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ORIGINAL PAPER

Pollinating birds differ in spectral sensitivity

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Abstract Pollinating animals and their angiosperm hosts often show strong co-adaptation in traits that increase the likelihood of a successful transfer of pollen and nutrient rewards. One such adaptation is the reported colour difference caused by unequal distribution of anthocyanidin pigments amongst plant species visited by hummingbirds and passerines. This phenomenon has been suggested to reflect possible differences in the colour vision of these pollinating birds. The presence of any such difference in colour vision would arguably affect the ecological and evolutionary interactions between flowers and their visitors, accentuating differences in floral displays and attractiveness of plants to the favoured avian pollinators. We have tested for differences in colour vision, as indicated by the amino acid present at certain key positions in the short-wavelength-sensitive type 1 (SWS1) visual pigment opsin, between the major groups of pollinating birds: the non-passerine Trochilidae (hummingbirds), the passerine Meliphagidae (honeyeaters) and Nectariniidae (sunbirds) plus five other Passerida passerine families. The results reveal gross spectral sensitivity differences between hummingbirds and honeyeaters, on the one hand, and the Passerida species, on the other.

Keywords Colour vision · Pollination · SWS1 pigment opsin · UV sensitivity · Ornithophily

List of abbreviations

bp	Base pair
λ_{max}	Wavelength of maximum absorbance
MSP	Microspectrophotometry
PCR	Polymerase chain reaction
SWS1	Short-wavelength-sensitive type one
UVS	Ultraviolet sensitive
VS	Violet sensitive

Introduction

The study of the evolutionary interaction between colouration of ornithophilous flowers and the colour vision of their avian pollinators is a promising field to both vision physiologists and ecologists, yet relatively unexplored. Diurnal birds have perhaps the most sophisticated visual system of all vertebrates, well developed for detecting colour, brightness and motion (Meyer 1977; Bowmaker et al. 1997). It drives many aspects of their behaviour, such as predator avoidance, mate selection and foraging (Walls 1942; Lythgoe 1979), including nectar feeding. Nectarivory/pollination has evolved independently in the ancestors of several different bird families (Cronk and Ojeda 2008), where at least two, Trochilidae and Nectariniidae (hummingbirds and sunbirds), have converged (see Ericson et al. 2006; Hackett et al. 2008) with a high degree of similarity, both in ecology and in plumage colouration. Vision physiological data on these groups is limited, but it has been suggested that differences in floral pigment mixtures may reflect potential differences in the colour vision of the pollinating birds (Scogin 1988).

The sequences presented in this study are available at GenBank with acc nos: GQ305950, GQ305951, GQ305954–GQ305968.

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Floral pigments such as anthocyanidins are important contributors to the light-reflecting characteristics of flower structures. The three major types of anthocyanidin are pelargonidin, cyanidin and delphinidin (Cronk and Ojeda 2008), where delphinidin pigmentation is relatively uncommon amongst ornithophilous flowers (Scogin 1988). The shift in floral colouration resulting from differences in pigment content appears to affect visibility to birds: red flowers being slightly more discriminable than those of other colours to the green-backed firecrown hummingbird *Sephanoides sephanoides* Lesson (Herrera et al. 2008). Intriguingly, there is also a difference in pigmentation among flowers pollinated by different bird species, with the prevalence of pelargonidin compared to cyanidin being relatively high in hummingbird-pollinated species, as opposed to those pollinated by other birds (Scogin 1988).

At least two discrete types of colour vision have been demonstrated in diurnal birds (Cuthill et al. 2000). They are distinguished by the maximum absorbance wavelengths ($\lambda_{\max}$) of the two cone classes that are sensitive to short wavelengths. On the basis of retinal microspectrophotometry (MSP) measurements and in vitro mutation studies, the short-wavelength-sensitive type 1 (SWS1) class shows the largest between-species variation of all cone classes (Hart and Hunt 2007). The SWS1 cone opsin generates visual pigments sensitive to the ultraviolet and violet region of the spectrum with the $\lambda_{\max}$ of the ultraviolet-sensitive type (UVS) falling between 355 and 380 nm and that of the violet-sensitive type (VS) between 402 and 426 nm (see MSP data references in Ödeen et al. 2009). The SWS2 cone class ($\lambda_{\max}$ 430–463 nm) is also shifted towards shorter wavelengths in UVS than in VS birds, but less so than SWS1 (Hart 2001, 2004).

