0035	33.570	< 0.0001	6.830	0.0016	51.200	< 0.0001
1 and 2[d]	24.812	< 0.025	46.777	< 0.025	22.939	< 0.025	46.475	< 0.025
1 and 3	17.712	> 0.100	42.071	< 0.025	13.751	> 0.100	44.786	< 0.025
1 and 4	34.235	< 0.025	42.185	< 0.025	33.256	< 0.025	54.627	< 0.025
1 and 5	23.450	< 0.050	34.742	< 0.025	11.735	> 0.100	24.907	< 0.100
2, 3, 4, 5[e]	16.523	> 0.100*	12.035	> 0.100**	21.521 19.504	< 0.050*** > 0.100****	29.720	< 0.025*****
Minus older/outlier specimens[c]								
ANOVA 1–5[b]	61.940	< 0.0001	33.210	< 0.0001	32.090	< 0.0001	49.940	< 0.0001
1 and 2[d]	30.247	< 0.025	44.090	< 0.025	29.642	< 0.025	41.172	< 0.025
1 and 3	23.147	< 0.050	42.071	< 0.025	20.473	< 0.050	44.786	< 0.025
1 and 4	39.670	< 0.025	42.185	< 0.025	39.978	< 0.025	44.667	< 0.025
1 and 5	28.885	< 0.025	34.742	< 0.025	18.457	< 0.100	24.907	< 0.025
2, 3, 4, 5[e]	16.523	> 0.100*	16.800	> 0.100**	21.521 19.504	< 0.050*** > 0.100****	25.784	< 0.050*****

[a]ANOVA performed in PROC GLM (SAS v9.4); significance of ANOVA based on Welch's correction, which is robust to assumptions for parametric models (unequal variances)

[b]Clade ID: UVS: 1 = trogons (Trogonidae). VS: 2 = woodpeckers (Picidae); 3 = Asian barbets (Megalaimidae); 4 = toucans (Ramphastidae); 5 = bee-eaters (Meropidae)

[c]Complete = all specimens included in analysis; no outliers = outlier specimens identified in box-and-whisker plots (Fig. 3) and Online Resource 3 omitted from analysis

[d]*A posteriori* contrasts performed with Tukey's studentized range test (HSD) in PROC GLM (SAS v9.4); P values are based on one-tailed test

[e]VS Clade IDs for significant *a posteriori* contrasts: *3, 4. **2, 5. ***4, 5. ****3, 4. *****4, 5

[f]ΔX = minimum difference between group means (nm)

due to uncertainty over the ancestral plumage pigment in trogons (Fig. 5).

Discussion

This comparative study provides critical support for earlier evidence that plumage signals express a characteristic integration with receptor sensitivities typical of each avian color vision system, which transcends idiosyncrasies in ecology and evolution. The robustness of this result requires a re-evaluation of the idea that avian color vision systems perform only generalized perceptual tasks (Vorobyev et al. 1998; Lind and Delhey 2015). Minimally, physical and chemical (spectral location of λR_{min}) specificity of plumage pigments in relation to visual system implies a corresponding specialization in signal form. The history of the association does not mandate that the visual system also evolved to match the signals (see ancestral character state reconstructions for the VS system). Nor is signal specialization incompatible with the idea that the color vision systems developed their properties for general-purpose color vision. However, the restriction of plumage pigments to birds pertaining to one or the other visual system based on characteristic pigment alignments to each visual system implies specialized *communication*, which only requires change in either signals or receptors; birds meet this criterion because both color vision systems appear to have evolved specialized signals. Thus, emphasis on the interplay between signals and receptors helps clarifies how specialized and generalized functions can coexist within the same color vision system.

Novel higher-level organizational patterns in avian visual communication systems also emerge from a consideration of the carotenoid-based signal specializations pertaining to each color vision system. Thus, a striking consequence of these signal specializations in near-passerines is that the absorption maxima (λR_{min}) of both their yellow and red plumage carotenoids are relatively blue shifted in VS compared to UVS species even though receptor absorption maxima ($e\lambda_{max}$) are relatively blue shifted in UVS compared to

Table 4 Phylogeny-based statistical test of differences in wavelength of reflectance minimum (λR_{min}) between UVS (Trogoniformes) and VS (Piciformes + Coraciiformes) near-passerines for all sex × carotenoid combinations; analyses based on the basal independent contrast method (Garland et al. 1993) assuming unit branch lengths (see "Materials and Methods")

