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Avian Visual Pigments: Characteristics, Spectral Tuning, and Evolution

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ABSTRACT: Birds are highly visual animals with complex visual systems. In this article, we discuss the spectral characteristics and genetic mechanisms of the spectral tuning of avian visual pigments. The avian retina contains a single type of rod, four spectrally distinct types of single cone, and a single type of double cone photoreceptor. Only the single cones are thought to be involved in color discrimination; double cones are thought to be involved in achromatic visual tasks, such as movement detection and pattern recognition. Visual pigment opsin protein genes in birds are orthologous to those in other vertebrates and have a common origin early in vertebrate evolution. Mechanisms of spectral tuning in the different classes of avian cone visual pigments show similarities in most instances to those in other vertebrates. The exception is the ultraviolet/violet (SWS1) class of pigments; phylogenetic evidence indicates that the ancestral vertebrate SWS1 pigment was ultraviolet sensitive (UVS), with different molecular mechanisms accounting for the generation of violet-sensitive (VS) pigments in different vertebrate classes. In birds, however, UVS visual pigments have re-evolved from an ancestral avian VS pigment by using a novel molecular mechanism not seen in other vertebrate classes. This has occurred independently in four of the 14 avian orders examined to date, although the adaptive significance of this is currently unknown.

Keywords: bird, visual pigment, opsin, cone oil droplet, visual ecology.

It is increasingly evident that the sensory perception of the world by other animals is very different from our own experience. With regard to the visual sense, differences between animals in the detection of the physical environment are due to variations in the anatomical, biochemical, and neurophysiological characteristics of the eyes and brain. To understand how other animals view the world and integrate the visual information they gather into a behavioral response, we must know how their visual systems work and what they are capable of doing under natural conditions (Lythgoe 1979).

The first step in the visual process occurs when photons of light reaching the retina at the back of the eye are absorbed by visual pigments contained in the outer segments of photoreceptor cells. There are two main types of photoreceptor cells in vertebrates: rods and cones. Rods are generally most abundant in the retinas of nocturnal species, are more sensitive to light than cones, and are used for vision under scotopic (dim light) conditions. Cones, which dominate the retinas of strongly diurnal species, are operational under brighter (photopic) levels of illumination, respond faster to light than rods, and are used for color vision where present (Ebrey and Koutalos 2001). The morphology, ultrastructure, and physiological properties of rods and cones vary considerably throughout the vertebrate classes, in some instances making it difficult to generalize about what exactly constitutes a rod or a cone (Rodieck 1973).

Regardless of photoreceptor structure, it is the spectral absorption properties of the visual pigments contained within their outer segments that determine the range of wavelengths to which an animal is sensitive and whether the animal has color vision. Visual pigment molecules consist of a protein, called an opsin, and a chromophore derived from vitamin A; it is the interactions between these two moieties that determine the spectral absorption properties of the visual pigment. In vertebrates, there are two different types of visual pigment: rhodopsins, where the chromophore is the aldehyde of vitamin A_1 (retinal), and porphyropsins, where the chromophore is the aldehyde of vitamin A_2 (3,4-didehydroretinal). The two chromophores may be used interchangeably with the same opsin protein, although a porphyropsin visual pigment will have a wavelength of maximum absorbance (λ_{max}) shifted toward longer wavelengths compared to a rhodopsin visual pigment using the same opsin, with the λ_{max} of the porphyropsin pigment becoming progressively more long-wave-

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shifted compared to the rhodopsin pigment as the λ_{max} increases (reviewed in Crescitelli 1972).

Several aquatic species, notably, some lampreys (Wald 1942; Hárosi and Kleinschmidt 1993), teleost fish (Dartnall and Lythgoe 1965), amphibians (Wald 1958), and elasmobranchs (Cohen et al. 1990), have both rhodopsin and porphyropsin visual pigments. Usually, the predominant type of chromophore present in the retina changes over a developmental timescale to coincide with an ontogentic shift in habitat or in response to changes in the photic environment (Liebman 1972; Loew and Dartnall 1976). In general, marine fish (or the marine phase in euryhaline species) have rhodopsins, whereas freshwater fish have porphyrospins. With the exception of some lizards (Provencio et al. 1992; Bowmaker et al. 2000; Loew et al. 2002), the visual pigments of terrestrial vertebrates are all rhodopsins. Thus, in birds, mammals, and most reptiles, the only way to alter the λ_{max} of a visual pigment is to change the structure of the opsin protein.

Changes in the tertiary structure of the opsin protein are caused by variations in amino acid sequence, which are a function of the genetic code. Four classes of cone and a single class of rod visual pigment opsin genes are present in vertebrates (reviewed in Yokoyama 2000), and the opsin proteins they encode are capable, when paired with an appropriate chromophore, of generating visual pigments with λ_{max} values ranging from approximately 355 nm in the ultraviolet (UV) to about 630 nm in the far red (Bowmaker and Hunt 1999). Cone pigments are classified according to their spectral sensitivity but are defined by the amino acid sequence of the opsin protein as follows (Bowmaker and Hunt 1999; Yokoyama 2000): (*a*) SWS1, ultraviolet-sensitive (UVS) or violet-sensitive (VS) cone visual pigments with λ_{max} values between 355 and 440 nm; (*b*) SWS2, short-wavelength-sensitive (SWS) cone visual pigments with λ_{max} values between 410 and 475 nm; (*c*) RH1 and RH2, medium-wavelength-sensitive (MWS) rod and cone visual pigments, respectively, with λ_{max} values between 460 and 540 nm; (*d*) LWS, long-wavelength-sensitive (LWS) cone visual pigments with λ_{max} values between 505 and 630 nm.

Evolution of the Major Visual Pigment Classes

The recent discovery in the southern hemisphere lamprey *Geotria australis* of multiple visual pigment opsin genes that are orthologous to the major classes of cone opsin genes found in jawed vertebrates (Collin et al. 2003*a*, 2003*b*) suggests that the major cone opsin types existed before the divergence of the jawed and jawless vertebrate lineages in the early Cambrian epoch some 540 million years ago. Phylogenetic analysis based on gene sequence identity shows that the evolution of cone pigments preceded the rod pigment, with the consequent deduction that photopic vision evolved before scotopic vision. The gene sequences for these cone opsins show an overall identity of around 40%. In contrast, the RH2 cone and RH1 rod opsins show a much higher identity of around 80%, indicating a more recent separation of the RH1 and RH2 gene lineages and consistent with the origin of the RH1 rod opsin gene from a duplication of the RH2 cone opsin gene. The absence of a rod pigment from agnathans indicates that the evolution of scotopic vision occurred early in the jawed vertebrate lineage.

In eutherian mammals, the cone opsin complement has been reduced to only two classes, LWS and SWS1, an event that is believed to have resulted from a nocturnal phase that mammals went through during their evolution. As a result of this loss, most eutherians are dichromats. In contrast, there is evidence that some marsupial mammals express additional pigments and possess trichromatic color vision (Arrese et al. 2002, 2006). In simian primates, this reduction in the number of cone pigments has been partially reversed, thereby achieving trichromacy (Nathans et al. 1986; Bowmaker et al. 1991; Ibbotson et al. 1992), although the evolutionary mechanism by which this has arisen differs in the two major simian groups, the New World (platyrrhines) primates from Central and South America and the Old World (catarrhines) primates from Africa and Asia. In New World primates, a polymorphic X-linked LWS gene is present, with different alleles specifying either red or green variants of the LWS pigment (Mollon et al. 1984; Williams et al. 1992). All males remain dichromats, but females that inherit a different form of the gene on each X chromosome possess trichromacy (Tovee et al. 1992). In Old World primates (Dulai et al. 1999) and in one species of New World primate, the howler monkey (*Alouatta* spp.; Jacobs et al. 1996), a duplication of the LWS gene has occurred such that one copy specifies a red pigment and the other a green pigment. This means that trichromacy is present in all individuals and in both sexes. In both cases, the major driving force behind the evolution of this trichromacy, with its improved color discrimination in the red/green region of the spectrum, is argued to be the detection and evaluation of ripe fruits (Mollon 1989; Osorio and Vorobyev 1996; Sumner and Mollon 2000; Regan et al. 2001) or young nutritious leaves (Dominy and Lucas 2001) against the green foliage of the rain forest.

Spectral Tuning of Vertebrate Visual Pigments

SWS Opsins

SWS pigments exist in two forms based on either SWS1 or SWS2 opsins. Although both may specify pigments with

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λ_{max} values in the violet/blue region of the spectrum, only SWS1 opsins can specify UVS pigments. The SWS1 pigments vary in different species—most notably among the birds and mammals—from a peak in the UV at around 360 nm to a peak in the violet at 390–435 nm. In so doing, they show some of the largest within-class variations in λ_{max} of any naturally occurring visual pigment.

Ancestral SWS1 Pigment. The presence of UVS and VS SWS1 pigments in the amphibians, avians, and mammals indicates that spectral shifts between UV and violet must have occurred several times in the evolution of these vertebrate classes. Phylogenetic analysis suggests that the ancestral vertebrate SWS1 pigment was UVS (Hunt et al. 2001; Shi and Yokoyama 2003; Hunt et al. 2004); with the exception of avian UVS pigments, the major evolutionary event therefore has been the tuning of SWS1 pigments from the UV to the violet region of the spectrum, with the consequent loss of UV sensitivity (fig. 1). The main evolutionary pressures for this to occur may be the protection of the retina from the damaging effect of UV light or an improvement in the quality of the image on the retina.

