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RESEARCH ARTICLE

Extrinsic Versus Intrinsic Control of Avian Communication Based on Colorful Plumage Porphyrins

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Abstract Studies of avian visual communication are often approached from the perspective of adaptation-based hypotheses couched in an ecological framework. Despite their exceptional ecological diversity, however, birds express relatively few pigment categories in their visual signals or receptors. The mismatch between ecologic and pigment diversity suggests the operation of non-ecological constraints on avian visual communication. Colorful plumage porphyrins (turacoverdin and turacin) were examined to determine if both signal and receptor pigment absorption patterns co-vary with ecology, if only plumage pigment absorption varies with ecology, or if plumage and receptor pigment absorption are tied to each other's physicochemical, physiological, and phylogenetic characteristics rather than to ecology. Physicochemical constraints on signal form were suggested by the persistence of the plumage pigments' diagnostic spectral structure across lineages despite dramatic ecological differences. Physiological constraints on communication were suggested by the occurrence of colorful porphyrins only in birds with violet-sensitive (VS) vision, whose receptor sensitivities aligned to colorful porphyrin spectral structure much more strongly than did receptors of alternative visual systems. Phylogenetic constraints on these associations were evidenced by restriction of colorful plumage porphyrins to just a few lineages, all non-passerines (galliforms, musophagiforms, and charadriiforms). Synthesis of these patterns indicated that VS visual systems always evolved prior to colorful plumage porphyrins, suggesting a sensory bias for plumage pigments based on signal-receptor alignment. Patterns for colorful porphyrins and violet-sensitive systems reinforce the functional coupling between signal and receptor pigments observed for carotenoid plumage pigments in ultraviolet-sensitive birds, but the pairings differ in details of their alignments.

Keywords Bird · Evolution · Opponent processing · Pigment · Signal · Turacoverdin · Turacin

Introduction

Visual communication systems often demonstrate strong and interdependent links to properties of the external signaling environment (Endler 1992; Endler and Basolo 1998; Proctor 1992; Boughman 2001; Rodd et al. 2002; Carleton et al. 2005; Garcia and Ramirez 2005; Seehausen et al. 2008). However, certain physical materials and processes also have the potential to influence and constrain the form and direction of evolution in communication systems (Kingsolver and Watt 1983; Auld et al. 2010). In particular, both visual signals and receptors derive many of their salient properties from their constituent pigments, which are materials that demonstrate wavelength-specific absorption of light (Hill and McGraw 2006). Although an extraordinary diversity of pigments exists in nature (Rodriguez-Amaya 2001; Sutthiwong and Dufossé 2014), many fewer pigments have absorption bands in the range of wavelengths that make them useful as components of visual signals (McGraw 2006b) or receptors (Hart and Hunt

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2007). Moreover, the chemistry of each pigment dictates exactly which wavelengths will be absorbed, imposing a characteristic absorption band signature for any pigment class despite other physical (e.g. amount and thickness of colorant, composition of the matrix) or ecological (diet, habitat, light environment) changes. These considerations also extend to interactions among pigments. In this regard, absorption by a visual receptor depends strongly not just on the chromophore pigment, but also on the chemical identity of amino acid residues at specific locations in the light-sensitive opsin protein that binds the chromophore (Bowmaker 2008; Hart and Hunt 2007; Carvalho et al. 2007). This interdependence highlights that mutations needed to adjust the amount and direction of change in receptor sensitivity may not always be available.

A consideration of these physical and biological constraints may be of particular importance in groups whose visual communication systems appear far less diverse than their ecological habits. Birds are famous for their extraordinary diversity of colors and ecologies, but their visual communication systems appear to be based on a much more limited range of signal and receptor properties than observed in comparably diverse groups (Brush 1990; Hill and McGraw 2006). Surprisingly, only a dozen or so distinct chemical classes of pigment are responsible for avian integumentary colors (Hill and McGraw 2006; LaFountain et al. 2010; Thomas et al. 2013). Furthermore, birds have lost the ability present in many other metazoans to synthesize important groups of these compounds (e.g. carotenoids) *de novo*, thereby constraining birds to acquire them through their diet (McGraw 2006b). Most diurnal terrestrial birds also share tetrachromatic (four single cone) color vision that encompasses variation divided into just a few subsystems that are more (ultraviolet sensitive, UVS) or less (violet sensitive, VS) sensitive to shorter wavelengths (Cuthill et al. 2000; Hart and Hunt 2007; Ödeen et al. 2011b, Ödeen and Håstad 2013). Such conservatism in pigments contrasts strongly with patterns in other organism with complex color vision. Thus, butterflies living in the same terrestrial environments as birds express much more diversity in signal (Morehouse et al. 2007) and in cone photoreceptor (Briscoe 2008; Frentiu and Briscoe 2008) pigments. Ecological correlates to visual communication are even more pronounced among fish-like vertebrates, which have undergone extensive speciation and ecological diversification in aquatic environments (Levine and MacNichol 1979; Lythgoe 1979; Cummings 2007; Carleton 2009; Sabbah et al. 2010).

One possible explanation for low diversity in avian communication components is simply that the attendant variation has been underestimated. Newly discovered pigments (McGraw et al. 2007; LaFountain et al. 2010; Thomas et al. 2013) and physical processes (Mendes-Pinto et al. 2012) have quantitatively expanded the known avian color palette to some degree. Moreover, direct measures of avian singe-cone spectral sensitivity through microspectrophotometry (MSP) has been conducted on only a few dozen of the more than 10,000 living species of birds, leading several authors to suggest that variation in receptor sensitivity has been greatly under-sampled (Carvalho et al. 2007; Hart and Hunt 2007; Beason and Loew 2008; Bowmaker 2008; Frentiu and Briscoe 2008; Yokoyama et al. 2008; Hunt et al. 2009; Renoult et al. 2011). Consistent with this view, the tetrachromatic color vision of most diurnal birds appears capable of adjusting to different environmental conditions by modulating the sensitivities of each receptor through filtering effects by the ocular media (Cuthill et al. 2000; Hart and Hunt 2007; Bowmaker 2008; Lind et al. 2014) and the carotenoid pigments present in the oil droplets that cap the three longer wavelength-sensitive cone classes (Partridge 1989; Hart and Vorobyev 2005). Sequence data now available for (the opsin component of) visual pigments from hundreds of additional avian species also indicates a more complex and labile phylogenetic distribution of avian color vision systems (Ödeen and Håstad 2013) than previously supposed (Cuthill et al. 2000; Ödeen and Håstad 2003). Nevertheless, the distinction between violet (VS) and ultraviolet (UVS) vision (Ödeen et al. 2011b, Ödeen and Håstad 2013), and the predominance of one or the other condition in all (Ödeen et al. 2011a) but a few (Ödeen et al. 2011b) avian families remains a basic pattern. More direct measures of color vision capacity via MSP studies also indicate relatively conserved variation in color vision within clades whose species vary greatly in plumage coloration and visual habitat (Coyle et al. 2012).

Another possibility is that the conservatism in avian visual systems is real but that ecological differences favor signal divergence even without major changes in the sensory system (Marchetti 1993; Coyle et al. 2012). It is reasonable to expect that selection will favor signals whose properties are tailored to environmental characteristics such as habitat noise, illumination, transmission, and background properties (Endler 1992; Endler and Mielke 2005; Doucet et al. 2007). On the other hand, birds may place a premium on those few general-purpose color vision systems that function best across different environments (Vorobyev et al. 1998; Hart and Hunt 2007). This interpretation is consistent with evidence that birds have visual systems that confer excellent color constancy (Goldsmith and Butler 2003; Lind et al. 2013), which means that variation in ambient and background visual properties have less impact on signal effectiveness (although the response may be non-linear at UV wavelengths; Chavez et al. 2014). Furthermore, a limited variety of visual systems could be reinforced by the restriction of avian breeding to terrestrial

habitats, which comprise just a few basic illumination profiles (Endler 1993; Fleishman et al. 1997; Chiao et al. 2000) except for the most extreme settings (see Leal and Fleishman 2004). By comparison, exceptional diversity in color vision systems is more typical of groups that are aquatic, a medium whose absorptive properties have a higher potential than air to influence variation in habitat light (Lythgoe 1979; Lythgoe and Partridge 1989; Chiao et al. 2000).