Tree[b]	Contrasts[a]		Test statistic		One-tailed test	
	Basal	SD (all—basal)	df[c]	t_s[d]	Critical value[e]	*P*
Complete[f]						
Yellow						
Male	27.01	12.214	50	2.206	1.676	< 0.05
Female	19.93	11.792	47	1.655	1.678	0.052
Red						
Male	35.34	14.478	52	2.396	1.675	< 0.05
Female	37.04	13.132	42	2.887	1.682	< 0.05
Minus older/outlier specimens[f]						
Yellow						
Male	28.14	10.889	49	2.559	1.677	< 0.05
Female	20.88	10.973	45	1.862	1.679	< 0.05
Red						
Male	34.71	14.02	51	3.125	1.675	< 0.05
Female	36.23	10.993	37	3.211	1.687	< 0.05

[a]Those species with carotenoid-based plumage coloration in one clade (trogons) are exclusively UVS, while those in the sister clade (woodpeckers, Asian barbets, toucans, bee-eaters) are exclusively VS. Thus, the basal contrast contains all information regarding clade differences in plumage coloration in relation to visual system independent of the phylogeny of subsidiary clade members

[b]Phylogeny-based independent contrasts were calculated within the PDTREE module in PDAP (Garland et al. 1993) based on the phylogeny shown in Fig. 2, using sub-trees for taxa with yellow or red carotenoid-based plumage patches for each sex

[c]The sample size (N) for each comparison depends on the number of taxa for each sex × pigment type (yellow, red carotenoid) sub-tree. Corresponding degrees of freedom were then calculated as N (sample size) − 1 (the number of contrasts) − 1 (the number of contrasts except the basal contrast) − 1, as indicated (see Garland et al. 1991, 1993)

[d]T-test of significant difference between the basal contrast and the sample of all remaining contrasts (see "Materials and Methods", and Garland et al. 1993)

[e]One-tailed tests justified by expectations based on two earlier studies (Bleiweiss 2014, 2015). Critical value to determine conventional significance ($P < 0.05$) based on a t-distribution is provided for each test statistic and associated degrees of freedom

[f]Complete = all specimens included in analysis; no outliers = outlier specimens identified in box-and-whisker plots (Fig. 3) and Online Resource 3 omitted from analysis

VS species (Figs. 1, 3, 4, 6). Mismatched blue shifts between signals and receptors reinforce the idea that change in signal designs can be uncoupled from change, or lack of change, in visual receptor designs. With the caveat that these considerations likely apply mainly to colorful plumages (those with pronounced and discrete absorption bands; see Bleiweiss 2015), alignments of λR_{min} to cone receptor sensitivities provide a surprisingly simple but useful way to investigate if and how plumage pigments are coded to visual system.

Concerted Pigment Absorption Shifts

If alignments between signal λR_{min} and cone sensitivities strongly determine the chemistry of plumage signals, then carotenoids should make excellent colorants because their absorption maxima (Rodriguez-Amaya 2001) fall in the sweet spot for avian cone sensitivities (Hart and Hunt 2007), especially for the V and S cones that most distinguish the VS and UVS visual systems. Although the yellow and red designations for carotenoids are based on human perceptions, these colors correlate with additional variations in chemical formulations and absorption maxima of the corresponding pigment. Compared to yellow carotenoids, red carotenoids typically absorb at longer wavelengths due to their more highly conjugated system of double bonds within the basic carotenoid hydrocarbon skeleton (Rodriguez-Amaya 2001; McGraw 2006). As documented herein, it follows that yellow and red carotenoids should align with cones whose maximal sensitivities are located at shorter and longer wavelengths, respectively. Thus, general aspects of carotenoid tuning in general, and of yellow and red carotenoids in particular, follow from well-known physical properties of carotenoids.

