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Ultraviolet vision and foraging in dip and plunge diving birds

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Many fishes are sensitive to ultraviolet (UV) light and display UV markings during courtship. As UV scatters more than longer wavelengths of light, these signals are only effective at short distances, reducing the risk of detection by swimming predators. Such underwater scattering will be insignificant for dip and plunge diving birds, which prey on fishes just below the water surface. One could therefore expect to find adaptations in the eyes of dip and plunge diving birds that tune colour reception to UV signals. We used a molecular method to survey the colour vision tuning of five families of dip or plunge divers and compared the results with those from sister taxa of other foraging methods. We found evidence of exten-ded UV vision only in gulls (Laridae). Based on available evidence, it is more probable that this trait is associated with their terrestrial foraging habits rather than piscivory.

Keywords: piscivory; SWS1 cone opsin; ultraviolet light; social communication; fishes; predation

1. INTRODUCTION

Visual sensitivity to ultraviolet (UV) light has been demonstrated in a variety of fishes, mainly freshwater living such as guppy (*Poecilia reticulate*; Smith *et al.* 2002), some cichlid fish (*Metriaclima zebra* and *Haplochromis burtoni*; Carleton *et al.* 2000), rainbow trout (*Salmo gairdneri*; Hawryshyn *et al.* 1989) and a number of coral reef fishes (Losey *et al.* 2003), but it also appears to apply to species in temperate saline waters (S. Östlund-Nilsson, personal communication). UV has been shown to play a part in fish communication (Carleton *et al.* 2000). Many of the markings on fishes that reflect UV are situated on parts of the body that are usually displayed in courtship behaviours, such as the face or the fins, suggesting a role of the UV patterns in social communication (Thresher 1983).

Light of different wavelengths differs in physical properties, causing the available spectrum in water to change with depth. UV is assumed to be available down to 200 m in clear seawater, but to use reflected UV light for signalling purposes, the intended receiver should be closer than 5 m, as scattering would otherwise blur the signal (Losey *et al.* 1999). UV cues are thus of limited use to underwater predators such as fishes and diving birds. To avian predators foraging close to the surface however, they could be of substantial value; the UV scattering between fishes at shallow depths and the surface is minor and the scattering in air is negligible (Ödeen & Håstad 2003). Accordingly, UV markings appear more frequently on the lateral than the dorsal surface of fishes, where they would be most visible to avian predators flying directly above (c.f. Losey *et al.* 1999). UV signals from fishes would also stand in stark contrast to the most abundant upwelling light, which is rich in wavelengths between 425 and 500 nm (Austin 1974, cited in Hart 2001).

All species of diurnal birds studied to date have retinal colour receptors with some sensitivity to UV (the SWS1 single cone; Honkavaara *et al.* 2002). The position of maximum absorbance (λ-max) of the SWS1 cone appears to fall into either of two classes in birds (Cuthill *et al.* 2000). UV-sensitive (UVS) birds have the SWS1 λ-max shifted towards shorter wavelengths than the violet-sensitive (VS) birds (figure 1). VS seems to be the avian ancestral state from which UVS has evolved independently in four lineages (Ödeen & Håstad 2003; Shi & Yokoyama 2003), one of which is gulls (family Laridae).

UV has been shown to be ecologically important in foraging (Viitala *et al.* 1995; Church *et al.* 1998; Siitari *et al.* 1999, 2002; Probst *et al.* 2002), but it is also associated with various costs (Bennett & Cuthill 1994; Losey *et al.* 1999). That gulls maintain the UVS system therefore indicates an adaptive value, such as improved foraging efficiency in dip or plunge diving. However, gulls are unique among seabirds in that they are also highly successful on land. Many species are terrestrial feeders and prey on invertebrates to a high degree. The adaptive value of UV in locating invertebrates has been demonstrated in blue tits (*Parus caeruleus*) searching for caterpillars (Church *et al.* 1998).