Origin of VS Pigments in Nonavian Vertebrates. In nonavian vertebrates, VS pigments have arisen directly from the ancestral UVS pigment. In birds, however, the situation is more complicated because phylogenetic data indicate that UVS pigments have arisen secondarily from an ancestral avian VS pigment. Therefore, to fully understand this process, it is necessary to examine the evolution of VS pigments in nonavian vertebrates before considering these events in the avian lineage.

Sequence comparisons of the UVS pigments in fish with the UVS and VS pigments in mammals have identified substitutions at site 86 as good candidates for spectral shifts between the UV and violet (Cowing et al. 2002*a*; Fasick et al. 2002). In fish and lamprey UVS pigments, this site is invariably occupied by Phe (fig. 1), and Phe is retained in UVS pigments of the mouse (*Mus musculus*) and rat (*Rattus norvegicus*). In the VS pigments of the cow (*Bos taurus*) and the pig (*Sus domesticus*), two species from the mammalian order Artiodactyla, or even-toed ungulates, Phe86 is replaced by Tyr86, and site-directed mutagenesis of goldfish (*Carassius auratus*) UVS and bovine VS pigments (Cowing et al. 2002*a*; Fasick et al. 2002) has confirmed that this substitution is responsible for the long-wavelength shift (table 1). The single replacement of Phe by Tyr at site 86 therefore accounts for the evolution of the bovine and porcine VS pigments from the ancestral UVS pigment. VS and UVS pigments are also present in marsupials; in the tammar wallaby (*Macropus eugenii*), a VS pigment is present (Deeb et al. 2003), whereas UVS pigments have been retained by the honey possum (*Tarsipes rostratus*) and the fat-tailed dunnart (*Sminthopsis crassicaudata*; Arrese et al. 2002). Sequencing of the SWS1 pigment in the latter two species reveals that both have retained Phe86 (D. M. Hunt, C. A. Arrese, J. A. Cowing, and Y. A. Oddy, personal observations), whereas the wallaby has Tyr86 (Deeb et al. 2003), identical to ungulate VS pigments. Therefore, a Phe86Tyr substitution is again responsible for long-wavelength tuning; however, this is an example of convergent evolution because the retention of Phe86 in UVS pigments of eutherians (mice and rats) and metatherians (fat-tailed dunnart and honey possum) clearly demonstrates that the Phe86Tyr substitution in VS pigments must have occurred separately in metatherian and eutherian lineages.

The separate origin of VS pigments is again seen in the order Rodentia. The rodents are divided into two suborders, the Sciurognathi, with 11 families, and the Hystricognathi, with 18 families. The mouse and rat, members of the Sciurognathi, both have UVS pigments, as does the hystricognathous caviomorph rodent the Chilean degu (*Octodon degus*; Chávez et al. 2003; Jacobs et al. 2003). However, VS pigments are found in the guinea pig (*Cavia porcellus*), a South American member of the Hystricognathi, and in the gray (*Sciurus carolinensis*) and ground squirrels (*Spermophilus* spp.), members of the Sciurognathi (Jacobs 1976; Jacobs et al. 1976; Jacobs and Deegan 1994; Peichl and Gonzalez-Soriano 1994). The UVS pigments in the mouse and rat have both retained Phe86, whereas the gray squirrel has Tyr86 (Carvalho et al. 2006), as found in ungulates and the tammar wallaby. In contrast, the guinea pig has substituted Phe86 with Val (Parry et al. 2004); the experimental replacement of this residue with Phe is sufficient to shift the λ_{max} of the pigment back into the UV, although the reverse mutation of Phe86Val into goldfish UVS pigment does not cause a long-wavelength shift in the λ_{max}, indicating that Val86 requires other changes in a UVS pigment to generate a long-wavelength shift. In other species with VS pigments, yet more differences are found at site 86. Leu is present in the VS pigment of primates (Nathans et al. 1986; Hunt et al. 1995), Met is present in the VS pigment of the clawed frog (*Xenopus laevis*; Starace and Knox 1998), and Ser is present in all VS pigments of birds (Okano et al. 1992; Das et al. 1999). However, none of these residues, when substituted into goldfish UVS pigment, alters the λ_{max} of the pigment (table 1), indicating that these changes are insufficient by themselves to generate VS pigments (Cowing et al. 2002*a*). In contrast, a Tyr86Ser substitution in bovine VS pigment yields only a minor short-wavelength shift in λ_{max} to 422 nm. Therefore, in the bovine pigment, Ser86 is able to maintain a VS pigment, whereas the same substitution in goldfish UVS does not result in a long-wavelength shift

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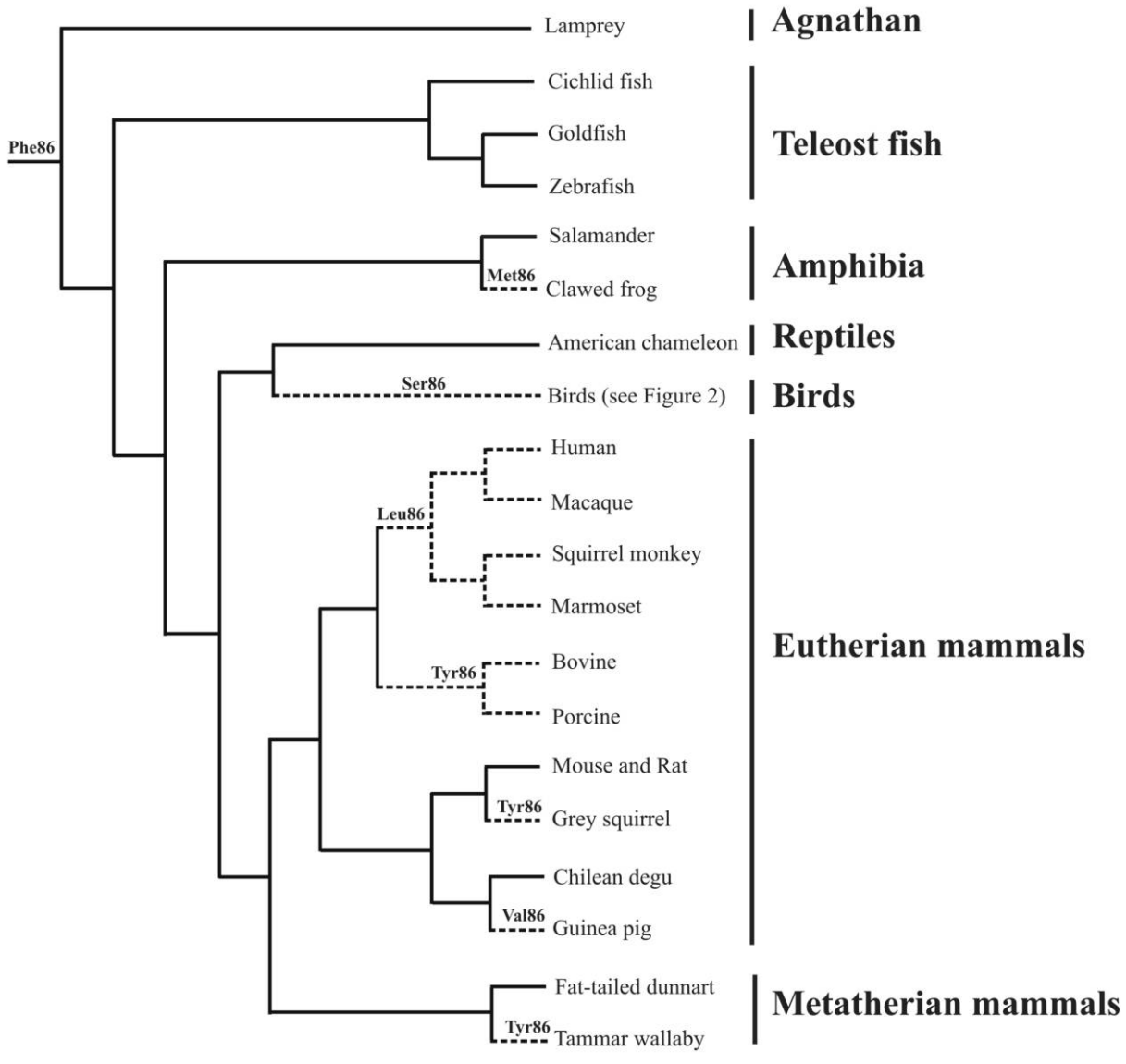

Figure 1: Phylogeny of ultraviolet-sensitive/violet-sensitive (UVS/VS) opsins showing amino acid changes at site 86. Only where a substitution has occurred is the new residue shown on the branches. Solid lines are UVS lineages; dashed lines are VS lineages.

into the violet. This again suggests that as for Val86 and unlike Tyr86, additional substitutions at other sites are required for changes at site 86 to generate a VS pigment.