However, concerted shifts in absorption properties of yellow and red carotenoids raise questions about the degree to which tuning patterns are physiologically independent

Table 5 Phylogeny-based statistical test of differences in wavelength of reflectance minimum (λR_{min}) between UVS (Trogoniformes) and VS (Piciformes + Coraciiformes) near-passerines for all sex × carotenoid combinations; analyses based on the basal independent contrast method (Garland et al. 1993) assuming Grafen's branch length transformations (see "Materials and Methods")

Tree[b]	Contrasts[a]		Test statistic		One-tailed test	
	Basal	SD (all—basal)	df[c]	t_s[d]	Critical value[e]	*P*
Complete[f]						
Yellow						
Male	26.69	4.486	49	5.989	1.677	< 0.0005
Female	22.08	4.394	46	4.92	1.679	< 0.0005
Red						
Male	40.7	5.169	51	8.906	1.675	< 0.0005
Female	40.8	5.046	41	8.079	1.683	< 0.0005
Minus older/outlier specimens[f]						
Yellow						
Male	30.84	4.052	48	7.54	1.677	< 0.0005
Female	26.77	4.155	44	6.314	1.680	< 0.0005
Red						
Male	39.46	5.044	50	9.554	1.676	< 0.0005
Female	37.34	4.363	36	8.335	1.688	< 0.0005

[a]Those species with carotenoid-based plumage coloration in one clade (trogons) are exclusively UVS, while those in the sister clade (woodpeckers, Asian barbets, toucans, bee-eaters) are exclusively VS. Thus, the basal contrast contains all information regarding clade differences in plumage coloration in relation to visual system independent of the phylogeny of subsidiary clade members

[b]Phylogeny-based independent contrasts were calculated within the PDTREE module in PDAP (Garland et al. 1993) based on the phylogeny shown in Fig. 2, using sub-trees for taxa with yellow or red carotenoid-based plumage patches for each sex

[c]The sample size (N) for each comparison depends on the number of taxa for each sex × pigment type (yellow, red carotenoid) sub-tree. Corresponding degrees of freedom were then calculated as N (sample size)—1 (the number of contrasts)—1 (the number of contrasts except the basal contrast)—1 (for estimating rho)—1, as indicated (see Garland et al. 1991, 1993)

[d]T test of significant difference between the basal contrast and the sample of all remaining contrasts (see "Materials and Methods", and Garland et al. 1993)

[e]One-tailed tests justified by expectations based on two earlier studies (Bleiweiss 2014, 2015). Critical value to determine conventional significance ($P < 0.05$) based on a t-distribution is provided for each test statistic and associated degrees of freedom

[f]Complete = all specimens included in analysis; no outliers = outlier specimens identified in box-and-whisker plots (Fig. 3) and Online Resource 3 omitted from analysis

from one another. Dietary yellow carotenoids are the typical substrate for endogenous production of red carotenoids (Hill 1996, 2002; Rodriguez-Amaya 2001; McGraw 2006). Thus, parallel shifts in λR_{min} among yellow and red carotenoids could arise if the same endogenous modifications were applied to different dietary precursors used by birds pertaining to each visual system. Nevertheless, birds are known to use the same native yellow precursor pigments to produce divergent pigments (McGraw 2006); these include the strongly blue-shifted yellow carotenoids called picofulvins, whose absorption maxima match those of the yellow carotenoids characteristic of VS taxa (Figs. 3, 4; Stradi et al. 1998). At the very least, therefore, the yellow pigments of VS taxa appear to be tailored downstream to align specifically to that visual system. Unfortunately, the specific chemical identities of yellow plumage carotenoids in trogons are unknown. Nevertheless, yellow carotenoid metabolites in other UVS birds (e.g. canary xanthophylls in passerines) lack the strong blue shifts of picofulvins, but instead, have absorption maxima that more closely match the absorption properties of the native yellow pigments as well as the maximal sensitivities of corresponding S cones (Bleiweiss 2014). Thus, selective modifications of both yellow and red carotenoids probably affiliate carotenoid pigments to visual system.

Characteristic alignment patterns for each visual system are aided by the apparent absence of major sexual dimorphism in avian visual receptor sensitivities (Hart and Hunt 2007; Coyle et al. 2012; but see; Bloch 2014 for dimorphic expression patterns). Conversely, the requirements of signal alignment may help explain why the avian sexes often share plumage pigment chemistries (embodied by λR_{min}) within each (yellow or red) carotenoid class (Hill and McGraw 2006), which does not preclude color dimorphisms by other means (pigment concentration or optical

Table 6 Visual system-specific Spearman's rank correlations (r_s) between shorter wavelength-sensitive (V or S) cone class maximum effective sensitivities ($e\lambda_{max}$) and wavelength of reflectance minimum (λR_{min}) partitioned by pigment type (yellow or red) and sex