A third possibility is that both signal and receptor pigment absorption patterns vary much less than do ecological habits. This proposal seems counterintuitive because avian visual signals *appear* to be so extraordinarily varied. Upon closer inspection of some avian clades, however, signal and receptor pigments used in communication appear constrained at several levels. For example, passerid (Passerida) passeriforms have only UVS type visual systems despite the group's remarkable adaptive radiation (Ödeen et al. 2011b). Given the mismatch between ecologic and receptor diversity, the strong alignment between the maximum sensitivities of the passerid tetrachromatic array and the most characteristic and prominent features of carotenoid-based plumage spectra (Bleiweiss 2005, 2007, 2008) is noteworthy. Indeed, different cone combinations of the same tetrachromatic array serve to index the major absorption and reflectance bands of both chemically distinct (yellow and red) classes of passerid plumage carotenoids (Bleiweiss 2014). Evidence that alignments are stronger for the diagnostic cones of the passerid UVS as compared to other (VS) visual systems reinforces the causal basis of the intra-system patterns. Thus, the passerid UVS-carotenoid communication system appears to encompass physicochemical, physiological, and phylogenetic constraints in addition to ones connected with the well-known inability of these birds to synthesize carotenoids *de novo* (McGraw 2006b)

To further document and understand such patterns in relation to extrinsic and intrinsic controls on avian communication, I examined signal and receptor properties associated with the use of colorful porphyrin pigments (Church 1870, 1892, 1913; McGraw 2006a). These novel colorants produce vibrant, human-visible green (turacoverdin) and red (turacin) plumages superficially similar to those produced by several other pigments or structural colors (McGraw 2006b). However, colorful porphyrins share a unique chemistry based on the chelation of a copper atom within a heterocyclic tetrapyrrole. The resulting compound produces a diagnostic series of absorption bands located at wavelengths quantitatively distinct even from those of other chemical classes of pigments (melanins, carotenoids, pterins) with a similar subjective appearance (Dyke 1992; McGraw 2006a, b; Toral et al. 2008). Colorful plumage porphyrins were long thought to be unique to turacos (Musophagiformes), and for that reason were speculated to evolve in associated with some of the characteristic habits of these birds, including their tropical rainforest haunts and strongly herbivorous diets (Moreau 1958; McGraw 2006a, b). More recently, however, some of the same colorful plumage porphyrins were discovered in pheasants (Galliformes) and shorebirds (Charadriiformes), whose life styles differ greatly from each other and from those of turacos (Dyke 1992).

The complex evolution of colorful porphyrins provides a suitable comparative framework for testing each of the three scenarios outlined above for the evolution of avian visual communication pigments in signals and receptors. These three hypotheses can be ordered with respect to their emphasis on extrinsic versus intrinsic effects on plumage pigmentation as entirely extrinsic (both pigments and visual systems co-vary with ecology), as partly extrinsic (only pigments co-vary with ecology), or as entirely intrinsic (neither pigments nor visual systems co-vary with ecology, but only with each other's evolutionary characteristics). I report that development of colorful plumage porphyrins appears strongly tied to physicochemical, physiological, and phylogenetic considerations. These patterns suggest that intrinsic properties of visual signals and receptors are an important consideration for understanding the evolution of avian visual communication systems.

Materials and Methods

Plumages and Taxa Examined

This study focused on the copper-chelating colorful porphyrins (McGraw 2006a) because "duller" forms (With 1973; Toral et al. 2008; Negro et al. 2009; Weidensaul et al. 2011) lack local minima and maxima suitable for alignment, and fade rapidly with feather age (Weidensaul et al. 2011). All genera and families known to display colorful porphyrins were sampled (Table 1; Dyke 1992; Turner 1997; Toral et al. 2008), including galliforms (*Rollulus*, *Ithaginis*), musophagiforms (various genera and species), and charadriiforms (*Jacana*) except for two depauperate turaco genera where this coloration is poorly developed (although published spectra for one of them, *Corythaeola cristata*, are virtually identical to those of confamilial taxa; Dyke 1992). Superficially similar (to turacin) plumages from the two male galliforms also were analyzed (Table 1). One putative adult per sex was scanned for each of ten turaco species, and up to three putative adults per sex were scanned for each of the remaining taxa except *Ithaginis*, where only males display colorful plumage. Details on the 14 species and 36 specimens (males: $\overline{X} = 1.3571$

Table 1 Plumages and pigments present in taxa examined

Taxon[d]		Plumage	Pigment	
		Human-visible color[a] Green/red	Class[b] Green/red	Location[c] Green/red
Galliformes (Pheasants)				
Crested wood-partridge	*Rollulus roulroul*	+/+	P/C?	B/B
Blood pheasant	*Ithaginis cruentus*	+/+	P/C	B/B
Musophagiformes (Turacos)				
Livingstone's Turaco	*Tauraco livingstonii*	+/+	P/P	B/W
Schalow's Turaco	*Tauraco schalowi*	+/+	P/P	B/W
Black-billed Turaco	*Tauraco schuetti*	+/+	P/P	B/W
White-crested Turaco	*Tauraco leucolophus*	+/+	P/P	B/W
Fischer's Turaco	*Tauraco fischeri*	+/+	P/P	B/W,B
Hartlaub's Turaco	*Tauraco hartlaubi*	+/+	P/P	B/W
Purple-crested Turaco	*Gallirex porphyreolophus*	+/+	P/P	B/W
Ruwenzori Turaco	*Ruwenzorornis johnstoni*	+/+	P/P	B/W,B
Violet Turaco	*Musophaga violacea*	−/+	P?/P	−/W,B
Ross's Turaco	*Musophaga rossae*	−/+	P?/P	−/W,B
Charadriiformes (Shorebirds)				
Wattled Jacana	*Jacana jacana*	+/−	P/R	W,B?/S
Northern Jacana	*Jacana spinosa*	+/−	P/Y	W,B?/S

[a] +visible; −not visible or indistinct

[b] P = porphyrin (green = turacoverdin; red = turacin); C = red carotenoid; R = bare red skin, Y = bare yellow skin

[c] B = body (contour) feathers; W = wing (primary flight) feathers; S = bare skin

[d] ? = Uncertain whether red crest of male *Rollulus* contains carotenoids, or dark body plumages of *Musophaga* and *Jacana* contain turacoverdin

individuals, SD = 0.6333; females: $\overline{X} = 1.2143$ individuals, SD = 0.6993) measured are provided in Online Resource Table 1.

Characterization of Porphyrin Spectral Diversity

Methods of data generation and processing followed earlier approaches (Bleiweiss 2005, 2007, 2008, 2014; see also Andersson and Prager 2006). Briefly, the same set of plumage subdivisions (hind crown added to ten prior patches; Bleiweiss 2014) was designated for all species, and spectra were recorded from all human-visible green or red patches (up to six). All spectra were obtained with a WP230-1-XRS fiber optic probe attached by a bifurcated cable to an Ocean Optics USB 2000 + spectrometer and to a PX-2 pulsed xenon light source. 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 (see also Andersson and Prager 2006). A Spectralon® WS-1-SL (Ocean Optics) diffuse reflectance white standard was scanned prior to obtaining all spectra from each specimen, and patches for each specimen were measured in random order. The probe tip was repositioned prior to obtaining replicate spectra from each patch. All spectra were analyzed over the avian visible range (320–700 nm), which includes the wavelengths visible to humans (400–700 nm).

Resolutions of the various reflectance minima (distinct absorption maxima) were of particular interest because these features appeared to provide important alignment features in carotenoids. Over the avian visible range, both colorful porphyrins have three reflectance minima (absorption maxima), whose prominence and spectral locations differ greatly within and between pigments (Dyke 1992; herein). In accordance with standard chemical terminology, these minima were numbered from deepest (λR_{minI}) to shallowest (λR_{minIII}), independent of their spectral location (Fig. 1). Thus, λR_{minI} for turacoverdin occurred at relatively short visible wavelengths (~410 nm) whereas λR_{minI} for turacin occurred at much longer wavelengths (~580 nm). This nomenclature was preferred to one numbering the minima based on spectral location because even the absorption bands at the longest or shortest wavelength occurred at different spectral locations across pigments, which also creates uncertainty regarding the homology of bands across pigments. In