Variation in visual sensitivity among dip and plunge diving birds is commonly assumed to be adaptive in foraging. However, studies devoted to the relative proportions of cone types between species have yielded inconclusive results (reviewed in Hart 2001). Therefore, we have focused on surveying the distribution of the UVS cone type. If UVS in seabirds is an adaptation to dip or plunge diving, then it should be more strongly associated with foraging method than phylogenetic relationship. We would expect to find it in all dip and plunge divers regardless of whether their close relatives with other feeding modes have the ancestral VS system. Conversely, if this trait is an adaptation to terrestrial foraging, then we should only find it in gulls among the seabirds.

To test these expectations, we have surveyed the vision system of five families of dip or plunge divers (figure 2) and related taxa of varying foraging methods. Five dip and plunge families form four monophyletic groups, each with a sister group of swimming piscivorous birds. The phylogenetic relationships allow for a pairwise comparison of vision specialization in relation to foraging method.

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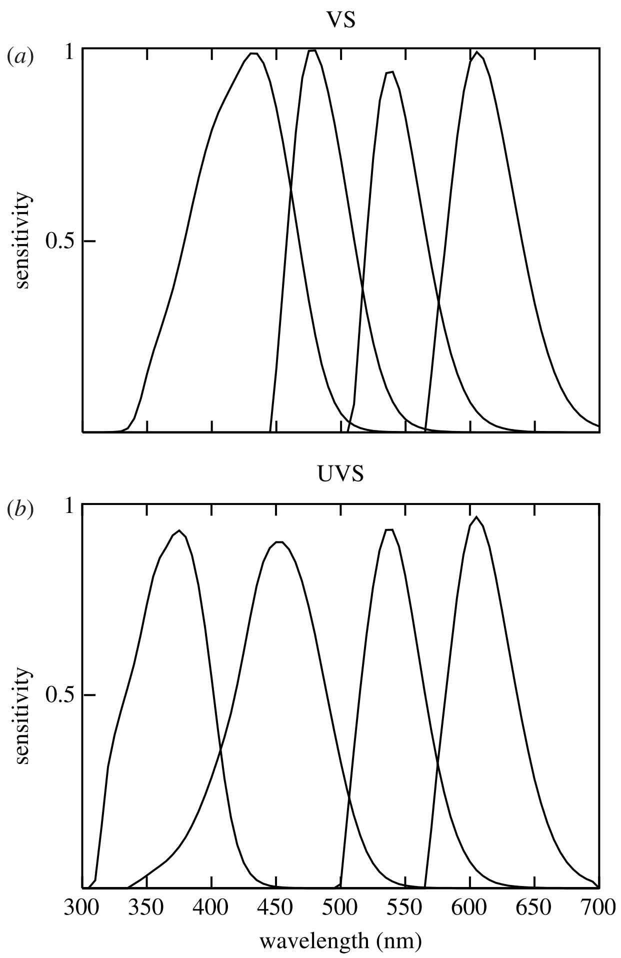

Figure 1. Spectral sensitivities (calculated relative photon catches) of cones belonging to different avian colour vision systems: (*a*) VS (peafowl, *Pavo cristatus*; Hart 2002) and (*b*) UVS (blue tit, *Parus caeruleus*; Hart *et al.* 2000). SWS1 is the first peak from the left.

2. MATERIAL AND METHODS

We used a recently developed molecular method for identification of avian colour vision systems (Ödeen & Håstad 2003). It takes advantage of the apparent tight integration of ocular transmission and cone sensitivities with sequence variation in the *SWS1 opsin* gene. By identifying a certain amino acid substitution, S90C, known to shift λ-max of *SWS1* − 35 nm (Wilkie *et al.* 2000), the UVS system can be identified.

We extracted total DNA from muscle tissues or feathers and performed a polymerase chain reaction (PCR) and sequencing following Ödeen & Håstad (2003) with the exception that we adjusted the annealing temperature depending on the primers used (52 ± 2 °C), and purified all PCR products with EXOsap-IT (USB) or Microcon YM-50 (Millipore).