The SWS1 $\lambda_{\max}$ in avian retinae closely follows amino acid sequence variation in the SWS1 opsin gene. In vitro mutation studies have demonstrated that $\lambda_{\max}$ can be predicted purely on the basis of the opsin's amino acid sequence (Wilkie et al. 2000; Yokoyama et al. 2000; Shi and Yokoyama 2003; Carvalho et al. 2007). The budgerigar wild-type pigment's $\lambda_{\max}$ of 371 nm is shifted by the substitution of alanine for serine in aa-position 86 (A86S: numbering referring to bovine rhodopsin) −1 nm (A86C not at all), cysteine for serine at 90 (C90S) +35 nm (+38 nm in the zebrafinch *Taeniopygia guttata*: Yokoyama et al. 2000), threonine for valine at 93 (T93V) +3 nm and alanine for threonine at 118 (A118T) +3 nm. Also S86F (serine to phenylalanine) has been demonstrated to short-wave shift pigeon and chicken SWS1 pigments in vitro, by 31 and 47 nm, respectively (Carvalho et al. 2007). The spectral absorptance properties of the pigmented cone oil droplets can be predicted on the basis of the $\lambda_{\max}$ of the visual pigment the cones contain (Hart and Vorobyev 2005), due to the covariance of these traits. The entire cone sensitivity including the filtering effects of the oil droplet can, therefore, be estimated from the opsin sequence alone. Since spectral tuning of the SWS1 single cone is under such simple genetic control, it becomes possible to reliably identify the type of short-wavelength sensitivity present in a bird merely from a sample of genomic DNA (Ödeen et al. 2009).

Using such an approach (Ödeen and Håstad 2003), we devoted this study to testing for gross differences in colour vision between primary families of passerine and non-passerine pollinating birds: the non-passerine Trochilidae (New World), the oscine passerine but non-Passerida Meliphagidae (honeyeaters, Australia, Oceania), and the Passerida Nectariniidae (Africa to Australasia), Promeropidae (sugarbirds, southern Africa), Icteridae (New World orioles), Zosteropidae (white eyes, Africa to Australasia), Thraupidae (honeycreepers, American tropics) and Drepanidinae (Family Fringillidae, Hawaiian honeycreepers). The presence of any such difference in colour vision would arguably affect the ecological and evolutionary interactions between ornithophilous flowers and their visitors, accentuating differences in floral displays and attractiveness of plant taxa to avian pollinators.

Materials and methods

Our material comprised up to five species from each of eight bird families (Table 1). We isolated genomic DNA from museum tissue collections, using a GeneMole® automated nucleic acid extraction instrument (Mole Genetics) and amplified a key fragment of the SWS1 opsin gene containing the residues of amino acid positions 81–94 (following bovine rhodopsin numbering), all located in the second α-helical transmembrane region. Nested PCR with the primer pair SU193a/SU306b was performed on Trochilidae PCR templates amplified with primer pair SU161a/SU306b (primers sequences in Ödeen and Håstad 2003). Otherwise, we followed the protocols outlined in Ödeen et al. (2009). After translating the DNA sequences, we calculated $\lambda_{\max}$ from amino acid substitutions in the spectral tuning sites 86, 90 and 93, using budgerigar *Melopsittacus undulatus* L. (A86, C90, T83; Wilkie et al. 2000) as a template (see above).

Results

PCR and sequencing produced up to 119 bp long double-stranded sequences. In contrast to hummingbirds (Trochilidae) and the basal (Barker et al. 2004) oscine passerine honeyeaters (Melphagidae), nectarivorous Passerida oscine passerines carry the UV-tuning amino acid cysteine in position 90 in their SWS1 opsin genes (Table 1). We found no

Table 1 Species of pollinating birds, with wavelength of maximum absorbance (λ_{max}) predicted from SWS1 opsin gene fragment amino acid sequences and type of colour vision distinguished by λ_{max} (see text)