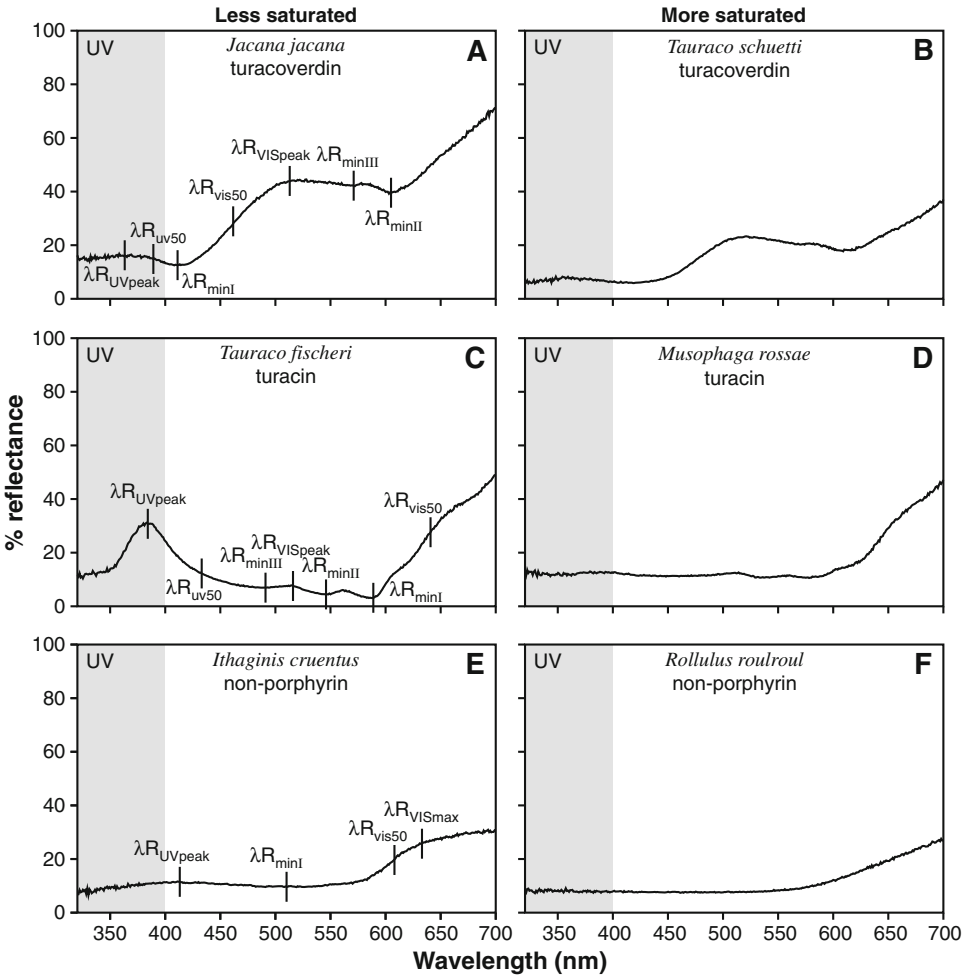

Fig. 1 Representative reflectance spectra obtained for unsaturated (*left*) and saturated (*right*) turacoverdin, turacin, and probable non-porphyrin (β-keto-carotenoid in *Ithaginis*) pigments. *Vertical bars* mark characteristic plumage reflectance features analyzed (see "Materials and methods" for definitions). Species common names, human visible color, and patch location are: Wattled Jacana, *Jacana jacana* (**a**, green wing primary), Black-billed Turaco, *Tauraco schuetti* (**b**, green face), Fischer's Turaco, *Tauraco fischeri* (**c**, red wing primary), Ross's Turaco, *Musophaga rossae* (**d**, red crown), Blood Pheasant, *Ithaginis cruentus* (**e**, red upper tail coverts), Crested Wood-Partridge, *Rollulus roulroul* (**f**, red crown). Near-ultraviolet (UV) wavelengths are *shaded*. Possible sub-forms (Moreau 1958; Dyke 1992), mixtures (Dyke 1992) or oxidation products (Church 1870, 1892) of colorful porphyrins were not distinguishable

addition to these various minima, spectral locations of the most prominent local maxima found at UV (λR_{UVpeak}) and human-visible ($\lambda R_{VISpeak}$) wavelengths also were calculated, as were the wavelengths of half-maximal reflectance [Fig. 1; measured from local minima to their associated peaks in the UV (left-facing slope, λR_{uv50}), in the human visible range (right-facing slope, λR_{vis50}) and for the steep rise in longest-wavelength reflectance expressed by turacins (left-facing slope, λR_{vis50})].

The spectra obtained from human-visible red plumages of both galliform species produced spectra with absorption and reflectance bands that were broader and rounder then those known for colorful porphyrins. Their spectral shapes closely resemble those of (possibly optically saturated) red (β-keto) carotenoids in that their single broad reflectance minima (absorption maxima) centered around 530 nm, and their reflectance plateau started (rising) around 600 nm. Chemical analysis supports this determination for *Ithaginis* (Thomas et al. 2014), but the identify of the red pigment in *Rollulus* remains uncertain (Thomas et al. 2014 concluded it was not a carotenoid, though this also was based on reflectance spectra). To avoid conflating analysis of different pigments, therefore, spectra from the red plumages of galliforms were analyzed separately. Features of the carotenoid-like galliform spectra (λR_{UVpeak}, λR_{minI}, λR_{vis50}, $\lambda R_{VISpeak}$) were calculated as in prior carotenoid studies (Fig. 1; Bleiweiss 2005, 2007, 2008, 2014).

Literature Survey of Ecologic and Visual System Diversity

Literature sources were consulted to characterize both ecologies and receptor sensitivities. Habitat, light environment, and diet were used to summarize ecological characteristics (del Hoyo et al. 1994, 1996, 1997) that may correlate with important physical and biotic factors relevant to signal production and reception (Hill and McGraw 2006). Standard abbreviations (Hart and Hunt 2007; Beason and Loew 2008) were used to refer to the (from shortest to longest) four wavelength-sensitive visual pigments (SWS1, SWS2, RH2 and LWS) and corresponding single cone receptors (V, S, M, and L). Sensitivities of visual pigments and receptors were estimated at two different levels of precision. First, visual opsin (gene

sequence) data for the SWS1 pigment characteristic of the VS and UVS systems were used to classify visual systems (e.g. Ödeen and Håstad 2013). Second, quantitative microspectrophotometry (MSP) data of effective single cone sensitivities ($e\lambda_{max}$ = whole cone sensitivities incorporating the filtering effects of ocular media and cone oil droplets; Goldsmith et al. 1984; Bowmaker et al. 1997; Hart et al. 2000; Cuthill 2006) were then used to test quantitatively whether (colorful porphyrin) plumage pigments align better to their own than to other visual systems with the null expectation of equal fit to both VS and UVS systems (see Bleiweiss 2014). The MSP data included only species for which all four single cones were characterized, which included 10 VS and 12 UVS systems (Hart and Hunt 2007; Coyle et al. 2012).

Phylogenetic Analyses

Visual system data (opsin, MSP) were available for few species with colorful porphyrins [e.g. *Gallirex* (*Tauraco*) *porphyreolophus*; Ödeen and Håstad 2013), However, these data were available for many related species in the orders (Galliformes, Musophagiformes, Charadriiformes) that display these pigments (e.g. Baker et al. 2007; Hackett et al. 2008; Ödeen and Håstad 2013; Wang et al. 2013), from which other visual systems were inferred through phylogenetic associations. Historical associations between visual system and plumage pigment were explored explicitly also by mapping colorful plumage porphyrins onto the most recent estimates of avian phylogeny. Maximum likelihood (as implemented in Mesquite version 3.02; Maddison and Maddison 2014) was used to reconstruct visual system ancestral character states in relation to the occurrence of colorful plumage porphyrins. The phylogeny was a composite based on studies using different kinds of molecular data (Hackett et al. 2008; Ödeen et al. 2010, 2011b; Ödeen and Håstad 2013; Jarvis et al. 2014), so branch lengths were set arbitrarily to one. For likelihood analyses, changes between character states were treated as equally likely, using the stored Mk1 model of evolution by maximum likelihood (Maddison and Maddison 2014). Significance of ancestral character state was determined from a likelihood decision threshold of T = 2, which indicates 7.4 times more support for one over the other character state (Schluter et al. 1997).

Statistical Analyses

A total of 248 spectral scans was analyzed, comprising two replicate scans for each of 124 plumage patches (minus some patch spectra with low absolute reflectance whose fine structure could not be accurately characterized, particularly for male *Rollulus* and certain turacos; see also Dyke 1992) across the 14 species. Turacoverdin spectra were homogeneous in fine structure (local reflectance maxima and minima) such that even extremes (Fig. 1a, b) could be grouped for analysis. However, each red pigment class produced distinctly unsaturated (pronounced fine structure) or saturated (muted fine structure) spectra that correlated with other objective divisions [for turacin: unsaturated pigment in flight feathers, saturated pigment in contour plumage (Fig. 1c, d); for non-porphyrin: unsaturated pigment in *Ithaginis* male upper tail coverts, saturated pigment in *Rollulus* male crest (Fig. 1e, f)]. Therefore, each red pigment × saturation class was analyzed separately.

Data processing and statistical analyses followed earlier procedures (Bleiweiss 2014; see also Butler et al. 2011). Non-parametric methods were used to test correlations between plumage and receptor ($e\lambda_{max}$) frequency distributions as a function of wavelength. The frequency distributions were constructed by allocating (plumage or receptor) data into 2 nm bins from 320 to 700 nm. Each cell therefore was assigned an integer or zero value and the statistical test were based on n = 190 bins. This approach allowed for various informative comparisons (to either VS or UVS systems) with the fewest assumptions (by limiting visual systems analyzed to those actually measure with MSP). Pseudoreplication was reduced further by averaging (two) replicate scans × patch × pigment class × individual for each sex and species, which gave a total of 28 patch averages for males and 26 patch averages for females. These average values for each sex for each species were then retained in the final analysis, and the sexes were analyzed separately (although less stringent analyses led to entirely similar patterns and conclusions).