3. RESULTS AND DISCUSSION

We amplified 54–107 bp overlapping *SWS1 opsin* sequences in 13 individuals from 14 species of seabirds and related families (GenBank accession numbers AY960709–AY960721). The amino acid sequences presented in table 1 confirm that the UVS (S90C) mutation is restricted to the monophyletic group of gulls, Laridae (figure 2). The gulls are also unique among seabirds in having isoleucine (I) in the minor tuning sites 86 and 93 (table 1). The closest relatives of the clade including the families Laridae, Sternidae and Alcidae are the waders (families Charadriidae, Haematopodidae, Recurvirostridae and Scolopacidae, respectively; Paton *et al.* 2003). Three of the wader families were previously known to be VS (Ödeen & Håstad 2003) and the three species of Scolopacidae examined here confirmed that this fourth family is VS as well.

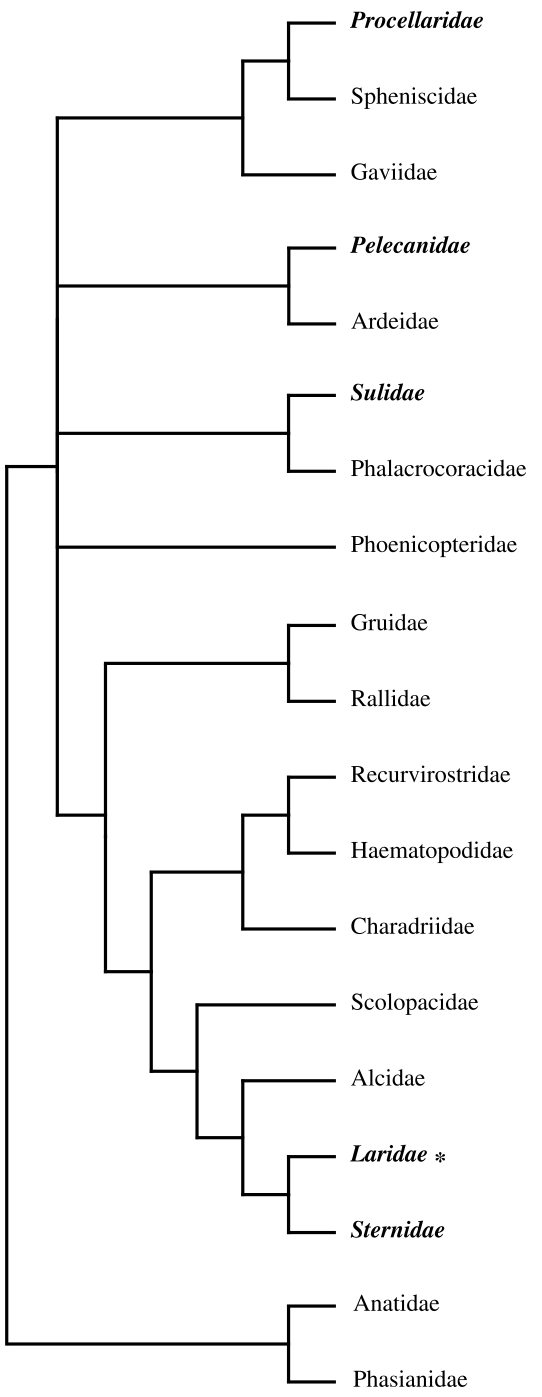

Figure 2. Phylogeny of seabirds and their closest relatives (Van Tuinen *et al.* 2001; Paton *et al.* 2003). Families of mainly dip or plunge divers are marked in bold. Laridae, the only family predisposed for UVS colour vision, is marked with an asterisk. Spectral tuning of SWS1 cones is determined from DNA sequencing (table 1) or retinal microspectrophotometry (Ödeen & Håstad 2003 and references therein; Hart 2004).