Order (clade)	Family	Species	Common name	Voucher/sample[a]	aa seq. 84–94	λ_{max} nm	Colour vision
Apodiformes	Trochilidae	*Phaethornis pretrei*	Planalto hermit	NRM 967134	FM**C**CIF**S**VF**T**V	406	VS
		Heliodoxa rubinoides	Fawn-breasted brilliant	NRM 20046023	FI**A**CIF**S**VF**T**V	406	VS
		Hylocharis chrysura	Gilded hummingbird	NRM 996701	XX**C**CIF**S**VF**T**V	406	VS
Passeriformes (Melephagoidea)	Meliphagidae	*Lichenostomus flavescens*	Yellow-tinted honeyeater	O. 66338	FM**C**CIF**S**VF**T**V	406	VS
		Philemon argenticeps	Silver-crowned friarbird	O. 65825	FM**C**CIF**S**VF**T**V	406	VS
		Phylidonyris novaehollandiae	New Holland honeyeater	O. 70854	FM**C**CIF**S**VF**T**V	406	VS
		Conopophila rufogularis	Rufous-throated honeyeater	O. 65927	FM**C**CIF**S**VF**T**V	406	VS
		Acanthorhynchus tenuirostris	Eastern spinebill	O. 70913	FM**C**CIF**S**VF**T**V	406	VS
Passeriformes (Passerida)	Zosteropidae	*Zosterops japonicus*	Japanese white eye	NRM 20026678	LM**M**CIF**C**IF**T**V	371[b]	UVS
		Zosterops senegalensis	African yellow white eye	NRM 20066253	LM**M**CIF**C**IF**T**V	371[b]	UVS
	Nectariniidae	*Aethopyga siparaja*	Crimson sunbird	NRM 20026613	LM**C**CVF**C**IF**T**V	371	UVS
		Chalcomitra senegalensis	Scarlet-chested sunbird	NRM 20056357	LM**C**CVF**C**IF**T**V	371	UVS
		Cinnyris pulchellus	Beautiful sunbird	NRM 20076163	LM**C**CVF**C**IF**T**V	371	UVS
	Promeropidae	*Promerops gurneyi*	Gurney's sugarbird	UWBM 70395	LM**C**CVF**C**IF**T**V	371	UVS
	Thraupidae	*Cyanerpes cyaneus*	Red-legged honeycreeper	FMNH 391637	LM**C**CVF**C**IF**T**V	371	UVS
	Icteridae	*Icterus galbula*	Baltimore oriole	FMNH 442567	LM**C**CVF**C**IF**T**V	371	UVS
	Fringillidae	*Himatione sanguinea*	'Apapane	UWBM 65834	LM**C**CVF**C**IF**T**V	371	UVS

Spectral tuning amino acid (aa) sites 86, 90 and 93 are marked in bold

[a] Swedish Museum of Natural History (NRM), Australian Museum (O.), The Field Museum, Chicago (FMNH), Burke Museum, University of Washington

[b] The spectral tuning effect of M86 is unknown

amino acids at key position 90 with unknown effect on λ_{max} (see Wilkie et al. 2000; Yokoyama et al. 2000) nor any previously unreported amino acid residues in pos. 86, 90 or 93 (see Ödeen and Håstad 2003 and references therein; Håstad et al. 2005a) (Table 1). The remaining sequences, all with serine in 90, predict a violet-sensitive (VS) type of photoreceptor in the retinae of the three hummingbird and five honeyeater species.

Discussion

Spectral sensitivity estimations

Molecular data from the SWS1 opsin gene suggest that the three major groups of avian pollinators have differently tuned colour vision systems: the hummingbirds and honeyeaters being VS, whilst the sunbirds and other nectarivorous Passerida passerines UVS. Predictions from amino acid sequences tend to underestimate extremes in λ_{max} by up to 16 nm, with sequence-estimated λ_{max} values being similar or lower than MSP results in VS birds and similar or higher in UVS birds (Ödeen et al. 2009). Ödeen and Håstad (2003) did not design a primer pair that amplified the tuning sites 116 and 118 in most birds, possibly due to an intron between bp 1 and 2 in amino acid position 121. Our calculations hence disregard the potential shift in λ_{max} that substitutions in these positions might produce. The, at least, 23 nm λ_{max} differences that exist between the VS and UVS opsins (Hart et al. 1999) are, however, greater than these discrepancies. The spectral tuning effect of M86 that we found in the two *Zosterops* species is unknown. Methionine in position 86 has previously been reported from the SWS1 opsin sequence of two other avian species, willow warbler *Phylloscopus trochilus* L. (Ödeen and Håstad 2003) and red-billed leiothrix *Leiothrix lutea* Scopoli (Ödeen et al. 2009), of which the latter has been analysed with retinal MSP (Maier and Bowmaker 1993). The MSP λ_{max} is 16 nm lower that that estimated from the gene sequence (Ödeen et al. 2009), which implies that even if M86 were to have an effect on spectral tuning it should not longwave shift the *Zosterops* SWS1 pigment from UVS to VS.