Visual System		VS		UVS	
Cone class		V	S	V	S
Complete[a,b]					
Yellow					
Male	r_s	0.50803	0.47190	−0.02852	0.18430
	P	<0.00010	0.51680	0.69530	0.01070
Female	r_s	0.37671	0.02267	−0.03197	0.15938
	P	<0.00010	0.75560	0.66060	0.02760
Red					
Male	r_s	0.07649	0.27503	−0.04076	−0.03764
	P	0.29290	0.00010	0.57560	0.60520
Female	r_s	0.11357	0.28950	−0.04336	−0.04003
	P	0.11770	<0.00010	0.55150	0.58240
Minus older/outlier specimens[a,b]					
Yellow					
Male	r_s	0.50803	0.47190	−0.02463	0.21984
	P	<0.00010	0.51680	0.73520	0.00220
Female	r_s	0.37671	0.02267	−0.02463	0.21984
	P	<0.00010	0.75560	0.73520	0.00220
Red					
Male	r_s	0.00264	0.28199	−0.04076	−0.03764
	P	0.97110	<0.00010	0.57560	0.60520
Female	r_s	0.02798	0.31220	−0.04336	−0.04003
	P	0.70080	<0.00010	0.55150	0.58240

[a]Spearman's rank correlations on raw values allocated into 2 nm bins, used as a compromise between maximum resolution and minimum sparseness of data. Similar analyses conducted on bin sizes of 5 and 10 yielded similar results. Analyses performed in PROC NPAR-1WAY (SAS v9.4); *P* values are based on two-tailed tests

[b]Complete = all specimens included in analysis; no outliers = outlier specimens identified in box-and-whisker plots (Fig. 3) and Online Resource 3 omitted from analysis

Table 7 Visual system-specific Spearman's rank correlations (r_s) between longer wavelength-sensitive (M or L) cone class maximum effective sensitivities ($e\lambda_{max}$) and wavelength of reflectance minimum (λR_{min}) partitioned by pigment type (yellow or red) and sex

Visual system		VS		UVS	
Cone class		M	L	M	L
Complete[a,b]					
Yellow					
Male	r_s	−0.05799	−0.05280	0.02398	−0.02633
	P	0.42550	0.46820	0.74200	0.71760
Female	r_s	−0.06483	−0.05903	0.02688	−0.02952
	P	0.37290	0.41730	0.71210	0.68520
Red					
Male	r_s	−0.07132	−0.06494	−0.03427	−0.03764
	P	0.32680	0.37210	0.63790	0.60520
Female	r_s	−0.06484	−0.05904	−0.03645	−0.04003
	P	0.37280	0.41720	0.61670	0.58240
Minus older/outlier specimens[a,b]					
Yellow					
Male	r_s	−0.05799	−0.05280	−0.02071	−0.02275
	P	0.42550	0.46820	0.77610	0.75480
Female	r_s	−0.06483	−0.05903	−0.02071	−0.02275
	P	0.37290	0.41730	0.77610	0.75480
Red					
Male	r_s	−0.06974	−0.06349	−0.03427	−0.03764
	P	0.33770	0.38290	0.63790	0.60520
Female	r_s	−0.06149	−0.05599	−0.03645	−0.04003
	P	0.39810	0.44170	0.61670	0.58240

[a]Spearman's rank correlations on raw values allocated into 2 nm bins, used as a compromise between maximum resolution and minimum sparseness of data. Similar analyses conducted on bin sizes of 5 and 10 yielded similar results. Analyses performed in PROC NPAR-1WAY (SAS v9.4); *P* values are based on two-tailed tests

[b]Complete = all specimens included in analysis; no outliers = outlier specimens identified in box-and-whisker plots (Fig. 3) and Online Resource 3 omitted from analysis

density, pigment × feather structure interactions, pigment allocations by patch).

General Alignment Patterns

Alignments of plumage carotenoid λR_{min} with visual system-specific cone $e\lambda_{max}$ in near-passerines mirror alignments between plumage and cone absorption properties described among other avian taxa, including for colorful yellow to red carotenoids in UVS passerines (Passeridae within Passeriformes; Bleiweiss 2014), and for colorful green to red porphryins in VS non-passerines (Galliformes, Musophagiformes, Charadriiformes; Bleiweiss 2015). Details of pigment chemistry, lineage identity, and the sequence of events that produced these alignments provide additional details regarding the processes by which such homoplasies arose. Thus in VS taxa, a convergent resemblance is consistent with the similar alignments of λR_{min} to V (for shorter wavelength-absorbing plumage pigments) and S (for longer wavelength-absorbing plumage pigments) cones across chemically, metabolically, and historically independently derived plumage pigments (picofulvin carotenoids, colorful porphyrins) and lineages (near-passerines, other non-passerines). The matching alignments are especially noteworthy given that morphology and ecology vary greatly within and among taxa that express colorful carotenoids (varied arboreal habits; Bleiweiss 2014, herein) and colorful porphyrins (terrestrial, aquatic, and arboreal habits; Bleiweiss 2015). In both cases, however, the matches between signals and receptors appear to have evolved through the fitting of appropriate signal