Alignments between the spectral locations of the local minima and maxima of plumage spectra with the single cone maximal sensitivities were then analyzed both for each spectral feature and single cone class separately, and for various combinations thereof (see below). Various behavioral paradigms suggest the presence of at least three single-cone opponent color processes (V and S, M and L, and a more complex S and M interaction) in species pertaining to both VS [chicken *Gallus gallus* (Osorio et al. 1999a, b), Japanese quail *Coturnix japonica* (Smith et al. 2002)] and UVS [budgerigar *Melopsittacus undulatus* (Goldsmith and Butler 2005), European starling *Sturnus vulgaris* (Smith et al. 2002)] type avian visual systems. I therefore examined alignment to these three explicit singe-cone opponent pairs, which contribute to the six possible ones specified for avian tetrachromats in the popular receptor noise-limited model of chromatic thresholds (Vorobyev et al. 1998; Cuthill 2006).

A few specimens that had been kept as aviary birds were grouped with the remainder of the sample based on their

similar spectra. However, I used General Linear Models to test for specimen age (year) and lineage (phylogeny) effects (McNett and Marchetti 2005; Armenta et al. 2006; Bleiweiss 2014). As before, strong associations were identified based on a nominal P value of 0.01 and large effect sizes (Cohen 1988; Nakagawa 2004). Statistical tests were two-tailed unless noted, and were conducted in SAS (version 9.1.3; SAS Inc. 2013).

Results

Plumage Pigment Spectra

Spectra of turacoverdin and turacin were distinct from each other, but spectra of each pigment were virtually identical in shape between the sexes and across taxa. Although specimen age spanned nearly a century (males: 1897–1973; females: 1896–1979), plumage reflectance showed no signs of significant chronological deterioration (Table 2). A caveat to this conclusion is that the most recent specimens were still almost fifty years old (1973), precluding detection of any initial change. Nevertheless, the spectra obtained herein closely resemble those from plumages (reflectance) and in vitro pigments (absorption) obtained in other studies (i.e. Dyke 1992; Toral et al. 2008), including from fresher material (Dyke 1992). The only notable exception to this uniformity was male *Rollulus*, whose dark dorsal plumage (altered for λR_{vis50} and weakly so for λR_{minI}) results from a mixture of turacoverdin and melanin (Table 2; see also Dyke 1992). Turacin was confirmed only for the musophagiforms (Church 1870, 1892, 1913; Moreau 1958; Rimington 1939; Toral et al. 2008; herein), whereas other red plumage pigments (carotenoids in *Ithaginis*, pigments with similar spectra in *Rollulus*) occurred only in the galliforms.

Turacoverdin plumages expressed three main absorption bands ($\lambda R_{minI} \sim 410$ nm, $\lambda R_{minII} \sim 605$ nm, $\lambda R_{minIII} \sim 570$ nm) and a main reflectance band ($\lambda R_{VIS\text{-}peak} \sim 510$–$530$ nm) over human-visible wavelengths (Fig. 1). The previously unmeasured UV portion of the turacoverdin spectrum indicated a relatively low ($\sim$5 %) hump around 350 nm. Turacin-based plumages were invariably present in the flight feathers of colorful turaco genera, and sometimes also in their contour plumages (crown or nape of *Ruwenzorornis johnstoni*, *Tauraco fischeri*, *Musophaga spp.*). In common with turacoverdins, turacins had three distinct reflectance minima, and a local reflectance maximum at intermediate wavelengths (Fig. 1). However, the turacin minima occurred at longer wavelengths ($\lambda R_{minI} \sim 570$ nm, $\lambda R_{minII} \sim 530$ nm, $\lambda R_{minIII} \sim 470$ nm), the weakest minimum ($\lambda R_{minIII} \sim 470$ nm) was the broadest, and the mid-wavelength peak was muted (<10 % reflectance). All plumage turacins reflected most strongly at the long wavelength limits of avian vision (starting around 650 nm and rising monotonically to 700 nm; see also Toral et al. 2008), and unsaturated turacins (in flight feathers) combined long wavelength reflectance with a prominent peak (up to 30 %) in the UV (Fig. 1). Unlike turacins, human-visible red pigments in male *Ithaginis* and *Rollulus* (putative carotenoids; Fig. 1) expressed a single broad minimum located between a principal

Table 2 General linear models testing effects of year, clade, and pigment class on spectrum features

Pigment[b]	Spectrum feature (dependent variable)[a]													
	λR_{UVpeak}		λR_{uv50}		λR_{minI}		λR_{vis50}		$\lambda R_{VISpeak}$		λR_{minII}		λR_{minIII}	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Males[c,d]														
Year[e]	1.07	0.312	0.59	0.453	0.23	0.637	0.04	0.841	0.25	0.619	0.47	0.501	0.02	0.895
Clade	0.49	0.621	0.09	0.914	**3.91**	**0.035**	**6.77**	**0.005**	0.49	0.618	0.67	0.525	0.58	0.570
Pigment	**5.59**	**0.027**	3.76	0.066	**9.44**	**0.005**	**46.4**	**0.000**	**18.1**	**0.000**	**29.6**	**0.000**	**195**	**0.000**
Females[c,d]														
Year[e]	1.09	0.309	0.73	0.403	0.71	0.411	0.32	0.578	0.65	0.431	0.63	0.435	1.06	0.315
Clade	0.03	0.972	0.81	0.461	0.42	0.665	0.91	0.418	3.20	0.062	0.46	0.641	0.07	0.934
Pigment	**5.30**	**0.032**	0.24	0.627	**11.3**	**0.003**	**65.4**	**0.000**	**23.1**	**0.000**	**19.3**	**0.000**	**490**	**0.000**

[a] Bolded associations $P < 0.05$. Statistics implemented in PROC GLM (SAS v9.1.3). Statistical tests based on type III sum of squares

[b] Turacoverdin, unsaturated turacin, saturated turacin, non-porphyrin

[c] Clade categories designated based on family (galliform, musophagiform, charadriiform) membership

[d] All dependent variables natural log transformed (SAS v9.1.3)

[e] Year effect not significant even without corrections for simultaneous comparisons, but see text for qualifications

reflectance band at long wavelengths, and a secondary, and much lower UV peak (which was virtually absent in the more saturated crest plumage of male *Rollulus*).

Plumage Pigment Spectra in Relation to Ecological Habits

Taxa with colorful plumage porphyrins vary greatly in ecological characteristics that might affect pigmentation (Table 3), either directly (available pigment precursors via diet) or indirectly (light environment via latitude, altitude, or vegetation type). Conversely, some plumage variation actually was greatest among birds with similar habits [e.g. terrestrial taxa have turacoverdin with low (male *Rollulus*) or high (*Ithaginis*, *Jacana*) reflectance]. The extensive development of colorful porphyrins in turacos has been tied to several characteristic features of these birds, including rainforest-dwelling habits and herbivorous diets (Moreau 1958; McGraw 2006b). However, these quintessential turaco characteristics do not extend to other taxa with colorful porphyrins (Tables 3-4; even if the red crown plumage of *Rollulus* is due to turacin). In this regard, the range of diets among the broader sampling of taxa is especially surprising given the suspicion that the herbivorous habits of turacos may help them synthesize colorful porphyrin by providing abundant copper (McGraw 2006a). However, this diet could give turacos the seemingly unique ability to produce jointly turacoverdin and turacin). Even among turacos, both turacoverdin and turacin occur in species that occupy a diversity of forest types (Table 3). The only ecological feature associated with development of colorful porphyrins across all taxa is high environmental humidity (typical of tropical, gallery, wetland, montane, and alpine zones), an association that applies to other pigments as well (Mayr 1963). Quantitatively, ecology was uncorrelated with colorful porphyrin reflectance minima and maxima except for regions of 50 % reflectance in males (light environment with λR_{vis50}) and females (marginally, diet with λR_{uv50}). Ecology did not correlate with any of the several regions of global (λR_{minI}) or local ($\lambda R_{minII-III}$) reflectance minima (absorption maxima) among porphyrin pigments.

Table 3 Ecology of study taxa that express colorful plumage porphyrins

Taxon[b]		Ecological characteristic[a]		
		Habitat	Light environment[c]	Diet[d]
Galliformes (Pheasants): turacoverdin				
Crested wood-partridge	*Rollulus roulroul*	Rainforest	Forest shade	Omnivorous
Blood pheasant	*Ithaginis cruentus*	Alpine	Gaps	Omnivorous
Musophagiformes (Turacos): turacoverdin + turacin				
Livingstone's Turaco	*Tauraco livingstonii*	Rainforest	Gaps	Herbivorous
Schalow's Turaco	*Tauraco schalowi*	Gallery forest	Gaps	Herbivorous
Black-billed Turaco	*Tauraco schuetti*	Rainforest	Gaps	Herbivorous
White-crested Turaco	*Tauraco leucolophus*	Gallery forest	Gaps	Omnivorous
Fischer's Turaco	*Tauraco fischeri*	Rainforest	Gaps	Omnivorous
Hartlaub's Turaco	*Tauraco hartlaubi*	Montane forest	Gaps	Omnivorous
Purple-crested Turaco	*Gallirex porphyreolophus*	Gallery forest	Gaps	Herbivorous
Ruwenzori Turaco	*Ruwenzornis johnstoni*	Montane forest	Gaps	Omnivorous
Violet Turaco	*Musophaga violacea*	Gallery forest	Gaps	Herbivorous
Ross's Turaco	*Musophaga rossae*	Gallery forest	Gaps	Omnivorous
Charadriiformes (Shorebirds): turacoverdin				
Wattled Jacana	*Jacana jacana*	Wetland	Open	Carnivorous
Northern Jacana	*Jacana spinosa*	Wetland	Open	Carnivorous