The tuning of primate VS pigments has been examined in great detail by Yokoyama and Shi (2000). A chimeric opsin comprising transmembrane helices (H) 1–3 from human SWS1 (VS) opsin and H4–7 from mouse SWS1 (UVS) opsin, when expressed and regenerated with retinal, was shown to produce a pigment with λ_{max} very close to that of the native human (VS) pigment. This therefore identified the same region of the opsin protein (H1–3) as important for violet spectral shifts in primates, as in other vertebrates. Subsequently, Shi et al. (2001) demonstrated by site-directed mutagenesis that the combination of the following human residues substituted into mouse UVS pigment—Phe86Leu, Thr93Pro, Ala114Gly, and Ser118Thr—resulted in a pigment with a λ_{max} at 399 nm. However, the residue present at site 114 is not conserved across other primate species and is therefore unlikely to be important, so the key substitutions in the evolution of primate VS pigments from an ancestral UVS pigment are probably Phe86Leu, Thr93Pro, and Ser118Thr.

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Table 1: Site-directed mutagenesis at sites 86, 90, and 116 of ultraviolet-sensitive (UVS) and violet-sensitive (VS) pigments from different species

Pigment and mutation	λ_{max} (nm)	Reference
Goldfish UVS:		
Wild type	358	
Phe86Tyr	413	Cowing et al. 2002*b*
Phe86Val	359	Cowing et al. 2002*b*
Phe86Ser	363	Cowing et al. 2002*b*
Phe86Leu	358	Cowing et al. 2002*b*
Bovine VS:		
Wild type	435	
Tyr86Phe	363	Cowing et al. 2002*b*
Tyr86Ser	422	Cowing et al. 2002*b*
Ser90Cys	431	Fasick et al. 2002
Mouse UVS:		
Wild type	358	
Phe86Tyr	424	Fasick et al. 2002
Guinea pig VS:		
Wild type	420	
Val86Phe	367	Parry et al. 2004
Pigeon VS:		
Wild type	388/393	
Ser90Cys	359	Yokoyama et al. 2000*b*
Budgerigar UVS:		
Wild type	360	
Cys90Ser	420	Wilkie et al. 2000
Chicken VS:		
Wild type	415	
Ser90Cys	369	Yokoyama et al. 2000*b*
Zebra finch UVS:		
Wild type	359	
Cys90Ser	397	Yokoyama et al. 2000*b*

Note: For each species, the indicated amino acid substitution was made into the wild-type sequence, and the resulting opsin was expressed in mammalian cells and regenerated with 11-*cis*-retinal.

Pro93 is also present in the clawed frog VS pigment, combined in this case with Met86. However, a Pro93Thr substitution into the VS pigment has essentially no effect on the λ_{max} of the mutant pigment (Dukkipati et al. 2001), and a Phe86Met substitution into goldfish UVS pigment (Cowing et al. 2002*a*) and a Met86Glu substitution in frog VS pigment (Dukkipati et al. 2001) both failed to generate any spectral shift. Therefore, neither substitution by itself is capable of generating the shift from UVS to VS in the evolution of the frog pigment. Nevertheless, given the role of these two sites in the tuning of other pigments, it would seem likely that both are involved in spectral tuning, although, like in the primate pigments, an additional change elsewhere must also be needed. The pattern of UVS to VS substitutions across the different vertebrate lineages is shown in figure 1.

Origin and Tuning of Avian VS Pigments. Sequence and spectral data exist for only three avian species with VS pigments, the Humboldt penguin (*Spheniscus humboldti*; Wilkie et al. 2000), the domestic pigeon (*Columba livia*; Yokoyama et al. 2000*b*), and the chicken (*Gallus gallus domesticus*; Okano et al. 1992); in all cases, Ser86 is present. In contrast, Ser86 is not found in any of the avian UVS pigments, making the Phe86Ser substitution a good candidate for the generation of avian VS pigments. However, the introduction of Ser86 by site-directed mutagenesis into the goldfish UVS opsin does not generate a spectral shift to longer wavelengths (Cowing et al. 2002*a*; table 1). Recent work by Shi and Yokoyama (2003) has shown that the triple substitution of Phe49Val, Phe86Ser, and Ser118Ala has the effect of shifting a UVS pigment from a λ_{max} of 360 to 374 nm and that the addition of a Leu116Val substitution produces a further shift to 393 nm. Because Val49 and Ala118 are already present in avian UVS pigments, they cannot be involved in the avian long-wavelength shift. The key substitutions in the evolution of avian VS pigments therefore may be Phe86Ser combined with Leu116Val.

The λ_{max} of native VS pigments in different avian species varies from 403 nm in the Humboldt penguin (Bowmaker and Martin 1985) to 418 nm in the chicken (Bowmaker et al. 1997). The SWS1 opsins in these species differ at certain sites that could potentially interact with the chromophore, and site-directed mutagenesis of the budgerigar UVS pigment (Wilkie et al. 2000) has shown that substitution at two of these, Thr93Val and Ala118Thr, which replace the pigeon/penguin residues with those present in chicken, each resulted in a 3-nm long-wavelength shift. If these substitutions cause similar shifts in VS pigments, they may account for the difference in λ_{max} values between the penguin, pigeon (Bowmaker et al. 1997), and chicken VS pigments.

Avian UVS Pigments. Uniquely, avian UVS pigments possess Cys rather than Ser at site 90, and a Cys90Ser substitution into the UVS pigments of the budgerigar (*Melopsittacus undulatus*) and the zebra finch (*Taeniopgyia guttata*) is sufficient to shift the λ_{max} of the pigment from 360 to 420 nm (Wilkie et al. 2000; Yokoyama et al. 2000*b*; Hunt et al. 2004; table 1). Equally, the reverse substitutions of Ser90Cys into the VS pigments of chicken and pigeon (Yokoyama et al. 2000*b*) cause a short-wavelength shift in the λ_{max} into the UV, although the same change in bovine VS pigment is without effect (Fasick et al. 2002). A Ser90Cys substitution into an avian VS pigment is therefore the major mechanism for the evolution of UVS pigments in birds. Note, therefore, that unlike UVS pigments in other vertebrate classes where the ancestral Phe86 residue has been retained, this represents a reinvention of

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UVS pigments from an avian VS ancestral pigment. In these pigments, site 86 may be occupied by Ala, Cys, Ile, Met, or Phe (Wilkie et al. 2000; Yokoyama et al. 2000*b*; Ödeen and Håstad 2003), demonstrating that the particular residue at this site is not important for UV sensitivity, although Ser is never present. It may also be significant that Val at site 116 is replaced in the three avian UVS pigments sequenced so far by either Ala or Met.

Our understanding of the evolution of avian SWS1 pigments has been extended by a recent study of the gene sequence of these pigments in 46 bird species distributed across 14 avian orders (Ödeen and Håstad 2003). The sequencing of a small region of the SWS1 gene that included sites 86–93 showed that although Ser90 is present in the SWS1 pigment of most species, a subset possess Cys90 as follows: three of 21 species from the order Ciconiiformes, four of the eight species from the order Passeriformes, both of two species from the order Psittaciformes, and one of the two species from the order Struthioniformes. From the phylogenetic relationships of the different orders (fig. 2), it would appear that the ancestral avian VS pigment had Ser86, Ser90, and Thr93 and that UVS pigments with Cys90 have evolved at least four times. However, in many of the species examined by Ödeen and Håstad (2003), the λ_{max} of the respective pigments has not been determined, so it has yet to be fully established that all these species possess a UVS pigment. Nevertheless, because site-directed mutagenesis has demonstrated that the possession of Cys90 is sufficient to generate an avian UVS pigment (Wilkie et al. 2000; Yokoyama et al. 2000*b*), it is probable that these species all possess UVS pigments.

Phe86 is substituted in all but two of the avian SWS1 sequences listed by Ödeen and Håstad (2003). The two exceptions are the pigments of the common rhea (*Rhea americana*) and the blue-crowned trogon (*Trogon curucui*). In the former case, Cys90 is present, so the pigment is most likely UVS, whereas Ser90 is present in the blue-crowned trogon, so either Phe86 has been retained in this species from the ancestral vertebrate UVS pigment or this represents a reverse mutation. It would be particularly interesting to obtain spectral data from this species because this may be the only example so far reported in birds where a shift into the UV has been achieved by a Phe86 substitution. Finally, Shi and Yokoyama (2003) have shown by site-directed mutagenesis that Cys86 will also generate a UV shift in a Ser90 pigment. Significantly, Cys86 is present with Ser90 in the pigments of eight of the bird species examined by Ödeen and Håstad (2003); if Cys86 does