The molecular method we have used to estimate visual tuning is indirect but robust. All data concur with that from retinal microspectrophotometry (see Ödeen & Håstad 2003), and the molecular change

Table 1. SWS1 cone types in species of seabirds and close relatives.
(The key tuning sites 86, 90 and 93 (Wilkie *et al.* 2000) are marked with bold in the amino acid sequences.)

Family	Species	Common name	Sequence	Type
Laridae	*Larus hartlaubii*	Hartlaub's gull	F I **I** C V F **C** I S **I** V	UVS
Laridae	*Larus hemprichii*	sooty gull	F I **I** C V L **C** I S **I** V	UVS
Laridae	*Larus ridibundus*	black-headed gull	F I **I** C V L **C** I S **I** V	UVS
Laridae	*Rissa tridactyla*	black-legged kittiwake	F I **I** C V F **C** I S **I** V	UVS
Pelecanidae	*Pelecanus onocrotalus*	great white pelican	F X **S** C X F **S** V F **T** V	VS
Phasianidae	*Lagopus mutus*	rock ptarmigan	F I **A** C I F **S** V F **T** V	VS
Procellariidae	*Fulmarus glacialis*	northern fulmar	F I **S** C I F **S** V F **T** V	VS
Scolopacidae	*Actitis hypoleucos*	common sandpiper	F I **A** C I F **S** V F **T** V	VS
Scolopacidae	*Gallinago gallinago*	common snipe	F I **A** C I F **S** V F **T** V	VS
Scolopacidae	*Phalaropus fulicarius*	red phalarope	F I **A** C I F **S** V F **T** V	VS
Sternidae	*Sterna paradisaea*	artic tern	F V **T** X I F **S** I X **T** V	VS
Sternidae	*Sterna sandvicensis*	sandwich tern	F V **T** C I F **S** I F **T** V	VS
Sulidae	*Morus bassanus*	northern gannet	F I **S** C I F **S** V F **T** V	VS

tuning SWS1 from VS to UVS coincides with changes in the transmittance of the ocular media (Hart *et al.* 2000). The effects on spectral tuning of T, C and I in position 86 and I in 93 are unknown, but the positions only marginally contribute to the tuning of the SWS1 cone with their previously reported amino acids (Wilkie *et al.* 2000; Yokoyama *et al.* 2000*b*), and previously sequenced species with 86C and 93I are not notably different in spectral tuning from species having amino acids with known effects in these positions (Ödeen & Håstad 2003). However, 86I or 86T (new to this study) might prove important for spectral tuning in gulls and terns, considering that position 86 has been shown to be a key site for tuning in mammals (Shi & Yokoyama 2003). Gulls also deviate from other UVS birds by having 92S instead of 92F (cf. Wilkie *et al.* 1998; Das *et al.* 1999; Yokoyama *et al.* 2000*a*; Ödeen & Håstad 2003) and terns are the only VS species with 91I instead of 91V (cf. Okano *et al.* 1992; Kawamura *et al.* 1999; Ödeen & Håstad 2003).

Dip and plunge diving birds apparently do not depend on UVS cones to locate fishes. However, there are other ways to change the relative spectral sensitivity of the eyes besides shifting the sensitivity maxima of the cones. As the sensitivity of VS birds extends into the upper part of UV, their UV vision can be enhanced by differentially decreasing the absorption of short wavelengths in the ocular media or by increasing the proportion of SWS1 cones in the retina. Nevertheless, UV signals will not stand in contrast to the upwelling light, which is rich in wavelengths to which the SWS1 cone of VS birds is also sensitive (figure 1).

For any association between the dip or plunge diving foraging method and vision system, we would have expected to find UVS species not only in Laridae, but also in the other four dip or plunge families (figure 2). Even the highly specialized piscivorous terns, Sternidae, which largely share feeding habits with gulls and are their closest relatives, turned out to be VS. Hence, our results hence do not support that the UVS vision found in gulls is an adaptation to dip or plunge diving. Therefore, the most plausible explanation for the UVS system in gulls is an adaptation enhancing their terrestrial, omnivorous foraging capabilities.

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