[a] Data from del Hoyo et al. 1994, 1996, 1997 (Volumes 2, 3, 4) and sources therein

[b] See Table 1 for pigments associated with each major taxon

[c] Based on classification scheme of Endler (1993)

[d] Omnivorous = plant and animal matter; herbivorous = largely fruits and leaves in differing proportions; carnivorous = arthropods, not apex predator

[e] Colorful porphyrins not extensive in *Corythaixoides* or *Corythaeola* (spectra were not analyzed here but appear to be identical to those obtained for other turacos (see Dyke 1992)

Table 4 General linear models testing effects of three ecological (habitat, light environment, diet) characteristics on spectrum features

Ecology[d]	Spectrum feature (dependent variable)[a,b,c]													
	λR_{UVpeak}		λR_{uv50}		λR_{minI}		λR_{vis50}		$\lambda R_{VISpeak}$		λR_{minII}		λR_{minIII}	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Males														
Habitat	0.94	0.446	2.01	0.153	1.25	0.324	1.31	0.305	1.66	0.214	0.43	0.735	0.78	0.523
Light	0.00	0.987	3.38	0.085	0.54	0.472	**14.74**	**0.001**	3.51	0.078	0.23	0.637	3.04	0.099
Diet	0.04	0.841	1.43	0.249	0.75	0.398	0.41	0.529	1.08	0.314	0.03	0.861	0.39	0.539
Pigment	**20.28**	**0.001**	**42.41**	**0.001**	**79.1**	**0.001**	**5615**	**0.001**	**21.84**	**0.001**	**118.9**	**0.001**	**127.6**	**0.001**
Females														
Habitat	2.85	0.085	2.30	0.131	1.65	0.221	0.01	0.995	0.00	0.997	0.62	0.552	2.35	0.125
Light	1.43	0.248	2.91	0.107	0.24	0.629	2.70	0.119	1.61	0.222	0.20	0.663	0.23	0.636
Diet	0.05	0.822	**4.89**	**0.041**	0.37	0.554	0.69	0.418	1.89	0.187	0.54	0.474	0.00	0.999
Pigment	**26.81**	**0.001**	**41.12**	**0.001**	**75.0**	**0.001**	**5916**	**0.001**	**28.57**	**0.001**	**93.36**	**0.001**	**310.9**	**0.001**

[a] Statistics implemented in PROC GLM (SAS v9.1.3). Statistical tests based on type III sum of squares. Bolded associations $P < 0.05$

[b] Model: reflectance feature = habitat + light + diet + pigment

[c] All dependent variables natural log transformed (SAS v9.1.3)

[d] Ecologic variables coded as follows: Pigment (1 = turacoverdin, 2 = unsaturated turacin, 3 = saturated turacin; carotenoids = excluded); Habitat (1 = rainforest, 2 = gallery forest, 3 = wetlands, 4 = montane forest; 5 = temperate alpine); Light environment (1 = forest shade, 2 = woodland shade, 3 = small or large gaps, 4 = open/cloudy); Diet (1 = herbivorous, 2 = omnivorous, 3 = carnivorous)

Plumage Pigment Spectra in Relation to Visual Habits

Despite their diversity of ecologic habits, only VS-type systems are known within higher (all non-passerine) taxa containing species that express bright plumage porphyrins, including Galliformes (6/6 species analyzed; Ödeen and Håstad 2003, 2013), Musophagiformes (1/1 species analyzed; Ödeen and Håstad 2013), and the paraphyletic, the long-legged shorebird component of Charadriiformes (11/11 species analyzed; Baker et al. 2007; Ödeen et al. 2010; Capuska et al. 2011). Among these larger and exclusively non-passerine clades, moreover, polymorphism in visual system that could compromise this approach occurred only in a clade lacking colorful porphyrins [e.g. the derived gull-tern-skimmer (Laridae-Sternidae-Rynchopidae) sub-clade within Charadriiformes, as well as among the Passeriformes (Ödeen et al. 2010, 2011a, b)].

Alignments Between Plumage Pigment Spectra and Visual Systems

Three or four VS single cones aligned strongly with prominent spectral features of unsaturated turacoverdins and turacins (Table 5; Fig. 2). These alignments differed between pigments in two respects. First, the L cone sensitivity closely matched a spectral feature of turacoverdin (λR_{minII}) but not of turacin. This difference arises from the far red-shifted long-wavelength fine structure for turacin, which lies well above the maximum sensitivity of the avian L cone. Second, cones indexed to both pigment spectra aligned to a minimum of one pigment but to a maximum or 50 % maximum of the other pigment, thus expressing a complementary pattern (Table 5). Alignment patterns were similar in both sexes except that the M cone was significantly associated with a turacoverdin spectral feature ($\lambda R_{VISpeak}$) only in males. Alignments were fewer and weaker ($P > 0.01$) for saturated turacins (Table 5; Fig. 2). Part of this latter discrepancy was associated with higher noise in the saturated spectra, whose reflectance was generally below 5 %, and part to a more pronounced reduction in alignment to female spectra (Table 5). No significant alignments were observed between cone sensitivities and (red) non-porphyrin (limited to males) reflectance (*Ithaginis* = unsaturated and *Rollulus* = saturated, r_s: $\lambda R_{UVpeak} = -0.01415$, $\lambda R_{minI} = -0.01306$, $\lambda R_{vis50} = -0.01306$; all $P > 0.800$), due to their distinctive means (*Ithaginis*: $\lambda R_{UVpeak} = 391.0$, $\lambda R_{minI} = 522.0$, $\lambda R_{vis50} = 614.8$; *Rollulus*: $\lambda R_{UVpeak} = 361.5$, $\lambda R_{minI} = 442.8$, $\lambda R_{vis50} = 605.3$) and high variances (*Ithaginis*: $\lambda R_{UVpeak} = 65.7$, $\lambda R_{minI} = 23.3$, $\lambda R_{vis50} = 17.9$; *Rollulus*: $\lambda R_{UVpeak} = 929.2$, $\lambda R_{minI} = 734.3$, $\lambda R_{vis50} = 3073.6$).

Known single-cone opponent pairs (Table 6) align both more consistently (number of significant *P* values) and more strongly (effect sizes) to turacoverdin (all three pairs) than to turacin (mainly the V–S pair), echoing the pattern observed for individual receptors (compare Table 5). The sexes differ to some extent in opponent alignments to

Table 5 Correlations between VS single cone receptors and plumage pigment spectrum features

Receptor[b]	Spectrum feature[a]		
	Turacoverdin correlation feature	Unsaturated turacin correlation feature	Saturated turacin correlation feature
Males[c]			
eV			
r_s	**0.55609 λR_{minI}**	**0.54697 λR_{uv50}**	**0.16298 λR_{minIII}**
P	**<0.00010**	**<0.00010**	**0.02430**
eS			
r_s	**0.56628 λR_{vis50}**	**0.26034 λR_{minIII}**	**0.17996 λR_{minIII}**
P	**<0.00010**	**0.00030**	**0.01270**
eM			
r_s	**0.26194 $\lambda R_{VISpeak}$**	**0.31260 λR_{minII}**	**0.18544 λR_{minII}**
P	**0.00030**	**<0.00010**	**0.01020**
eL			
r_s	**0.43873 λR_{minII}**	−0.03427	−0.02398
P	**<0.00010**	0.63790	0.74200
Females[c]			
eV			
r_s	**0.66507 λR_{minI}**	**0.64509 λR_{uv50}**	**0.16298 λR_{minIII}**
P	**<0.00010**	**<0.00010**	**0.02430**
eS			
r_s	**0.66473 λR_{vis50}**	**0.48371 λR_{minIII}**	−0.02634
P	**<0.00010**	**<0.00010**	0.71760
eM			
r_s	−0.02952	**0.34146 λR_{minII}**	−0.02634
P	0.68520	**<0.00010**	0.71760
eL			
r_s	**0.50238 λR_{minII}**	−0.03197	−0.02398
P	**<0.00010**	0.63060	0.74200

Note that many correlations are highly significant ($P < 0.01$), with moderate (>0.25) to large (>0.45) effect sizes (Cohen 1988). Some associations differ among pigments

[a] Spearman rank correlations (top) with two-tailed probabilities (bottom). Bolded correlations $P < 0.05$. Non-significant correlations are strongest relationship of that cone with any reflectance feature. Statistics implemented in PROC CORR (SAS v9.1.3)

[b] Cone maximal sensitivities (e = effective λ_{max}; adjusted for effects of oil droplet and ocular medium absorption) as reported in Hart and Hunt (2007)

[c] Turacoverdins and saturated turacins are from body (contour) plumage patches, unsaturated turacins are from wing (primary flight) feathers

turacins (both align the V–S pair to the unsaturated pigment, but differ otherwise for the V–S and S–M pairs; Table 6) but not turacoverdins (all three singe-cone pairs in both sexes).