Table 8 Visual system-specific Spearman's rank correlations (r_s) between wavelength of equal (o = overlap) sensitivity between adjacent cone classes and wavelength of reflectance minimum (λR_{min}) partitioned by pigment type (yellow or red) and sex

Visual system		VS		UVS	
Cone class		VoS	SoM[c]	VoS	SoM[c]
Complete[a,b]					
Yellow					
Male	r_s	0.22877	−0.06733	0.03057	−0.02852
	P	0.00150	0.35470	0.67460	0.69530
Female	r_s	0.35950	−0.07527	0.03427	−0.03197
	P	< 0.00010	0.30070	0.63790	0.66060
Red					
Male	r_s	0.26149	−0.01032	−0.04369	0.09535
	P	0.00030	0.88720	0.54840	0.18950
Female	r_s	0.36509	−0.07528	0.04648	−0.04336
	P	< 0.00010	0.30070	0.52320	0.55150
Minus Older/Outlier Specimens [a,b]					
Yellow					
Male	r_s	0.22877	−0.06733	−0.02641	−0.02463
	P	0.00150	0.35470	0.71690	0.73520
Female	r_s	0.35950	−0.07527	0.02641	−0.02463
	P	< 0.00010	0.30070	0.71690	0.73520
Red					
Male	r_s	0.26805	−0.00726	−0.04369	0.09535
	P	0.00020	0.92060	0.54840	0.18950
Female	r_s	0.39037	−0.07139	−0.04648	−0.04336
	P	< 0.00010	0.32640	0.52320	0.55150

[a]Spearman's rank correlations on raw values allocated into 2 nm bins, used as a compromise between maximum resolution and minimum sparseness of data. Similar analyses conducted on bin sizes of 5 and 10 yielded similar results. Analyses performed in PROC NPAR-1WAY (SAS v9.4); *P* values are based on two-tailed tests

[b]Complete = all specimens included in analysis; no outliers = outlier specimens identified in box-and-whisker plots (Fig. 5) and Online Resource 3 omitted from analysis.

[c]MoL values are out of range for observed λR_{min} values

pigments to pre-existing sensitivities of the VS cone array (Bleiweiss 2015, herein) by an intrinsic process reminiscent of sensory exploitation (Shaw 1995; Rodd et al. 2002), rather than by an extrinsic process related to occupancy of different habitats à la sensory drive (Bleiweiss 2015; Bloch et al. 2015). Thus, both convergence (chemically distinct and independently derived plumage pigments) and parallelism (the same ancestral visual system) play a role in tuning plumage pigments to the VS visual system.

In UVS taxa, alignments of plumage pigment λR_{min} to diagnostic cone sensitivities have been examined only for carotenoids. However, short wavelength-absorbing (yellow to orange) plumage carotenoids align λR_{min} to S cone $e\lambda_{max}$ in each of the distinct UVS lineages [trogons within near-passerines (herein), passerids within passerines (Bleiweiss 2014)] examined so far. Beyond this overall resemblance, subtle differences between the plumage-based carotenoid pigments of these two UVS lineages suggest that this resemblance also embodies some homoplastic features. Thus, the three-fingered absorption band structures typical of yellow and orange carotenoids are more muted and pointed in the near-passerine trogons (Fig. 1) than in the passerid passerines (Bleiweiss 2008, 2014). Moreover, yellow plumages in trogons absorb maximally at slightly longer wavelengths (λR_{min} = 458–460 nm) than do most yellow plumages in passerines (λR_{min} = 450–454 nm). Perhaps most surprisingly, orange plumage in trogons (i.e. *Harpactes oreskios*) absorb maximally at slightly shorter wavelengths (452 nm) than their yellow plumages, whereas the opposite relationship occurs in passerines (Bleiweiss 2008). Trogons are also unusual in the dramatic tendency of their plumage carotenoids to fade, and in the laxness of their feathers (Johnsgard 2000). These distinctive properties suggest that trogons differ from passerids in their plumage pigment chemistry, in how these pigments interact with the keratin matrix of the feather, or both. However, further study is needed before the nature of these more subtle differences can be fully characterized and related to processes of homoplastic resemblance in the absorbance properties of plumage carotenoids in UVS birds.