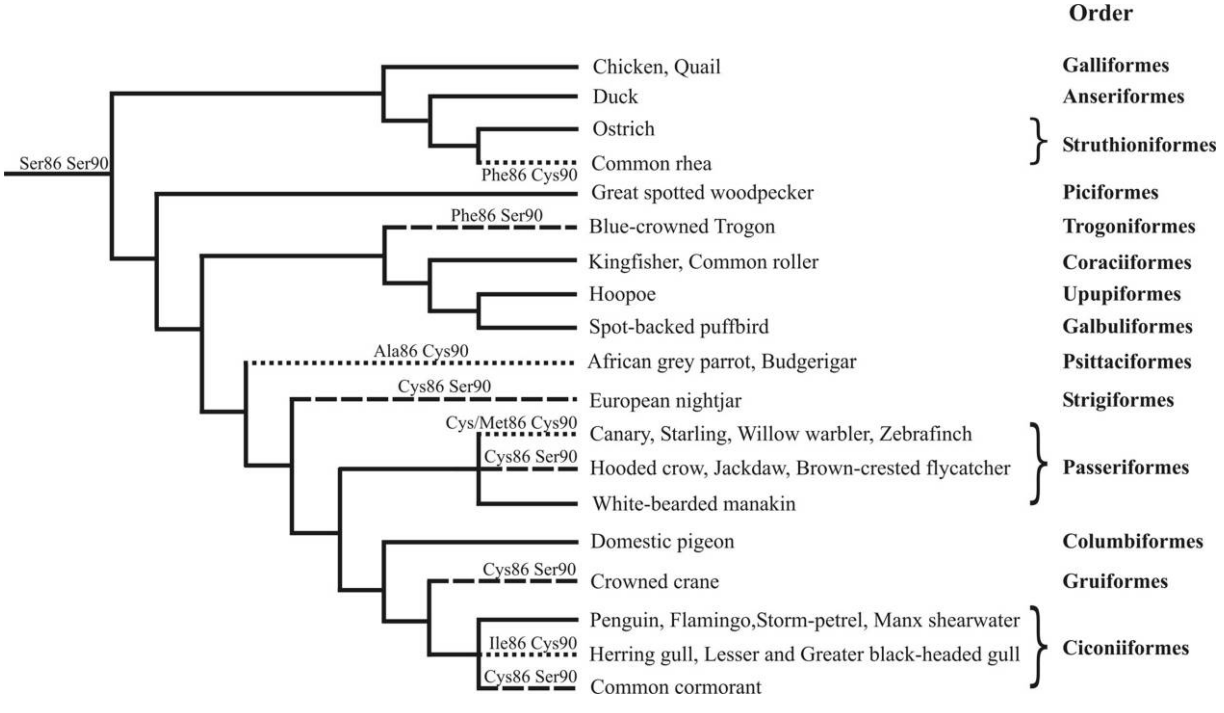

Figure 2: Phylogenetic relationship of the different avian orders showing presence of violet-sensitive (VS) and ultraviolet-sensitive (UVS) ultraviolet/violet (SWS1) pigments in the species so far examined. Dotted lines are UVS lineages with Cys90. Dashed lines are possible UVS lineages with either Phe86 or Cys86. The ancestral avian VS pigment was probably Ser86 and Ser90. Substitutions at these sites are shown on the respective branches. The tree is based on DNA-DNA hybridization data (Sibley and Ahlquist 1990) and is redrawn from Ödeen and Håstad (2003).

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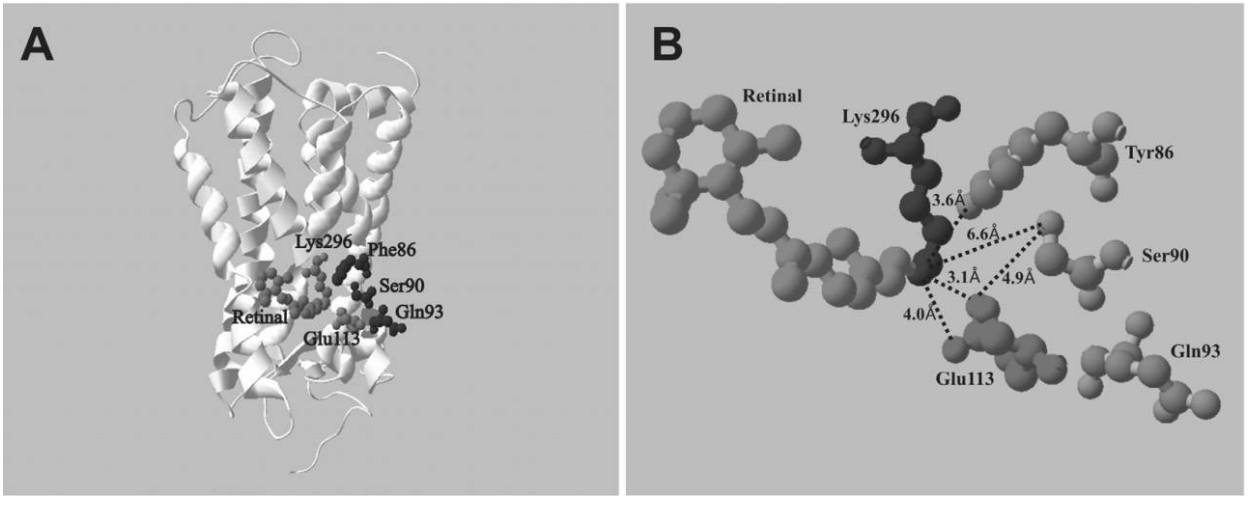

Figure 3: Structural model of goldfish wild-type and mutant ultraviolet/violet (SWS1) pigments. *A*, View of wild-type pigment showing the complete molecule but with portions of helices 3 and 5–7 cut away to reveal retinal, Lys296, the Schiff's base linkage, Glu113, and residues at sites Phe86, Ser90, and Gln93. *B*, Enlarged view showing retinal and key amino acid residues only, with the Phe86Tyr substitution. The model was created using Swiss Model (Guex and Peitsch 1997) and is based on the crystal structure of bovine rhodopsin (Palczewski et al. 2000).

result in a UVS pigment, then this will substantially increase the number of different occasions on which UVS pigments have evolved. It is therefore important to assess this in an avian species with Cys86 in its SWS1 pigment. The full pattern of substitutions at sites 86 and 90 involved in UV/violet shifts in the evolution of SWS1 visual pigments in birds is shown in detail in figure 2.

Generation of UVS and VS Pigments. The generation of UVS pigments can be achieved most simply by the loss of protonation of the Schiff's base. Protonation requires the presence of a charged counterion that is provided by a negatively charged residue (almost always Glu) at site 113 (Nathans 1990); substitution of Glu113Gln in a VS pigment causes a short-wavelength shift in the λ_{max} into the UV, a shift that is reversible at acid pH by an elevated chloride ion concentration, indicating that a protonated VS pigment can be generated by a chloride counterion from solution (Fasick et al. 2002). Replacement of this residue in mouse UVS pigment with uncharged Gln and consequent loss of protonation does not prevent the generation of a UVS pigment (Shi et al. 2001), which again indicates that UVS pigments are unprotonated.

All UVS pigments have retained a Glu113 residue; the alternative mechanism for the generation of a UVS pigment by replacement of this residue with an uncharged residue is never seen. The reason may be that protonation is required even in UVS pigments for the production and breakdown of photointermediates during photoactivation (Dukkipati et al. 2001, 2002). For example, the metarhodopsin I and II forms of mutant frog VS opsins that lack a charged residue at site 113 are substantially more stable than the wild type, thereby prolonging these steps in the photobleaching cycle (Babu et al. 2001).

All the sites found to be involved in the production of VS SWS1 pigments are in the vicinity of the retinylidine Schiff's base linkage and may act to stabilize protonation in pigments with λ_{max} values >390 nm. As shown in figure 3, residues at site 86 and 90, modeled on to the bovine rhodopsin template (Palczewski et al. 2000), are sufficiently close to the Schiff's base to stabilize protonation. In bovine, porcine, wallaby, and squirrel VS pigments, the replacement of Phe by Tyr at site 86 may therefore serve to facilitate the electrostatic stabilization of protonation, although it is less clear how Val86 interacts.

In UVS pigments, a nonpolar amino acid is invariably found at site 86, indicating that the short-wavelength shift may be attributable to the loss of electrostatic stabilization of protonation. In avian pigments, a similar mechanism may account for the shift from VS to UVS arising from the replacement of polar Ser by Cys at site 90. Yokoyama et al. (2000*b*) have proposed that the hydrophobicity of Cys90 removes a water molecule from the vicinity of the Schiff's base and thereby displaces its positive charge. Therefore, under these conditions, the Schiff's base would be effectively unprotonated.

All avian VS pigments possess Ser at sites 86 and 90; Ser at both sites would therefore appear to be required for the stabilization of protonation in avian VS pigments. Significantly, however, a Phe86Ser substitution in goldfish

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(with Ser90) does not by itself generate a long-wavelength shift (Cowing et al. 2002*b*). An additional change is required, identified by Shi and Yokoyama (2003) as a Leu to Val substitution at site 116. The mechanism here may be a conformational change that brings Ser86 to a position within the opsin protein to stabilize protonation.

SWS2 Opsins

The coding sequences for SWS2 opsins have been obtained for only a few species, and spectral tuning studies are limited to the pigment in the newt (*Cynops pyrrhogaster*; Takahashi and Ebrey 2003) and those in the species flock of cottoid fish in Lake Baikal (Bowmaker et al. 1994; Cowing et al. 2002*b*). The newt pigment with a λ_{max} at 474 nm is red shifted compared to pigments in other species, and a comparison of the amino acid sequence of the newt opsin with that of the bullfrog (*Rana catesbeiana*) with a λ_{max} at 430 nm (Hisatomi et al. 1999) identified seven candidate amino acid differences for the spectral shift. Site-directed mutagenesis confirmed that replacement of each of the amino acids present in the newt opsin with those in the bullfrog caused a short-wavelength shift in the λ_{max}, although substitutions at sites 91, 94, 122, 261, and 292 had the greatest effect. In contrast, substitutions at only two sites were identified as causing short-wavelength shifts in the SWS2 visual pigments of the Baikal cottoids; the replacement of Thr with either Gly or Ala at site 116 generates a 5–11-nm shift, whereas a Thr to Ala substitution at site 269 produces a 10-nm shift (Cowing et al. 2002*b*).