Hummingbird colour sensitivity

Judged by our results from Hermits, Brilliants and Emeralds, three relatively distant primary Trochilidae clades of the nine identified in the molecular phylogenetic work of McGuire et al. (2007), hummingbirds seem to carry VS rather than UVS SWS1 pigments. These results are in line with available information on the phylogenetic distribution of avian VS and UVS pigments (Ödeen and Håstad 2003 and references therein), but differ from the recently published study by Herrera et al. (2008) on the spectral sensitivities of the green-backed firecrown hummingbird. Herrera et al. (2008) argue that the presence of a UVS cone can be inferred from the presence of a UV-transparent ocular medium (referring to a study by Hart and Vorobyev 2005). This correlation is real, but inferences based on it are only reliable when applied to the reverse case; a UV-opaque ocular medium indicates that the λ_{max} of the SWS1 is located within the human visual range, i.e. being a VS pigment. The opposite is not always true; the SWS1 cone of the wedge-tailed shearwater *Puffinus pacificus* Gmelin contains a VS opsin (λ_{max}=402 nm), but the cone is still functionally sensitive to UV, due to a UV-transparent ocular medium ($\lambda_{T0.5}$=335 nm) (Hart 2004).

VS birds are not as homogeneous a group as are the UVS birds, with regard to their retinal sensitivity parameters. In addition to the ocular transmittance variation, there is also a fairly large variation in λ_{max} within the group (Hart 2001). In VS species investigated with MSP, λ_{max} ranges from 402 nm in the Manx shearwater *Puffinus puffinus* Brünnich and wedge-tailed shearwater (Hart 2004) to 424 nm in the peafowl *Pavo cristatus* L. Herrera et al. (2008) choose between a VS type with λ_{max} at 420 nm and a UVS type with λ_{max} at 371 nm, but we suggest the possibility of a more short-wavelength tuned type of VS pigment. Based on our results and those of Herrera et al. (2008), it seems that hummingbirds are of the VS type, but with the SWS1 single cone pigment tuned towards the shorter end of the VS-type sensitivity range, e.g. 406 nm. This would give them a limited UV sensitivity, mediated by the β-band absorbance of the SWS1 and UV-transmitting ocular media. One should however not overlook the possibility of low-taxonomic level variation or within-species polymorphism in the SWS1 opsin, as exemplified in the bobolink *Dolichonyx oryzivorus* (Beason and Loew 2008).

Evolutionary interactions

The presence of UVS SWS1 opsins in the Passerida pollinating passerines, VS opsins in the non-passeriform hummingbirds and the passeriform but non-Passerida (Melephagoidea) honeyeaters may have a phylogenetic explanation. The VS opsin appears to be ancestral and the most common state in birds (Yokoyama 2002; Ödeen and Håstad 2003), but all investigated members of the monophyletic Passerida passerine clade (Ericson et al. 2002; Barker et al. 2004) share the UVS type (9 species in this study and 11 investigated previously: Maier and Bowmaker 1993; Bowmaker et al. 1997; Hart et al. 1998, Das et al. 1999, Hart et al. 2000a, b; Ödeen and Håstad 2003). This evidence points to a single shift from VS to UVS opsins in an ancestor of Passerida. One should, however, keep in mind that non-Passerida passerines have only been sparsely sampled for spectral tuning data (two species each of Tyrannidae and *Corvus* in addition to this study: Ödeen and Håstad 2003), rendering such an argument of phylogenetic constraints somewhat speculative.

Another possibility to consider is that these intergroup differences in colour vision may be the results of nectarivory-mediated selection. In contrast to the insects (Chittka 1996), it is possible for bird vision to have adapted to flower colouration, rather than vice versa. The emergence of flowering plants, which occurred at the latest in lower Cretaceous (see review in Soltis et al. 2008), predated the change from VS to UVS vision in passerines, since these began diversifying in the upper Cretaceous (Ericson et al. 2002; Barker et al. 2004). Nevertheless, systematic evidence in plants points to several independent origins for ornithophily, mainly from bee-pollinated ancestors (see Cronk and Ojeda 2008), compared to the single shift in spectral sensitivity found in avian pollinators. Thus, flowers would have had to adapt to the visual system of their avian pollinators in the majority of cases.