The colorful porphyrin spectra do not align nearly as well to receptors of the UVS system (Table 7), whose species are not known to display these pigments. Thus, the number of correlations and their effect sizes were roughly half that for UVS compare to VS systems. Unlike VS systems, moreover, UVS systems lacked the complementary alignment pattern to different (unsaturated) colorful porphyrins. Rather, most of the alignments involved the M and L cones, whose sensitivities are more similar than are those of the V and S cones between systems. Other alignments between colorful porphyrin spectra and the UVS system are of questionable salience given the overall low reflectance associated with these plumage features [UV for turacoverdin (both sexes) and saturated turacin (males)].

Phylogenetic Patterns

Colorful plumage porhyrins arose at least four times, including three times across families (galliformes, musophagiforms, charadriiforms; Fig. 3), and twice within galliforms (distant relations of *Rollulus* and *Ithaginis*; Wang et al. 2013). Moreover, the VS visual system was widespread, directly ancestral to, and conserved in those

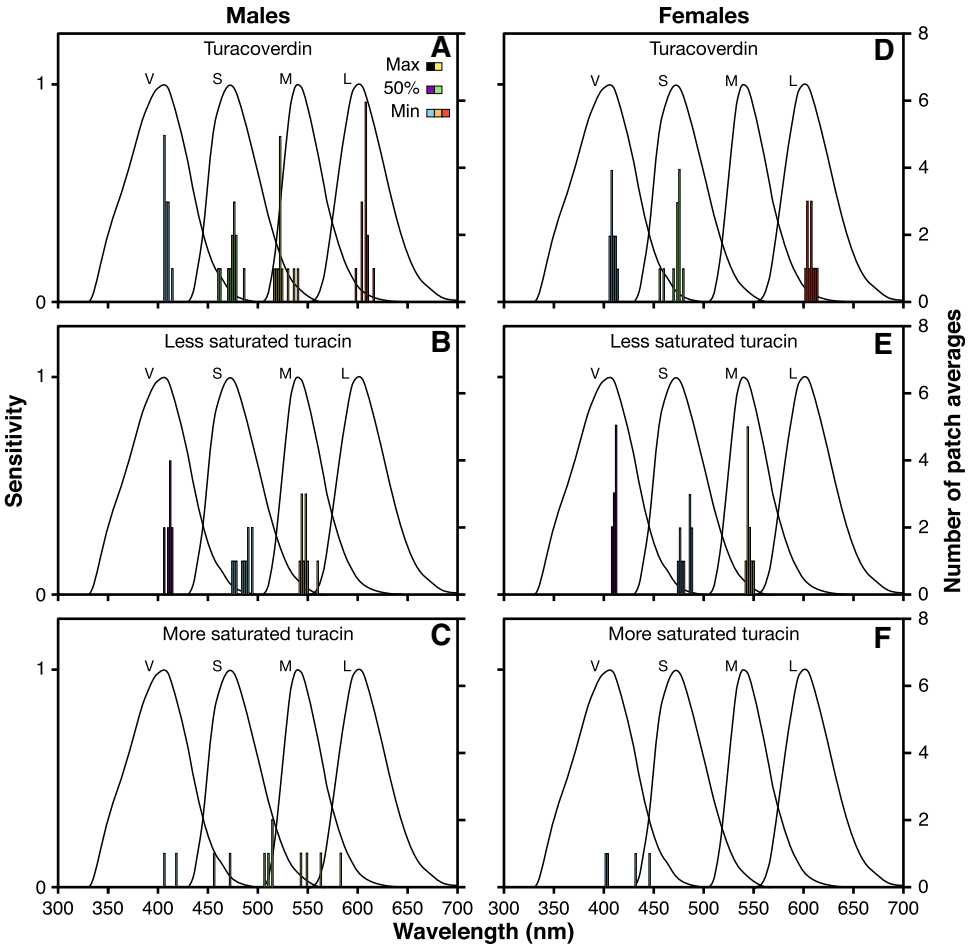

Fig. 2 Spectral distribution of significantly aligned ($P < 0.0010$ for turacoverdin and unsaturated turacin, $P < 0.0250$ for saturated turacin) male and female spectrum features in relation to the spectral location of the single-cone array (see also Tables 5, 6). Note strong effective cone sensitivity alignments to regions of maximal and minimal reflectance, which imply strong sensory inputs from several known two-cone opponent receptor combinations (V–S, S–M, M–L). Cone spectral sensitivities based on VS species, the Wedge-tailed Shearwater *Puffinus pacificus* (Cuthill et al. 2000; Hart and Hunt 2007). Abbreviations are as defined in text and Fig. 1

avian lineages that express colorful plumage porphyrins (Fig. 3). In combination, these patterns suggest that the VS visual system always was present before the evolution of colorful plumage porphyrins. Moreover, greater opponent stimulation achieved through strong alignments between VS cone sensitivities and colorful plumage porphyrin reflectance provides a plausible selective advantage for colorful plumage porphyrins in VS species, through greater conspicuousness, information content, or both (Bleiweiss 2014). Thus, a synthesis of signal and receptor pigment absorption and alignment patterns in a phylogenetic context suggests that colorful plumage porphyrins may be favored in VS species through an intrinsic bias described by the pattern of sensory exploitation (Shaw 1995).

Discussion

Consideration of Alternative Hypotheses

The strong associations between colorful porphyrin spectra and VS cone λ_{max} independent of ecology supports the hypothesis that broad-scale characteristics of signals and receptors are linked mainly to each other's intrinsic (physicochemical, physiological, and phylogenetic) properties, reinforcing earlier results with carotenoids (Bleiweiss 2014). The similar absorption maxima of the plumage pigments in vitro and in vivo (see Dyke 1992) further attests to the physical constraints imposed on signal form. While incomplete sampling of plumage pigments or visual systems cannot be entirely dismissed, it remains the case that available information strongly supports a link between colorful porphyrins and VS visual systems (Ödeen and Håstad 2013). Furthermore, the physical and phylogenetic associations of colorful porphyrins with VS cone sensitivities reveal levels of functional integration between signal and receptor that transcend generalized perceptual tasks (Vorobyev et al. 1998; Stoddard and Prum 2008).

The evidence for sensory exploitation as an overarching process encompassing these various intrinsic associations is conceptually satisfying because it reconciles the constraints on signal form and limits on phylogenetic distribution (rarity, evolutionary lag) with the communicative function of coloration suggested by the signal-receptor

Table 6 Correlations between VS single cone receptors and plumage pigment spectrum features for possible opponent pairs of cones

Opponent pair[b]	Receptor-opponent with plumage reflectance pairings[a]		
	eV + eS	eS + eM	eM + eL
Plumage reflectance pair[c]			
Turacoverdin	$\lambda R_{minI} + \lambda R_{vis50}$	$\lambda R_{vis50} + \lambda R_{VISpeak}$	$\lambda R_{VISpeak} + \lambda R_{minII}$
Turacin (unsaturated)	$\lambda R_{uv50} + \lambda R_{minIII}$	$\lambda R_{minIII} + \lambda R_{VISpeak}$	$\lambda R_{VISpeak} + \lambda R_{vis50}$
Turacin (saturated)	$\lambda R_{uv50} + \lambda R_{minIII}$	$\lambda R_{minIII} + \lambda R_{VISpeak}$	$\lambda R_{VISpeak} + \lambda R_{vis50}$
Males			
Turacoverdin			
r_s	**0.53893**	**0.39392**	**0.31290**
P	**<0.00010**	**<0.00010**	**<0.00010**
Turacin (unsaturated)			
r_s	**0.35622**	0.10784	−0.05493
P	**<0.00010**	0.13760	0.45040
Turacin (saturated)			
r_s	0.16150	0.06010	−0.04819
P	0.02560	0.40890	0.50800
Females			
Turacoverdin			
r_s	**0.65754**	**0.31389**	**0.22467**
P	**<0.00010**	**<0.00010**	**0.00180**
Turacin (unsaturated)			
r_s	**0.53139**	**0.21272**	−0.06105
P	**<0.00010**	**0.00310**	0.40150
Turacin (saturated)			
r_s	0.04398	−0.04660	−0.04449
P	0.54580	0.52210	0.54110

Note that many correlations are highly significant ($P < 0.01$), with moderate (> 0.25) to large (> 0.45) effect sizes (Cohen 1988). Some associations differ among pigments

[a] Spearman rank correlations (top) with two-tailed probabilities (bottom). Bolded correlations $P < 0.05$. Non-significant correlations are strongest relationship of that cone pair with any reflectance features. Statistics implemented in PROC CORR (SAS v9.1.3)

[b] Cone maximal sensitivities (e = effective λ_{max}; adjusted for effects of oil droplet and ocular medium absorption) as reported in Hart and Hunt (2007)

[c] Turacoverdins and saturated turacins are from body (contour) plumage patches, unsaturated turacins are from wing (primary flight) feathers

alignments. By comparison, dull plumage porphyrins for which spectra are available lack any fine structure (Toral et al. 2008), and are widely distributed among both VS (Columbidae, Cuculidae, Caprimulgidae, Eurypygidae, Strigidae, Accipitridae, Halcyonidae) and UVS (Trogonidae, Passeridae) birds (Völker 1938). This disparity between porphyrin subclasses further supports the functional basis and perceptual link between colorful plumage pigments and their VS type vision. Indeed, these signal-receptor alignments provide physical evidence that colorful porphyrins are important in communication, a function that is otherwise poorly studied for this class of pigment (McGraw 2006a). However, the association of colorful plumage porphyrins with the VS system makes it unlikely that these pigments provide a private communication channel to avoid detection by avian predators, which have the same general visual system (cf. Håstad et al. 2005). Consistent with these interpretations, several authors have noted that the turacoverdin-based green plumage even in the terrestrial galliform *Rollulus* (female) is remarkably "bright" (del Hoyo et al. 1994) not cryptic. Thus, alignment data support subjective human impressions that turacoverdin and turacin deserve the moniker of colorful pigments.