The avian SWS2 opsins that have been sequenced range in λ_{max} from 427 nm in the zebra finch and 440 nm in the canary (*Serinus canaria*) to 452 nm in the pigeon and 453 nm in the chicken (Okano et al. 1989; Bowmaker et al. 1997). Amino acid alignments show that none of the sites mutated by Takahashi and Ebrey (2003) shows variation across the avian sequences, whereas site 269 does differ, with Ser present in the two more red-shifted pigments (pigeon and chicken) compared to Cys in the two more blue-shifted pigments (canary and zebra finch). Thr/Ala substitutions at site 269 are a common mechanism for spectral tuning in vertebrate rod and cone pigments (Neitz et al. 1991; Ibbotson et al. 1992; Williams et al. 1992; Shyue et al. 1995; Sun et al. 1997; Das et al. 1999), and expression studies have shown that Thr269Ala results in a 14–15-nm shift in primate and fish RH2 and LWS cone pigments (Asenjo et al. 1994; Yokoyama and Radlwimmer 1999) and in mammalian rod (RH1) pigments (Chan et al. 1992). The red-shifted pigment always possesses a polar residue with a hydroxyl side chain (usually Thr), whereas a nonpolar residue is present in the blue-shifted pigment. This is usually Ala but is Cys with a sulfhydryl side chain in the avian pigments. In a study of the evolution of SWS2 visual pigments, Yokoyama and Tada (2003) also identified substitutions at site 269, together with substitutions at sites 46, 49, and 52, as important in the tuning of avian SWS2 pigments.

RH1 and RH2 Opsins

As mentioned previously, the RH1 rod pigments and the RH2 cone pigments show a much higher identity with each other than with any other class of opsin, consistent with the origin of the RH1 pigment as a duplication of the RH2 cone opsin gene subsequent to the evolution of the four cone pigment classes in vertebrates. Values of λ_{max} for avian RH1 and RH2 pigments have been obtained for >20 species, and in all cases, the two pigments show similar values, with peaks between 497 and 509 nm. This raises the question of whether similar mechanisms are used to spectrally tune the pigments. The two opsins differ at site 122, with Gln in RH2 cone pigments replaced by Glu in RH1 rod pigments. The amino acid at site 122 is one of the residues that forms the chromophore-binding pocket (Palczewski et al. 2000), therefore with the potential to interact directly with the chromophore. This site has been implicated in the determination of the rate of formation and decay of metarhodopsin II, a photointermediate in the activation cycle of rod and cone pigments (Imai et al. 1997). The replacement of Gln in RH2 opsins by Glu in RH1 opsins also constitutes a nonconservative change (polar to charged residue) that, when replicated by site-directed mutagenesis in bovine rod opsin, results in a 15–20-nm shift to shorter wavelengths (Sakmar et al. 1989; Zhukovsky and Oprian 1989). If the presence of Gln122 in the RH2 pigments causes a similar shift in bird pigments, then other substitutions must be present to compensate for this short-wavelength shift. All avian RH1 and RH2 pigments so far sequenced differ at two sites, 222 with Cys in RH1 and Ser in RH2 and 295 with Ala in RH1 and Ser in RH2. As originally proposed by Heath et al. (1997), changes at these two sites may be responsible for causing a long-wavelength shift in the λ_{max} of the RH2 pigments to a spectral location similar to that of the RH1 pigments.

LWS Opsins

The λ_{max} values of avian LWS pigments are mostly between 560 and 570 nm (table 2). However, relatively few sequences are available to assess the mechanisms of spectral tuning. In the LWS opsins of the chicken (Okano et al. 1992), canary (Das et al. 1999), zebra finch (Yokoyama et al. 2000*a*), and pigeon (Kawamura et al. 1999), at least part of the long-wavelength shift is achieved by the presence of a chloride-binding pocket determined by His194

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and Lys197, equivalent to sites 197 and 200 in mammalian LWS opsins (Wang et al. 1993). In mammals, chloride binding is responsible for a long-wavelength shift of >20 nm; where it is absent, as in the mouse LWS pigment as a result of a His194Tyr substitution, the λ_{max} is blue shifted by around 22 nm (Sun et al. 1997).

In primates, the LWS opsin gene exists in two spectral forms that encode the red and green variants of the LWS pigment (Nathans et al. 1986; Ibbotson et al. 1992). The spectral difference of around 30 nm between these two pigments is largely determined by substitution at three sites, 180, 277, and 285, with a polar residue replacing a nonpolar residue in the red-shifted variant (Merbs and Nathans 1993; Asenjo et al. 1994). The same three amino acid substitutions are found in the red and green variants of *Astyanax fasciatus*, the blind cave fish (Yokoyama and Yokoyama 1990). The λ_{max} values of avian LWS pigments are similar to the red variants of primate pigments, and it is not surprising to find that avian pigments possess the same polar residues at these three sites. A few avian species possess LWS pigments that are significantly shortwave shifted (e.g., the Humboldt penguin and the tawny owl *Strix aluco*; see table 2), and it will be interesting to see whether the short-wavelength shifts of these pigments have been achieved by the replacement of polar residues at one or more of the previously mentioned sites. Therefore, overall, the LWS pigments show a level of convergent evolution, with common substitutions at sites 180, 277, and 285 accounting for most of the spectral shifts seen in the evolution of these pigments in the different vertebrate classes (Yokoyama and Radlwimmer 2001).

Avian Photoreceptors

Photoreceptor Types

The avian retina contains a single type of rod photoreceptor, four spectrally distinct classes of single cone, and a single spectral type of double cone. Double cones consist of a larger principal and smaller accessory member, the closely opposed outer segments of which are separated from the outer segments of other photoreceptors—but not each other—by the processes of pigmented epithelium cells (Morris and Shorey 1967); the two members of the double cone are thought to be both optically and electrically coupled (Young and Martin 1984; Smith et al. 1985).

Cone Oil Droplets

The single cones and the principal member of the double cones contain oil droplets at the distal end of their inner segments. In all but one of the single cone types, the oil droplets contain short-wavelength-absorbing carotenoid pigments that spectrally filter the incident light before it reaches the visual pigment in the outer segments (Goldsmith et al. 1984). Pigmented oil droplets act as long-pass cutoff filters and shift the effective sensitivity peak of the cone to a wavelength longer than the λ_{max} of the visual pigment contained in the outer segment (Bowmaker 1977). They also narrow the spectral sensitivity function of the cone and reduce the overlap with adjacent spectral types (Govardovskii 1983; fig. 4). Oil droplets are usually classified according to their cutoff wavelength (λ_{cut}), which is defined as the wavelength of the intercept at the value of maximum absorptance by the line tangent to the long-wavelength limb of the absorptance spectrum at half maximum absorptance (λ_{mid}; Lipetz 1984). Because the optical density of the pigmented oil droplets is usually very high, the λ_{cut} is effectively the wavelength below which no light is transmitted by the oil droplet.

Pigmented oil droplets are found in other vertebrate groups, including turtles (Liebman and Granda 1971, 1975; Loew and Govardovskii 2001), lizards (Barbour et al. 2002; Loew et al. 2002), and lungfish (Robinson 1994). Colorless oil droplets are found in marsupials (Arrese et al. 2002), some monotremes (Walls 1942), geckos (Ellingson et al. 1995), anuran amphibians (Hailman 1976), and chondrostean fishes (Walls 1942); colorless oil droplets are presumably retained in these taxa for their ability to capture and focus light into the outer segments and therefore enhance sensitivity (Ives et al. 1983). Oil droplets are absent from the cones of teleost and elasmobranch fishes (Walls 1942), snakes (Sillman et al. 1997, 2001), crocodilians (Sillman et al. 1991), and placental mammals (Walls 1942).

Visual Pigments

UVS/VS Single Cone Visual Pigments (SWS1 Opsins). The avian SWS1 visual pigment is located in the single cones containing the so-called transparent T-type oil droplets. T-type oil droplets have negligible absorptance from at least 330 to 800 nm and do not contain carotenoid pigments (Goldsmith et al. 1984; Bowmaker et al. 1997; Hart et al. 2000*a*). Consequently, and unlike the oil droplets found in all the other cone types, the T-type droplets do not act as cutoff filters and do not shift the peak sensitivity of the cone relative to the λ_{max} of the visual pigment it contains (Maier and Bowmaker 1993; Goldsmith and Butler 2003).