Other aspects of the alignment patterns also are consistent despite the different signal and receptor pigments and lineages involved. Thus, VS taxa align short and long wavelength-absorbing plumage pigments in tandem to the V and S cones, whereas UVS taxa align only short-wavelength-absorbing pigments to the S cone. Moreover, the alignments of λR_{min} to cone classes within visual systems are consistently tighter for shorter (yellow, green) compared to longer (red) wavelength-absorbing pigments. Inherent levels of pigment-specific variability, or nanometer-scale alignment tolerances, or both may account for these surprising similarities.

Carotenoid Alignment Patterns

Alignments of plumage carotenoids with the avian visual system is consistent with much other evidence that these pigments play an important role in avian communication (McGraw 2006), including in near-passerines (Noble 1936; Leniowski and Wegrzyn 2013; Musgrove and Wiebe 2016). However, alignments specific to certain carotenoids and color vision systems provide further insights into these well-studied systems. For example, differences in plumage carotenoid λR_{min} between VS and UVS birds imply corresponding differences in carotenoid-based communication because the absorption properties of a pigment embody its physical and chemical properties. For example, the

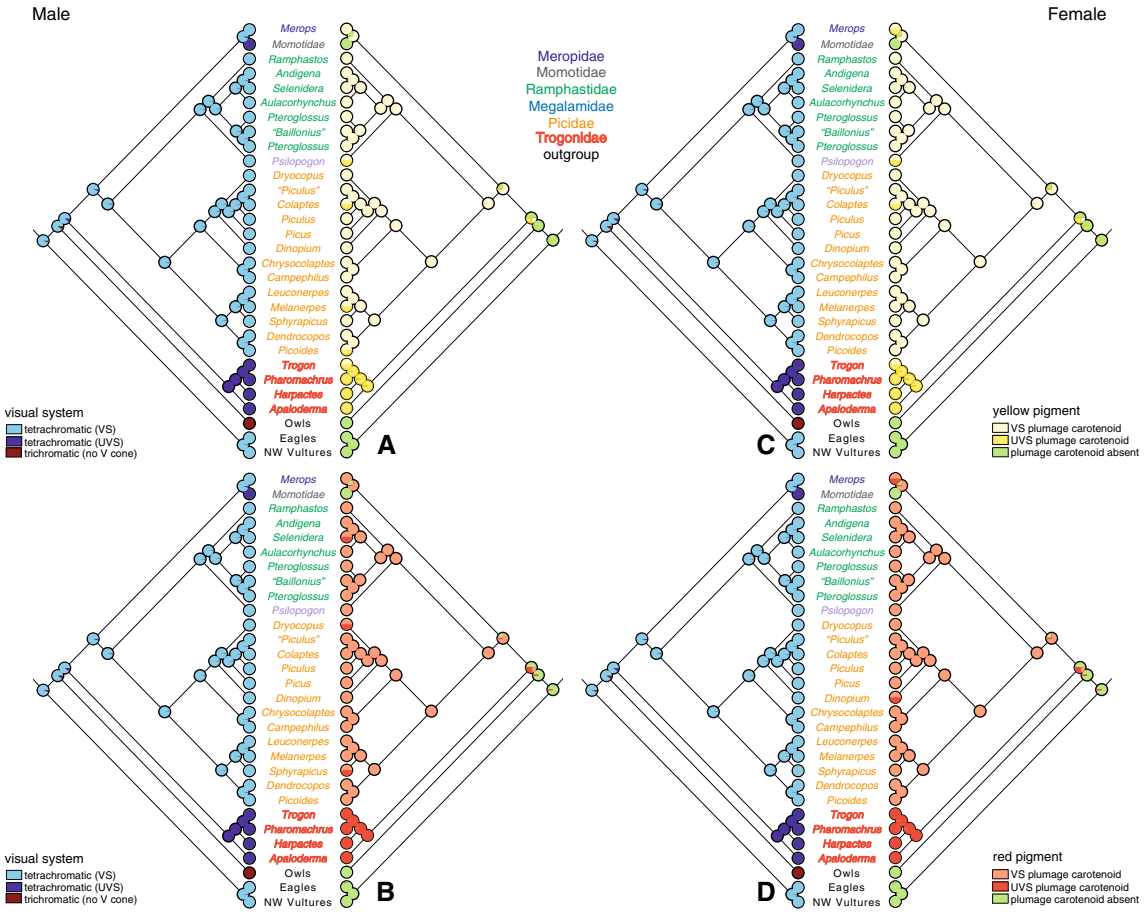

Fig. 5 Genus-level maximum likelihood ancestral character state reconstructions for all four sex × pigment combinations among near-passerines analyzed (Fig. 2); species-level reconstructions for plumage pigments are provided in Online Resource 4. To improve estimates of ancestral character states, the phylogeny includes UVS motmots (Momotidae, Coraciiformes) and three nearest outgroups [owls (Strigiformes), eagles (Accipitriformes), New World vultures (Cathartidae)] with known visual systems. Owls are coded as trichromatic due to their ubiquitous loss of the V cone, but members of Tytonidae have also lost functional MWS pigments (Wu et al. 2016). Family level ingroup clades are color coded as in Fig. 2. Reconstructions (see "Materials and Methods" for details) based on the default Mk1 model implemented in Mesquite v3.04 (Maddison and Maddison 2015) indicated that