These considerations do not exclude possible fine-scale changes in visual system or plumage reflectance in relation to ecology. Variation in VS visual systems encompasses the galliform "chicken" (longer wavelength) and remaining "pigeon" (shorter wavelength) variants, which may correlate with the terrestrial (closed) versus arboreal (open) habits of these groups (Cuthill et al. 2000). Notably, the lowest reflectance associated with turacoverdin (perhaps

Table 7 Correlations between UVS single cone receptors and plumage pigment spectrum features

Receptor[b]	Spectrum feature[a]		
	Turacoverdin correlation feature	Unsaturated turacin correlation feature	Saturated turacin correlation feature
Males[c]			
eV			
r_s	**0.38751 λR_{uv50}**	−0.03512	**0.20177 λR_{uv50}**
P	**<0.00010**	0.62960	**0.00550**
eS			
r_s	0.11210	−0.03764	−0.02634
P	0.12260	0.60520	0.71760
eM			
r_s	−0.03427	**0.53639 λR_{minII}**	**0.20177 λR_{minII}**
P	0.63790	**<0.00010**	**0.00550**
eL			
r_s	**0.60575 λR_{minII}**	−0.03764	−0.02634
P	**<0.00010**	0.60520	0.71760
Females[c]			
eV			
r_s	**0.34617 λR_{uv50}**	−0.03511	**0.17113 λR_{uv50}**
P	**<0.00010**	0.62960	**0.01790**
eS			
r_s	−0.04003	−0.03512	−0.17996
P	0.58240	0.62960	0.01270
eM			
r_s	−0.03645	**0.59574 λR_{minII}**	**0.20980 λR_{minI}**
P	0.61670	**<0.00010**	**0.00360**
eL			
r_s	**0.92481 λR_{minII}**	−0.03512	−0.02634
P	**<0.00010**	0.62960	0.71760

Note that highly significant correlations ($P < 0.01$) are fewer and effect sizes are weaker than for similar comparisons based on VS cone receptors

[a] Spearman rank correlations (top) with two-tailed probabilities (bottom). Bolded correlations $P < 0.05$. Non-significant correlations are strongest relationship of that cone with any reflectance feature. Statistics implemented in PROC CORR (SAS v9.1.3)

[b] Cone maximal sensitivities (e = effective λ_{max}; adjusted for effects of oil droplet and ocular medium absorption) as reported in Hart and Hunt (2007)

[c] Turacoverdins and saturated turacins are from body (contour) plumage patches, unsaturated turacins are from wing (primary flight) feathers

due to mixing with melanins; Dyke 1992) occurs in the male dorsal plumage of the galliform *Rollulus*, a species that lives in closed habitats with low ambient illumination. Conversely, the highest reflectance associated with turacoverdin occurs in *Jacana*, waterbirds that live in open habitats with high illumination (Tables 1, 3; body region also may play a role). Moreover, although the overall reflectance profiles of both plumages are similar due to the diagnostic absorption properties of colorful porphyrins (Fig. 1), small differences in their local minima and maxima (see also Dyke 1992) could correlate with different VS sensitivity patterns. Thus, it appears to be important to distinguish different aspects of the physical composition of a signal for the purposes of understanding overall signal and receptor design.

Alignment Patterns within Pigment Classes

Organizational properties of avian visual communication based on physical and physiological considerations are highlighted by parallel results for porphyrins (this study) and carotenoids (Bleiweiss 2014): (1) prominent absorption and reflection maxima of avian integumentary pigments are important alignment features in relation to the maximum

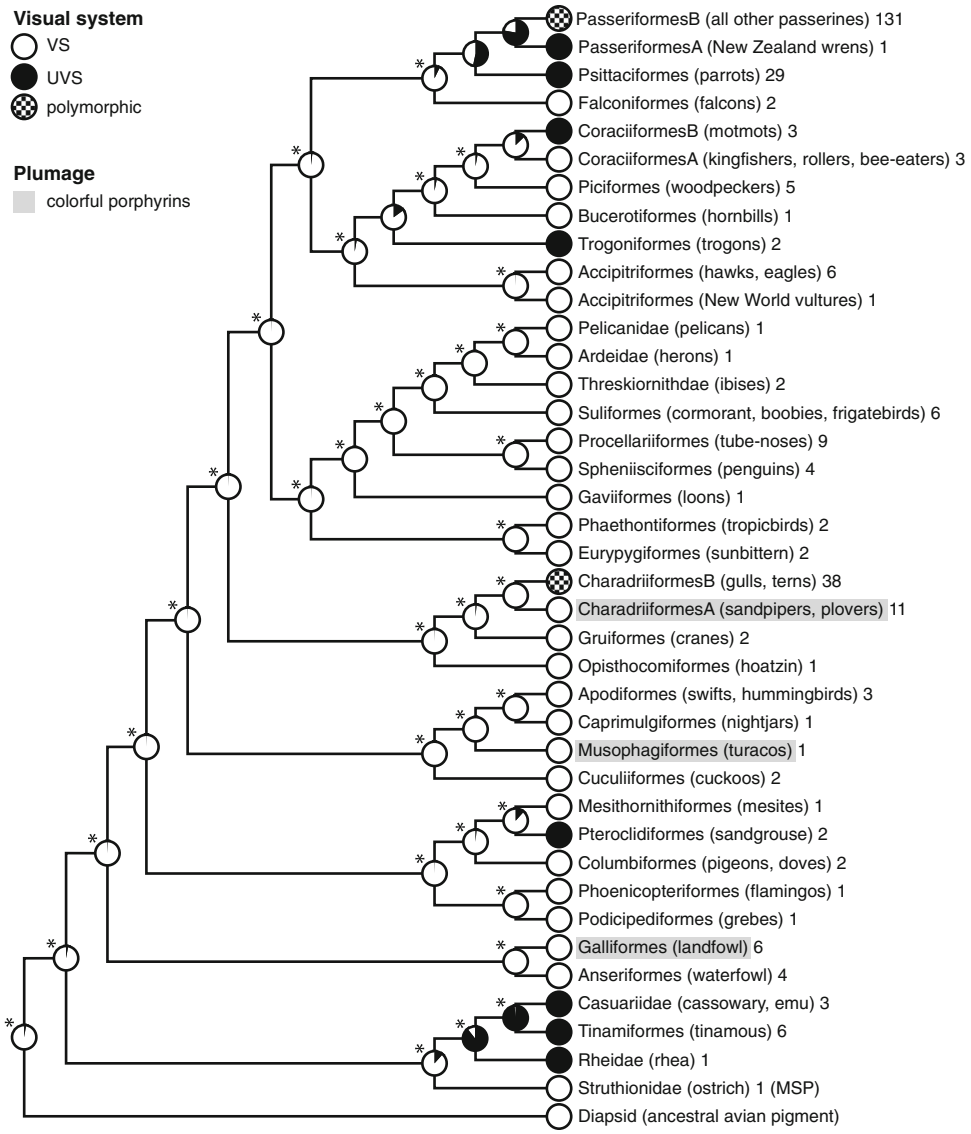

Fig. 3 Phylogeny and ancestral-state reconstructions of color vision (VS or UVS) macroevolution (*pie diagrams*) in major avian lineages in relation to the occurrence of colorful porphyrins (*grey bars*). Visual system data for paleognaths (Aidala et al. 2012) and neognaths (Ödeen et al. 2011b; Ödeen and Håstad 2013) based on SWS1 opein sequence data for V cone, except for Struthionidae (MSP; Hart and Hunt 2007). Numbers after common names tally species in that lineage for which SWS1 opsin sequence (visual system) data were available. All paleognaths share similar UVS-type SWS1 opsins, but the one species measured directly with MSP (ostrich, Struthionidae) has a functional VS-type retina, which could apply to the remaining diurnal paleognaths and to certain other (basal Austrialian passerine) taxa (see Ödeen and Håstad 2013). Regardless of these uncertainties, the current coding scheme (based primarily on the opsins) provides a conservative (under) estimate for the phylogenetic distribution of VS vision. The ancestral avian SWS1 visual pigment was presumed to be of the VS type (Hart and Hunt 2007; Bowmaker 2008). Maximum likelihood analysis based on the stored Mkl model as implemented in Mesquite (version 3.02, Maddison and Maddison 2014). Areas of pie slices indicate relative support for ancestral color vision character state in relation to the occurrence of colorful porphyrins. Asterisks indicate significant support for ancestral-state reconstruction at that node based on $T = 2$ criterion (support 7.4 times greater for one over the other state) of Schluter et al. (1997). Note that clades with species expressing colorful porphyrins appear to be exclusively VS and descend from taxa with that same visual system. Ordinal level genomic avian phylogenetic framework based on Jarvis et al. (2014) and Hackett et al. (2008). Reconstructions obtained at basal dichotomies for Charadriiforms [split between VS shorebirds versus alcids, gulls and terns (see species in Capuska et al. 2011; Ödeen et al. 2010)], and passerines [split between UVS New Zealand wrens versus remaining passerines (see species in Ödeen et al. 2011b)] were based on more detailed intra-ordinal phylogenies to accommodate intra-clade variation in color vision system