The SWS1 visual pigments of birds are the most variable in their spectral tuning properties (fig. 5). The measured λ_{max} values fall into two main categories: the UVS visual pigments, with λ_{max} values ranging from approximately 355 nm in the red-billed leothrix (*Leothrix lutea*; Maier and Bowmaker 1993) to 373 nm in the European blackbird

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Table 2: Spectral parameters of cone visual pigments, oil droplets, and ocular media in different bird species and predicted cone spectral sensitivity peaks

Order and specific name	Common name	Visual pigment λ_{max} (nm)				Ocular media $\lambda_{T0.5}$ (nm)	Oil droplet λ_{cut} (nm)			Predicted cone spectral sensitivity peak (nm)				Reference
		SWS1	SWS2	RH2	LWS		C	Y	R	UVS/VS	SWS	MWS	LWS	
Anseriformes:														
Anas platyrhynchos	Mallard duck	415	452	506	567	371	445	506	561	415 (420)	475	535	601	Jane and Bowmaker 1988
Anas platyrhynchos dom.	Aylesbury duck	415	449	501	570	377	445	506	561	415 (420)	473	534	601	Jane and Bowmaker 1988
Anas platyrhynchos dom.	Khaki Campbell duck	426	456	501	570	378	445	506	561	426 (427)	475	534	601	Jane and Bowmaker 1988
Ciconiiformes:														
Puffinus pacificus	Wedge-tailed shearwater	406	450	503	566	335	445	506	562	406 (407)	472	539	601	Hart 2004
Puffinus puffinus	Manx shearwater	402	452	…	…	…	…	…	…	…	…	…	…	Bowmaker et al. 1997
Spheniscus humboldti	Humboldt penguin	403	450	…	543	…	…	…	…	…	…	…	…	Bowmaker and Martin 1985
Columbiformes:														
Columba livia	Feral pigeon	404	452	506	566	S	448	514	586	404 (406)	480	547	620	Bowmaker et al. 1997
Galliformes:														
Coturnix coturnix japonica	Japanese quail	418	450	505	567	P	446	511	566	418 (428)	473	538	603	Bowmaker et al. 1993
Gallus gallus dom.	Chicken	418	453	507	571	P	443	505	561	418 (428)	475	537	603	Bowmaker et al. 1997
Meleagris gallopavo	Turkey	420	460	505	563	358	437	490	514	…	…	…	…	Hart et al. 1999
Pavo cristatus	Peafowl	424	458	505	567	365	449	511	569	424 (432)	479	539	607	Hart 2002
Passeriformes:														
Amadina fasciata	Cutthroat finch	370	447	500	563	318	423	516	575	370 (374)	461	543	609	Hart et al. 2000*a*
Corvus frugilegus	Rook	…	…	497	565	…	…	…	…	…	…	…	…	Bowmaker 1979
Erythrura gouldiae	Gouldian finch	370	440	500	562	317	422	513	572	370 (374)	453	541	607	Hart et al. 2000*a*
Leothrix lutea	Red-billed leothrix	355[a]	454	499	568	S	392	506	566	355 (362)	462	538	605	Maier and Bowmaker 1993
Lonchura maja	White-headed munia	373	446	500	562	318	422	510	567	373 (376)	457	535	603	Hart et al. 2000*a*
Neochmia modesta	Plum-headed finch	373	442	500	565	316	415	514	568	373 (375)	451	543	605	Hart et al. 2000*a*

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Parus caeruleus	Blue tit	372	449	502	563	317	413	508	573	372 (374)	453	539	607	Hart et al. 2000*b*
Passer domesticus	House sparrow	…	445	503	563	…	…	…	…	…	…	…	…	N. S. Hart and J. C. Partridge, unpublished data
Serinus canaria	Canary	363	440	501	567	S	414	506	578	363 (370)	451	540	613	Das et al. 1999
Sturnus vulgaris	Starling	362	449	504	563	338	399	515	573	362 (369)	453	545	607	Hart et al. 1998
Taeniopygia guttata	Zebra finch	359[b]	427	505	566	G	414	510	571	359 (359)	445	546	608	Bowmaker et al. 1997; Yokoyama et al. 2000*a*
Turdus merula	Blackbird	373	454	504	557	343	414	515	570	373 (378)	461	543	603	Hart et al. 2000*b*
Psittaciformes:														
Melopsittacus undulatus	Budgerigar	371	440	499	566	S	411	507	566	371 (376)	448	545	605	Bowmaker et al. 1997
Strigiformes:														
Strix aluco	Tawny owl	…	463	503	555	…	…	…	…	…	…	…	…	Bowmaker and Martin 1978
Struthioniformes:														
Rhea Americana	Rhea	…	447	506	571	O	417	506	556	…	463	537	601	Wright and Bowmaker 2001
Struthio camelus	Ostrich	405	445	506	570	377	417	506	552	405 (412)	459	539	601	Wright and Bowmaker 2001
Tinamiformes:														
Nothoprocta cinerascens cinerascens	Brushland tinamou	…	…	?498	564	…	…	…	…	…	…	…	…	Sillman et al. 1981
Nothoprocta perdicaria sanborni	Chilean tinamou	…	…	…	566	…	…	…	…	…	…	…	…	Sillman et al. 1981

Note: λ_{cut} = cut-off wavelength, λ_{max} = wavelength of maximum absorbance, $\lambda_{T0.5}$ = wavelength of 0.5 transmittance. Predicted spectral sensitivities take into account the spectral filtering effect of the C-, Y-, and R-type oil droplets located in the short- (SWS), medium- (MWS), and long-wavelength-sensitive (LWS) single cones and the preretinal ocular media. Values in parentheses in the ultraviolet-sensitive/violet-sensitive (UVS/VS) spectral sensitivity column represent peak wavelengths when the effect of absorption by the ocular media is also taken into account. The spectral locations of the SWS, MWS, and LWS single cone sensitivity peaks are not affected by ocular media absorption. Where ocular media spectra (complete or lens) were not available for the calculations of spectral sensitivity, the ocular media of a phylogenetically closely related species were used for the purposes of comparison: S = starling ocular media, P = peafowl ocular media, O = ostrich ocular media, G = gouldian finch ocular media. Visual pigment absorptance was modeled using the A_1 visual pigment templates of Govardovskii et al. (2000). Outer segments were assumed to be 16 μm long (Morris and Shorey 1967) and to have a specific (decadic) absorbance of 0.014 μm^{-1} (Bowmaker and Knowles 1977). Spectral sensitivities were not calculated for species for which oil droplet spectra were not available or showed evidence of carotenoid depletion.

[a] Approximate λ_{max} value only, because of limited spectral data.

[b] λ_{max} obtained from spectrophotometric measurement of reconstituted, in vitro expressed SWS1 opsin protein.

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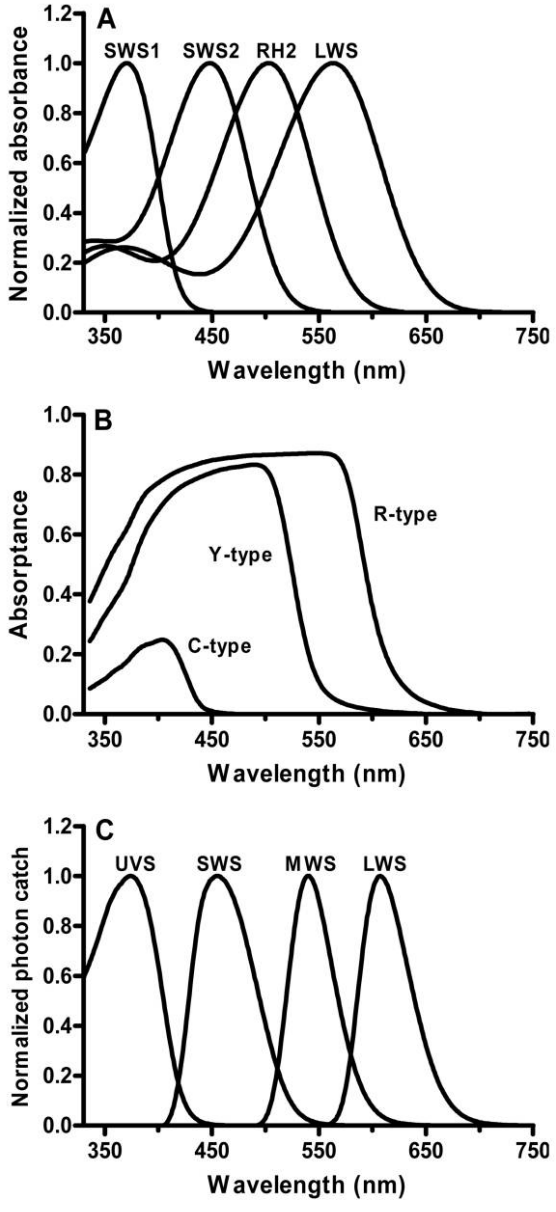

Figure 4: Spectral characteristics of single cone photoreceptors in the blue tit (*Parus caeruleus*; Hart et al. 2000*b*). *A*, Visual pigment absorbance spectra with λ_{max} values at 372 (ultraviolet/violet pigments [SWS1]), 449 (short-wavelength-sensitive pigments [SWS2]), 502 (medium-wavelength-sensitive pigments [MWS; RH2]), and 563 nm (long-wavelength-sensitive pigments [LWS]) are represented using the visual pigment templates given by Govardovskii et al. (2000). *B*, Absorptance spectra of pigmented C-, Y-, and R-type oil droplets found in the SWS (SWS2 opsin), MWS (RH2 opsin), and LWS (LWS opsin) single cones. T-type oil droplets found in the ultraviolet-sensitive/violet-sensitive single cones have negligible absorption from 300 to 800 nm and are not shown. *C*, Predicted photon catches (quantal spectral sensitivities) for the four types of single cone photoreceptor when the effect of spectral filtering by the oil droplets is taken into consideration (for more details, see note to table 2).