the VS visual system preceded the appearance of VS-specific plumage carotenoids, but could not resolve timing for the appearance of UVS specific plumage carotenoids (see "Results " for details). Quotes indicate distinctive taxa shown by molecular data to be nested within other genera. Complex taxonomies among *Colaptes* and *Melanerpes* woodpeckers (see Fig. 2) were simplified compared to their treatment in the full phylogeny, but the results and their interpretation remained unaffected. Near-passerines with plumage pigments absorbing at wavelengths more typical of the other visual system (bicolored pie chart for genus) are as follows: male yellow: *Trogon chionurus, Colaptes auratus, Psilopogon rafflesii, Melanerpes flavifrons, Picoides tridactylus*; male red: *Merops nubicus, Dryocopus pileatus, Sphyrapicus varius, Selenidera spectabilis*; female yellow: *Trogon viridis, Trogon chionurus, Psilopogon australis, Colaptes auratus, Merops pusillus, Merops ornatus*; female red: *Merops nubicus, Dinopium benghalense*. (Color figure online)

characteristic absorption maxima of the blue shifted picofulvin yellow carotenoids (around 405–430 nm; Figs. 3, 4) align to the V cone sensitivity of the VS system, and these pigments occur only in birds (selected near-passerines, herein; Eurylamidae among passerines, Prum et al. 2014) likely to be VS. Conversely, the characteristic absorption maxima of canary xanthophyll yellow carotenoids (445–450 nm) align to the S cone of the UVS system, and these pigments appear to be plumage colorants mainly among birds with that visual system (Fox 1976; McGraw 2006; Bleiweiss 2014). VS birds may produce picofulvins (McGraw 2006; Stradi et al. 1998) and colorful porphyrins (Bleiweiss 2015) through their own specialized metabolic pathways. However, both VS and UVS birds can produce canary xanthophylls (Fox 1976). Therefore, regulation of transport and deposition may be involved in other cases of plumage pigment selectivity (McGraw et al. 2003; Hudon et al. 2015). Under both scenarios for proximate origin of plumage pigments, alignments with the visual system provide a plausible foundation for understanding the ultimate origins of the form and distribution of colorful plumage pigment diversity among birds.