sensitivities of avian single-cones (Table 5); (2) these features are encoded by opponent cone pairs, suggesting perceptual salience (Table 6); (3) multiple pigment subclasses (turacoverdin and turacin) can be aligned to a single receptor array through exploitation of different cone combinations (Tables 5, 6); (4) unsaturated signals align

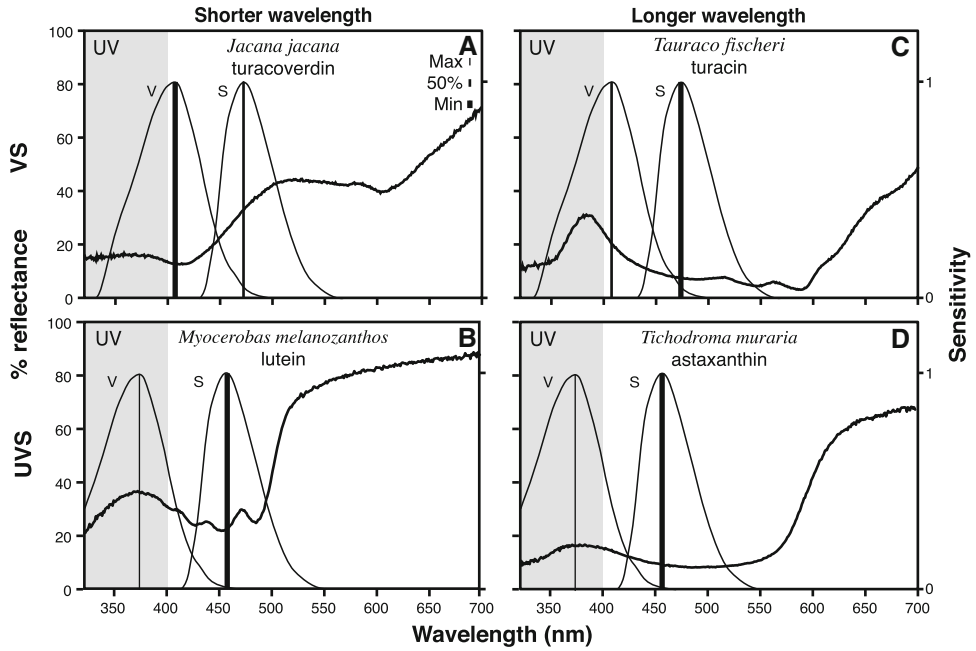

Fig. 4 Generalized alignment patterns of reflectance spectra with diagnostic cones (V and S) of the VS and UVS visual systems, for both shorter (*left*) and longer (*right*) wavelength-absorbing pigments. *Vertical lines* indicate key reflectance alignments: *thickest lines* index minimal reflectance, *intermediate lines* index 50 % reflectance, and *thinnest lines* index maximal reflectance (**a**). Note that cones of the VS and UVS systems differ most in alignment patterns for shorter wavelength-absorbing plumage pigments (see text). In addition, regions near maximum slope (50 % reflectance) appear to be more important ecologic (Table 4) and alignment (Table 5) features for VS system whereas regions of maximum reflectance (peak reflectance) appear more important for UVS systems (Bleiweiss 2014). VS species common names: Wattled Jacana, *Jacana jacana* (**a**, green wing primary), Fischer's Turaco, *Tauraco fischeri* (**b**, red wing primary). UVS species common names: Spot-winged Grosbeak, *Myocerobas melanozanthos* (**c**, yellow belly), Wallcreeper, *Tichodroma muraria* (**d**, red wing coverts). Pigment names indicated below species names (**a** and **c** are green and red porphyrins respectively, **b** and **d** are yellow and red carotenoids respectively). Near-ultraviolet (UV) wavelengths are shaded. Other features and abbreviations as defined in text and Figs. 1 and 2. Short wavelength-absorbing carotenoids also occur in many VS species, but the present study predicts that their spectra will show similarities to those of short wavelength-absorbing porphyrins

more closely than saturated ones (Tables 5, 6). Together, these patterns appear sufficient to index the diversity of colorful plumage porphyrins just as they did the diversity of carotenoids (despite the different visual systems involved). The alignment potential contained in avian cone arrays can be further appreciated by considering that avian M and L cones, which express broadly similar sensitivities in the VS and UVS systems (Hart and Hunt 2007), can encompass alignments to both porphyrins *and* carotenoids. Despite the latent capacity of fixed receptor arrays to align with diverse plumage spectra, limits to this flexibility are revealed by the failure of VS cones to align to the reflectance minima (M) and maxima (L) of the unidentified (carotenoid or other) red pigments in the two galliforms (*Rollulus*, *Ithaginis*).

The importance of reflectance minima (absorption maxima) as alignment features reinforces thinking about alignment in terms of the opponent pairs of cones (e.g. V-S, S-M, and M-L) that constitute functional units of perception (Hurvich 1981; Vorobyev et al. 1998). Absorption bands by themselves cannot determine distinct chromatic sensations, not because they correspond to regions of low reflectance, but because inputs from two or more cones are required to produce the relative receptor excitation patterns essential for distinguishing spectral waveforms (Hurvich 1981; Vorobyev et al. 1998). However, aligning one member of an opponent pair of cones to a reflectance minimum and the other to a reflectance maximum (Table 6) effectively encodes the pigment's absorptive properties (Bleiweiss 2014). Extending this strategy to different opponent cone groupings and different reflectance minima and maxima should further enhance perceived conspicuousness, variation, and information content of the signal.

The complementary alignment patterns among two or more signal pigments further reinforce the importance of intrinsic organizational features in avian visual communication. Thus, each (VS) single cone that indexed a reflectance minimum of one colorful porphyrin indexed a reflectance (sub)maximum of the other and vice versa (Table 5). This internal relationship should heighten contrast and reinforce the relative conspicuousness of

turacoverdin and turacin when these pigments color different patches in the same bird (e.g. as in many turacos). Indeed, this complementary alignment probably indicates perceptually complementary colors in that the combination of (reflected light from) turacoverdin and turacin in the right proportions should yield white (theoretically) or black (e.g. contour plumage patches in *Ruwenzorornis johnstoni*, *Tauraco fischeri*, *Musophaga spp.*). Indeed, signals with strong reflectance bands at one or both ends of the avian visible spectrum always occur in species that express middle wavelength-reflecting plumage due to turacoverdin: turacin in turacos, putative red carotenoids in galliforms, and red to yellow skin wattles or frontal shields in jacanas (Table 1; Fig. 1). Thus, the principal of maximal stimulation may favor certain plumage pigment combinations in the same way that it favors certain cone combinations.

Alignment Patterns Between Pigment Classes

Both the VS-porphyrin and UVS-carotenoid pairings demonstrate the importance of cone maximal sensitivities (λ_{max}) for understanding physical alignments between properties of the plumage and receptor pigments. For their diagnostic (V and S) cones, however, alignments observed for the two pairings differ in detail (Fig. 4). For shorter-wavelength reflecting pigments, the plumage reflectance minimum (λR_{minI}) aligns with the V cone in the VS systems (to turacoverdin) but with the S cone (to yellow carotenoids) in the UVS systems and vice versa for plumage reflectance (sub)maxima. Plumage pigments that reflect at longer-wavelengths (turacin, β-keto-carotenoids) align in more similar ways to each visual system, perhaps because the pigments' absorption bands are broader, more similar, and shifted to wavelengths where the respective cone sensitivities (e.g. S cones) are more similar (Fig. 4). Thus, use of red carotenoids by both VS (galliforms such as *Ithaginis*) and UVS (passerines such as passerids; see Bleiweiss 2014, Thomas et al. 2014) birds may arise from the undifferentiated nature of the relevant pigment spectra, paralleling the pattern observed for dull porphyrins (see above). Regardless of the historical scenarios responsible for these associations, avian plumage chemistries and receptor sensitivities appear interrelated and specialized to different degrees.

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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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