(*Turdus merula*; Hart et al. 2000*b*), and the VS visual pigments, with λ_{max} values ranging from 402 nm in the Manx shearwater (*Puffinus pacificus*; Bowmaker et al. 1997) to 426 nm in the Khaki Campbell duck (*Anas platyrhynchos domesticus*; Jane and Bowmaker 1988).

The large variation in avian SWS1 visual pigment λ_{max} is intriguing, and there is as yet no clearly defined functional explanation. Certainly, the λ_{max} of the SWS1 visual pigment may be determined to some extent by phylogeny because closely related species tend to have similar SWS1 visual pigment λ_{max} values. For example, galliform species such as the chicken (*Gallus gallus domesticus*; Bowmaker et al. 1997), turkey (*Meleagris gallopavo*; Hart et al. 1999), and peafowl (*Pavo cristatus*; Hart 2002) have VS SWS1 visual pigments with λ_{max} around 418–424 nm. Columbiform (domestic pigeon; Bowmaker et al. 1997) and ciconiiform (Manx shearwater: Bowmaker et al. 1997; Humboldt penguin: Bowmaker and Martin 1985; wedge-tailed shearwater *Puffinus pacificus*: Hart 2004) species, which are more closely related to each other than they are to other bird orders (Sibley and Ahlquist 1990), have slightly different VS SWS1 visual pigments, with λ_{max} around 402–406 nm. Candidate amino acid substitutions potentially responsible for these variations in avian VS visual pigment λ_{max} are discussed in "Origin and Tuning of Avian VS Pigments." Passeriforms are generally characterized by UVS SWS1 visual pigments (table 2). However, results from microspectrophotometric studies are limited to around 25 of the almost 10,000 extant bird species (Peterson 1999; Clements 2000), and so the scope for comparison is currently limited. Further insights may be obtained from the study of SWS1 opsin gene sequences.

Optical factors may also influence the spectral tuning of the SWS1 visual pigment. The short-wavelength limit to photoreception is set by the spectral absorption properties of the ocular media, principally the cornea and lens. From measurements of only a handful of species (see table 2), it is evident that birds with UVS SWS1 visual pigments tend to have ocular media that transmit more short-wavelength light than the ocular media of species with VS SWS1 visual pigments, although it is not known whether the ocular media drive the spectral tuning of the SWS1 visual pigment or vice versa (Hart 2001*b*). Moreover, in the species from which these data have been obtained, it is not known whether the increase in transmission of short wavelengths is a result of a reduction in corneal/lenticular pigmentation or a direct consequence of the reduction in optical path length in the smaller eyes.

The independent evolution of UVS SWS1 visual pigments in several different bird orders suggests that there is a selective advantage to be gained from the ability to detect UV wavelengths, despite the considerable costs associated with the transmission of UV light to the retina.

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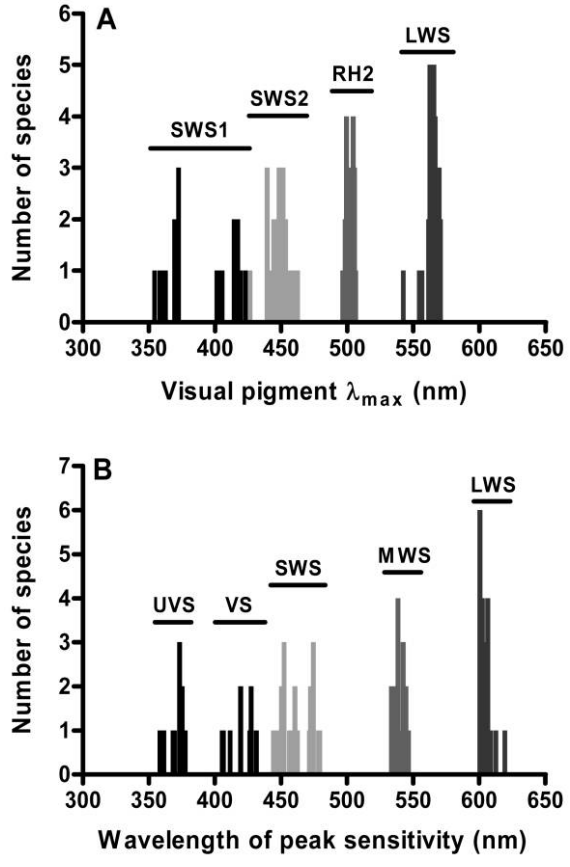

Figure 5: Histograms showing the spectral distribution of (*A*) avian cone visual pigment peak absorbance (λ_{max}) values and (*B*) the predicted spectral sensitivity peaks of the different single cones. SWS1, SWS2, RH2, and LWS refer to the visual pigment opsin types found in the ultraviolet-sensitive/violet-sensitive, short-wavelength-sensitive, medium-wavelength-sensitive, and long-wavelength-sensitive single cones, respectively.

For example, UV wavelengths are known to cause damage to the retina (Ham et al. 1976; Organisciak and Winkler 1994), and this is often cited as a reason for the presence of short-wavelength-absorbing (yellow) filters in the eyes of mammals (Douglas and Marshall 1999). Allowing UV wavelengths to enter the eye also has consequences for optical performance. The UV wavelengths are scattered by the ocular tissues to a greater extent than longer wavelengths, potentially degrading the retinal image (Lythgoe 1979). Moreover, longitudinal chromatic aberration (LCA) in the optical apparatus means that short-wavelength light will be focused in a different plane than longer wavelengths, leading to defocus and blurring of the retinal image (Mandelman and Sivak 1983; Rohrer et al. 1992). Therefore, we might expect birds with larger eyes to use VS SWS1 visual pigments in order to improve image quality, and this is generally the case, although the importance of the defocus due to LCA is dependent, among other things, on the spacing of the different cone types in the retina (i.e., resolving power). We might also expect birds that must detect objects at a distance to use VS rather than UVS SWS1 visual pigments because scattering of light by the atmosphere is inversely proportional to the fourth power of the wavelength and, as such, is considerably worse at UV wavelengths compared to violet (or longer) wavelengths. Evidence from the analysis of SWS1 opsin sequences suggests that birds of prey, such as the buzzard (*Buteo buteo*), which are well known for their excellent visual acuity, do probably have VS rather than UVS SWS1 visual pigments (Ödeen and Håstad 2003).

SWS Single Cone Visual Pigments (SWS2 Opsins). The SWS2 visual pigments of birds are found in the SWS single cones with colorless C-type oil droplets. Visual pigment λ_{max} values measured microspectrophotometrically range from 427 nm in the zebra finch (Bowmaker et al. 1997) to 463 nm in the tawny owl (Bowmaker and Martin 1978). The C-type oil droplets contain carotenoid pigments that absorb strongly below about 450 nm and appear either colorless or pale green, depending on the spectral location of the λ_{cut} (Goldsmith et al. 1984; Partridge 1989; Hart 2001*a*), which varies considerably between species (392–449 nm; table 2).

Selective absorption of short wavelengths by the C-type oil droplet will shift the spectral sensitivity of the SWS cones to longer wavelengths than the λ_{max} of the SWS2 visual pigment by up to 28 nm (table 2; fig. 4). Moreover, the λ_{cut} of the C-type oil droplet (Spearman's $r_s = 0.774$, $P < .001$, $n = 18$), the λ_{max} of the SWS2 visual pigment (Spearman's $r_s = 0.738$, $P < .001$, $n = 21$), and, consequently, the estimated wavelength of peak sensitivity of the SWS cone (Spearman's $r_s = 0.791$, $P < .001$, $n = 18$) are all positively correlated with the λ_{max} of the UVS/VS SWS1 visual pigment. This can clearly be seen in the bimodal distribution of SWS cone spectral sensitivity peaks shown in figure 5. This finding suggests that the spectral tuning of UVS/VS and SWS cone types within a given species are functionally and/or evolutionarily related. It has been proposed that a reduction in the overlap of adjacent spectral classes improves color constancy (Osorio et al. 1997; Dyer 1999, 2001) and increases chromatic contrast (Barlow 1982; Vorobyev et al. 1998; Vorobyev 2003). This principle holds for the effect of all the colored oil droplets on their respective cone spectral sensitivities but in particular may help to explain why birds with VS SWS1 visual pigments have SWS cones with a longwave-shifted sensitivity peak compared to species with UVS SWS1 visual pigments.

Rod Visual Pigments (RH1 Opsins). The avian RH1 visual

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pigment is located in the rod photoreceptors and shows little interspecific variation (λ_{max} 501–509 nm). The RH1 visual pigment is spectrally very similar to the avian RH2 visual pigment located in the MWS single cones. Most vertebrates have their rod RH1 visual pigment λ_{max} close to 500 nm, although systematic variations in rod λ_{max} are often seen in fish, with deep-sea species having λ_{max} values shifted toward shorter wavelengths to match the most abundant wavelengths available for vision at depth (Denton and Warren 1957; Munz 1957; Crescitelli et al. 1985; Lythgoe and Partridge 1989).

MWS Single Cone Visual Pigments (RH2 Opsins). The RH2 visual pigment is located in the MWS single cone that contains a golden yellow Y-type oil droplet. Within a given bird species, the λ_{max} of the RH2 visual pigment (499–506 nm) is spectrally almost identical to that of the rod RH1 visual pigment (Bowmaker et al. 1997; Hart 2001*b*). However, the Y-type oil droplets absorb strongly below about 530 nm (λ_{cut} 505–516 nm) and shift the effective peak spectral sensitivity of the MWS cones some 30–40 nm toward longer wavelengths (table 2).