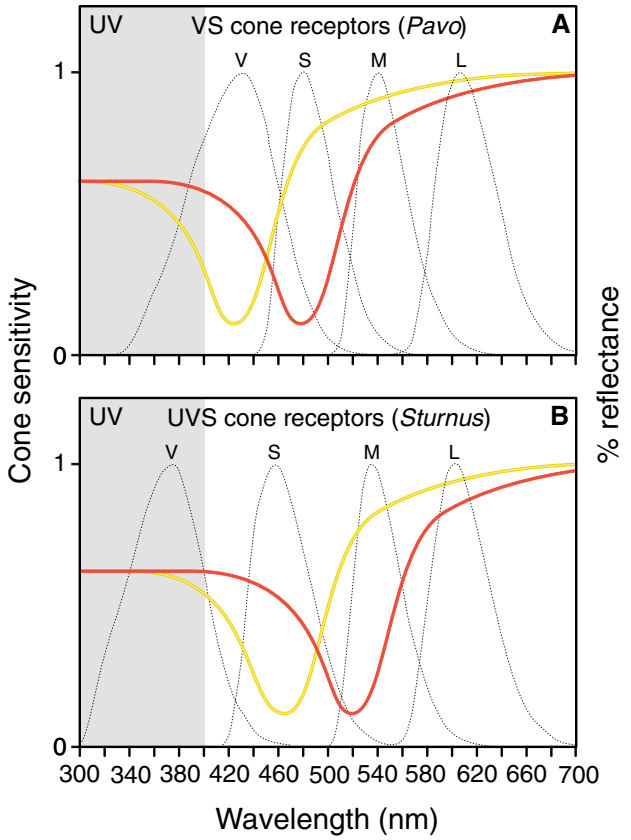

Fig. 6 Generalized alignments of yellow versus red plumage carotenoid reflectance patterns (color-coded lines) in relation to corresponding MSP-based, single-cone spectral sensitivities (grey lines) for each (VS, UVS) avian color vision system. Key aspects of alignment relate the wavelength of reflectance minimum (λR_{min}) to the single-cone sensitivity maximum ($e\lambda_{max}$), as described in text. In near-passerines, each visual communication system expresses concerted shifts in pigment absorption, but these shifts are in opposite directions for signals (λR_{min} blue shifted in VS taxa) and for receptors ($e\lambda_{max}$ blue shifted in UVS taxa). Shift differences are associated with alignment pairings of signals to receptors that are diagnostic of each visual system, encompassing both yellow (with V) and red (with S) plumage carotenoids in the VS system but only yellow (with S) plumage carotenoids in the UVS system. Cone spectral sensitivities are from species (VS non-passerine, UVS passerine) whose cone properties have been measured directly with MSP. Shaded regions correspond to ultraviolet (UV) wavelengths visible to birds but not normal humans. (Color figure online)

In addition, the signal content contained in λR_{min} is apparently tuned in different ways to each visual system. For yellow plumage carotenoids in VS near-passerines, endogenously derived picofulvins align their λR_{min} with the V cone peaks (405–430 nm) whereas native hydroxycarotenoids align their λR_{min} to the V and S cone overlaps (445–455 nm). As far as is known for UVS passerids, both endogenously metabolized (canary xanthophylls) and native (hydroxy−) yellow carotenoids align with the S cone peak (Bleiweiss 2014), though this pattern needs to be clarified for trogons (herein). Compared to yellow carotenoids, red carotenoids may have a stronger bias towards endogenous production overall (Hill 1996; McGraw 2006). In addition, red carotenoids align λR_{min} to the S cone in the VS system but to no cone in the UVS system. These various distinctions suggest that the two avian visual systems handle visual information differently both within and between yellow and red carotenoid classes. Therefore, visual system-specific alignments of cone peaks (conspicuousness) versus overlaps (discrimination) in relation to opponent perceptions of color (Hurvich 1981) could affect how birds in the two visual systems communicate with carotenoid pigments.

Notably, signal tuning differences between birds with VS and UVS visual systems may be enhanced by patterns of visual opsin expression, even if opsin wavelength sensitivities have not changed to match signal characteristics (see General Alignment Patterns). In particular, SWS2 opsins of the S cone are the most strongly expressed single cone opsins in UVS birds that have elaborated plumage carotenoids (parulid warblers, Bloch 2014; Bloch et al. 2015). Thus, opsin expression and plumage tuning (λR_{min} of yellow carotenoids aligned to the S cone) patterns share some remarkable similarities in UVS birds. Indeed, these considerations provide a basis for describing the avian UVS system as "S cone dominant". Extrapolating this pattern to VS species predicts a boost in expression for the SWS1 opsins of V cones and SWS2 opsins of S cones, with a possible bias towards SWS1 (Tables 6, 8). A suite of neural, chemical, and genetic components therefore appears to co-vary with the VS vs UVS distinction, which seem likely to influence how each system acquires and processes visual information. Evidence that avian color vision systems have evolved distinctive visual signals should therefore expand consideration from whether one or the other form of color vision is quantitatively superior to whether the two systems differ qualitatively in how they communicate with chromatic information.

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Compliance with Ethical Standards

Conflict of interest The author declares that he has no conflict of interest.

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