Whilst it is known that the colour receptor sensitivities of bees are optimally distributed across the spectrum for detecting insect-pollinated flower colours (Chittka and Menzel 1992) and that those of the green-backed firecrown hummingbird allow for greater discriminability of colours of preferred flowers than those of other flowers (Herrera et al. 2008), it is currently unknown whether the conspicuousness of ornithophilous flowers is greater to their preferred pollinators than to less fitness-conferring avian visitors, such as nectar robbers and birds that destroy flowers, or sometimes even generalist pollinators. Even minor changes in reflectance might determine detectability of a signal if they occur in an area where the spectral sensitivity of the avian eye is relatively high (Schaefer et al. 2007). The different, UVS and VS, types of colour vision will most likely emphasise contrasts against the background or within the flower in different parts of the spectrum. Selection of a plant species to maximise conspicuousness to the preferred pollinator, whilst minimising it for other birds, should therefore favour floral signals that exploit those differences. In a similar fashion, birds have themselves optimised plumage colouration to spectral sensitivity differences to avoid predation (Håstad et al. 2005b). Colour contrast variation between UVS bird- and VS bird-pollinated flowers is, hence, likely to be found in the wavelength range below 500 nm, where the spectral sensitivities of the UVS Passerida pollinators differ the most from those of the VS hummingbirds and honeyeaters (Fig. 1). To resolve these issues, ecological and behavioural information is needed from areas where groups of pollinators with differing spectral sensitivity overlap, both on the spectral reflectance of the flowers and the relative importance of pollinators.

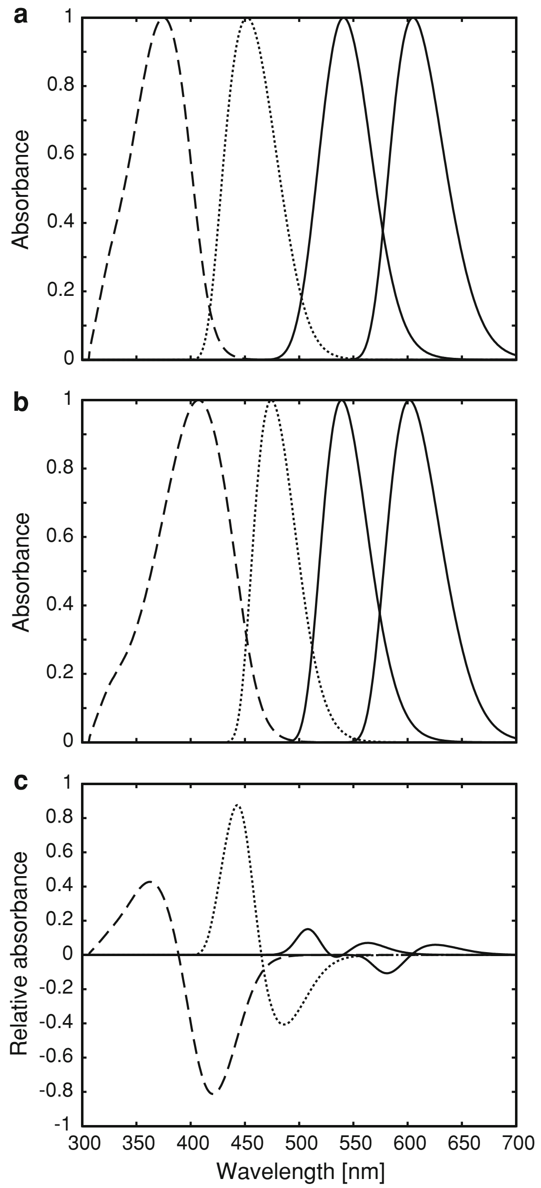

Fig. 1 Predicted spectral sensitivities for the four single cone classes of **a** a UVS-type bird, e.g. Passerida oscine passerine pollinating species and **b** a VS-type, e.g. a Trochilidae or Meliphagidae ditto. The cone classes are, from *left* to *right*, SWS1, SWS2, MWS and LWS. Maximum absorbance wavelengths ($\lambda_{\max}$) were taken from Table 1, and sensitivity calculations and other vision parameters from Hart and Vorobyev (2005), using *Serinus canaria* L. and *Puffinus puffinus* Gmelin for (**a**) and (**b**), respectively. All sensitivities were normalised to a maximum of 1. Since hummingbird ocular media are UV transmitting (Herrera et al. 2008), we used transmittance from the UVS *Sturnus vulgaris* L. (Hart et al. 1998) for both (**a**) and (**b**). **c** Difference in sensitivity (**a**, **b**), where positive values indicate higher sensitivity for the UVS-type birds compared to the VS-type birds, whilst negative values indicate the opposite relationship

The results of this study indicate that major groups of nectar-feeding birds have significantly different colour sensitivities. Whether or not this disparity is associated with variation in floral colouration as perceived by the preferred pollinator, and if so, whether the colour diversity of the plants has been affected by differences in avian colour vision or vice versa, remains to be investigated.

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