LWS Single and Double Cone Visual Pigments (LWS Opsins). The avian LWS opsin is located in the LWS single cones containing orange or red R-type oil droplets and both the principal and accessory members of the LWS double cone pair. LWS visual pigment λ_{max} values range from 543 nm in the Humboldt penguin (Bowmaker and Martin 1985) to 571 nm in the rhea (Wright and Bowmaker 2001). The R-type droplets absorb strongly below about 600 nm (λ_{cut} 552–586 nm; table 2) and shift the effective peak spectral sensitivity of the LWS single cone toward longer wavelengths (peak 601–620 nm). As previously described, the majority of avian LWS visual pigments have their λ_{max} between 555 and 571 nm. The short-wavelength-shifted LWS visual pigment of the Humboldt penguin (together with a less densely pigmented R-type droplet) is presumably an adaptation to increase visual sensitivity at depth in the ocean where longer wavelengths of light are attenuated more rapidly than the rest of the visible spectrum (Bowmaker and Martin 1985).

The principal member of the double cone pair always contains an oil droplet (P-type) that can appear colorless, pale green, or even yellow, depending on λ_{cut} (Partridge 1989; Hart 2001*a*). The spectral absorptance characteristics of P-type oil droplets vary both between species and across the retina. For example, in European starlings (*Sturnus vulgaris*; Hart et al. 1998), peafowl (Hart 2002), and white-headed munias (*Lonchura maja*; Hart et al. 2000*a*), P-type oil droplets in the ventral retina have λ_{cut} values at considerably longer wavelengths (471–489 nm) than those in the dorsal retina (407–419 nm). This intraretinal variation in spectral filtering may be related to differences in the relative intensity and spectral distribution of light impinging on the dorsal retina (from the ground) compared to the ventral retina (from the sky; Hart 2001*b*). The accessory member of the double cone pair sometimes contains a small oil droplet (A-type) or a diffuse aggregation of carotenoid at the distal end of the inner segment (Bowmaker and Knowles 1977; Jane and Bowmaker 1988; Maier and Bowmaker 1993; Bowmaker et al. 1997; Hart et al. 1998).

The spectral absorptance properties of both the P- and A-type droplets are usually sufficient to block transmission of short wavelengths to the outer segment but will not shift the peak sensitivity of the double cones away from that of the LWS visual pigment. Because double cones are the most abundant cone type in the majority of avian retinas, accounting for 29%–56% of the cone photoreceptor population (Hart 2001*a*), and because the wavelength of peak sensitivity of the LWS single cones is determined largely by the spectral transmittance properties of the R-type oil droplets, it is possible that selection pressures determining the precise λ_{max} of the LWS visual pigment are acting predominantly on the double cones.

Double cones are found in the retinas of birds, amphibians and reptiles, marsupial and some monotreme (but not placental) mammals, and teleost, holostean, chondrostean, and some dipnoan (but not chondrichthian) fishes (Walls 1942; Fang et al. 2004). In teleosts, paired cones are commonly referred to as twin rather than double cones because in many instances the two members are more equal in size and more symmetrical in shape than those of other taxa, which usually appear quite distinct in size and morphology. The function of double or twin cones in any animal is still largely a matter of conjecture, although in birds, at least, there is some evidence that they subserve achromatic (rather than chromatic) visual tasks, such as the detection of motion or the discrimination of fine spatial detail. Extracellular recordings from single cells in the nuclei of the accessory optic system, which mediates compensatory optomotor movements of the eyes (or head) when the head (or body) moves relative to the surroundings, show that the spectral sensitivity of this response closely matches the spectral sensitivity of the double cones, at least in pigeons (von Campenhausen and Kirschfeld 1998). However, motion-sensitive neurons in the optic tectum of the pigeon still respond to equiluminant chromatic borders (Sun and Frost 1997), suggesting that not all motion detection is color-blind.

Behaviorally measured spectral sensitivity thresholds in the pigeon (Remy and Emmerton 1989), red-billed leothrix (Maier 1992), and budgerigar (Goldsmith and Butler 2003) conform closely to the receptor-noise-modulated spectral sensitivity functions of the four single

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cone types in their retinas, implying that double cones are not used for color discrimination (Vorobyev and Osorio 1998; Goldsmith and Butler 2003). Moreover, chickens are unable to discriminate between fine textures with balanced second-order spatial statistics (isodipole textures; reviewed in Victor and Conte 1996; Osorio et al. 1999*b*) and textures that differ only in the orientation of their elements (Jones and Osorio 2004), when the textures present either an intensity or a chromatic contrast to the single cones but are equiluminant to the double cones. This suggests that visual mechanisms for form vision in birds are achromatic and mediated largely by the double cones (Osorio and Vorobyev 2005).

Double cones have also been implicated in the detection of the orientation of the electric vector (e-vector; plane of polarization) of polarized light (Young and Martin 1984). Polarization vision has been investigated in teleost fish using both behavioral (e.g., Hawryshyn and Bolger 1990) and electrophysiological paradigms (e.g., Hawryshyn et al. 2003), and it appears that only species with photoreceptor mosaics comprising regular, orthogonally orientated double (twin) cones are capable of e-vector discrimination, although the precise mechanism is still unclear (Hawryshyn 2000). However, there is as yet no direct evidence for the ability of birds to detect the e-vector of polarized light (see Coemans et al. 1994; Vos Hzn et al. 1995; Greenwood et al. 2003), and this issue remains controversial.

Visual Ecology and the Spectral Tuning of Photoreceptor Sensitivities

Some vertebrates, most notably fish, exhibit large interspecific variations in the number and spectral absorbance characteristics of their photoreceptors. In particular, the rod and cone visual pigments of deep-dwelling fish are usually shifted toward shorter wavelengths to match the spectral distribution of the ambient light at depth (Denton and Warren 1957; Munz 1958; Crescitelli et al. 1985; Bowmaker et al. 1994; Douglas et al. 1995). More subtle variations in cone visual pigment λ_{max} are observed between closely related fish species that inhabit different water bodies with differing spectral transmission properties (Lythgoe et al. 1994; Jokela et al. 2003) or even different microhabitats within a single body of water (Cummings and Partridge 2001).

With the exception of the variation in SWS1 visual pigment λ_{max}, the spectral sensitivities of the different cone types in birds are remarkably similar, despite considerable interspecific variation in habitat type and foraging method (Hart and Vorobyev 2005; table 2; fig. 5). The only exception identified to date is the penguin, the LWS visual pigment λ_{max} of which occurs at considerably shorter wavelengths than in other birds and is evidently an adaptation to the restricted spectral distribution of light at depth underwater. The avian visual system is also very similar to that of the turtles, which occupy quite different habitats than most diurnal terrestrial birds (Liebman and Granda 1971; Loew and Govardovskii 2001). The possession of four cone types is also shared by the lizards, and the spectral tuning of their cone photoreceptors is similar, the only notable difference being the presence of a yellow rather than a red oil droplet in the LWS single cones (Barbour et al. 2002; Loew et al. 2002).

Animals with four cone types and evenly spaced spectral sensitivities probably have a color vision system that is capable of making fine spectral discriminations over much of the visible spectrum. Therefore, in order to modulate their spectral sensitivities in response to specific microhabitat conditions, birds may resort to varying the relative proportions of the different cone types (Goldsmith et al. 1984; Partridge 1989; Hart 2001*a*). Some fish are thought to use a similar strategy (Fuller et al. 2003) or even change the relative expression of the different opsin proteins (Fuller et al. 2004). Given the elaborate and often (at least to our eyes) brightly colored plumage of birds and its potential significance as an indicator of genetic fitness (e.g., Hamilton and Zuk 1982; Petrie 1994; Limbourg et al. 2004), it is tempting to try to correlate aspects of the visual system with plumage coloration. Indeed, the behavioral significance of plumage reflectance in the UV region of the spectrum, where, coincidentally, there is the most interspecific variability in avian photoreceptor spectral tuning, has received much attention in recent years, largely because this waveband has been overlooked in most earlier assessments of color (see Bennett et al. 1994). It is evident that UV reflectance is integral to the assessment of color by birds (Osorio et al. 1999*a*; Smith et al. 2002) and may even have special significance for intraspecific communication (e.g., Bennett et al. 1996; Hausmann et al. 2003; Håstad et al. 2005). However, there is as yet no evidence that avian visual systems have evolved to facilitate the detection of specific types of plumage reflectance (UV reflecting or otherwise). Indeed, a study on the visual systems of four estrildid finches that differed markedly in their plumage reflectance spectra both within and between species failed to show any significant differences in the spectral tuning of their visual pigments (Hart et al. 2000*a*). It may be that body coloration is designed to take advantage of existing visual mechanisms that have evolved for other tasks, such as prey detection and predator avoidance (Lythgoe 1979). However, because so little is known about the visual abilities and specializations of the vast majority of bird species and the types of visual task they must perform on a daily basis, it is perhaps too early to speculate on adaptive variation in photoreceptor spectral tuning char-

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acteristics, and there is clearly much scope for further investigation in this area.

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