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UVS is rare in seabirds

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ABSTRACT

Ultraviolet-sensitive vision (UVS), believed to have evolved from an ancestral state of violet-sensitive vision (VS), is widespread among terrestrial birds, where it is thought to play a role in orientation, foraging, and sexual selection. Less is known, however, about the distribution and significance of UVS in seabirds. To date UVS has been definitively demonstrated only in two families (Laridae and Sternidae), although indirect evidence has been used to argue for a more widespread occurrence. In this study we analyzed short-wavelength sensitive (SWS1) opsin DNA sequences to determine the distribution of ancestral (VS) and derived (UVS) amino acid spectral tuning sites in 16 seabird species representing 8 families with diverse ecological niches. Our results revealed sequences associated with UVS pigments (UVSs) in the Black-backed gull (*Larus dominicanus*), providing further evidence of its widespread occurrence within the Laridae. The Caspian tern (*Hydroprogne caspia*) and White-fronted tern (*Sterna striata*), however, were found to have VSs, suggesting an evolutionary reversion to the ancestral state within Sternidae. VSs were also detected in an additional six families. Our results raise interesting questions about the functions of UV vision in marine environments.

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1. Introduction

In most birds vision is fundamental for communication, foraging, and reproduction. Birds perceive a wide range of color through at least four retinal cone photoreceptors that harbor light-sensitive oil droplets and visual pigments (Bowmaker, 1991). A small number of birds have short-wavelength sensitive (SWS1) pigments that respond to light from the ultraviolet spectrum (Wilkie et al., 1998). Violet sensitivity (VS) is the ancestral avian state (Yokoyama, 2000) from which ultraviolet sensitivity (UVS) evolved through a single amino acid substitution at position 90 in the retinal protein SWS1 opsin (Hunt, Wilkie, Bowmaker, & Poopalasundaram, 2001). Additional amino acids in SWS1 at positions 86 and 93 also confer sensitivity to short-wavelength light (Wilkie et al., 2000).

UVS is widespread among terrestrial birds, to date having been demonstrated in eight families (Ödeen & Håstad, 2003). Several functions have been ascribed to UVS in terrestrial birds, including a role in breaking camouflage of prey (Johnsen, 2002), signaling during mate selection (Dresp, Jouventin, & Langley, 2005), parent–offspring communication (Parejo, Aviles, & Rodriguez, 2010), and interspecific communication (Cuthill et al., 2000).

In seabirds, however, the distribution of UVS, and its functional role(s) are less clear. Indirect evidence has been used to argue for the existence of UVS in some seabird taxa, but these cases have yet to be resolved. Bowmaker and Martin (1985) showed that Humboldt penguins (*Spheniscus humboldti*) were sensitive to light wavelengths of 403 nm, and suggested that these birds may also be sensitive to ultraviolet wavelengths. Furthermore, UV reflection has been detected in the plumage and beaks of Emperor penguins (*Aptenodytes forsteri*) (Burkhardt & Finger, 1991) and King penguins (*Aptenodytes patagonicus*) (Jouventin, Nolan, Örnborg, & Dobson, 2005). For these reasons, penguins have been referred to as sensitive to the UV spectral range despite a lack of evidence for the presence of UV visual receptors (Meyer-Rochow & Shimoyama, 2008, 2009).

An important advance in the field was the demonstration by Wilkie et al. (2000) that the incorporation of a single amino acid, cysteine (C), at amino acid position 90, leads to a substantial shift in UV light perception. Based on this observation, Ödeen and Håstad (2003) developed a molecular method to assess shortwave sensitivity by sequencing a small fragment of the SWS1 opsin gene flanking position 90 to determine color perception in a number of avian species. Ödeen and Håstad (2003) provided the first report of UVS in seabirds (three species of gulls; family Laridae), and Håstad, Ernstdotter, and Ödeen (2005) extended the list to include a further three species of gulls. Recently, Ödeen, Håstad, and Alström (2010) have demonstrated the presence of UVS pigment-associated

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sequences (UVSs) in an additional six species of gulls, and in three species of tern (Sternidae). UVSs have thus been identified only in 16 species of seabirds, thirteen of which are in a single family (Laridae) and three in the closely related Sternidae (Table 1).

It should be borne in mind, however, that the demonstration of UVS pigments *per se* is not conclusive evidence for functional UV vision, which depends also on other factors such as spectral filters and neural circuitry. The presence of UVSs does, however, provide a strong indication of UVS vision, and is far more practicable for comparative analyses than the behavioral experiments required to definitively demonstrate visual sensitivity.

To understand the evolution and ecological significance of UVS in seabirds, an immediate priority is to establish whether UVSs are, as the data currently suggest, rare among birds living in the marine environment, or whether the apparently restricted distribution compared with terrestrial birds is an artifact of limited sampling. Further information on the distribution of VSs and UVSs among seabirds will also provide a basis for a better understanding of the selection pressures that favor UVS within the marine environment.

To help illuminate these issues, we analyzed SWS1 opsin DNA sequences that cover the main VS/UVS spectral tuning amino acids in SWS1 to determine the distribution of the ancestral VSs and derived UVSs in 16 seabird species representing 8 families from diverse ecological niches. Our results suggest that UVS is sparsely distributed among seabirds and show that two species of tern have lost UVSs by reversion to the ancestral VSs state.

2. Methods

We targeted the amino acids used for identification of avian color vision systems as determined by Ödeen and Håstad (2003) and validated by Ödeen, Hart, and Håstad (2009). Using a set of newly designed SWS1 primers we amplified a coding region containing the VS and UVS amino acids at positions 86, 90, and 93 (Wilkie et al., 2000).

For feathers, DNA was extracted from 1 to 2 feather bulbs by incubation overnight at 56 °C, with rotation, in 40 µl of 1 mg/ml proteinase K and 40 µl of Chelex100. A 1–2 µl of the extract was used in a 10 µl PCR mix containing 50 mM Tris–Cl pH 8.8, 20 mM (NH₄)₂SO₄, 2.5 mM MgCl₂, 1 mg/ml BSA, 200 µM of each dNTP, 40 ng of each primer, sws1F + F (5′-agtcgacgcttctagcttTACATCCTG GTGAACATCT) and sws1R + R (5′-catgctactgctactgtTATCCCTGs GAGCTGGmGAT), and ~0.3 U of platinum Taq (Invitrogen). Primers sws1F + F and sws1R + R were tailed with generic sequencing primers F and R respectively to allow direct sequencing of small

amplification products. The reaction mix was overlaid with mineral oil and subjected to amplification in a Hybaid OmniGene thermal cycler using the following parameters; 94 °C for 2 min (×1), 94 °C for 20 s, 55 °C for 20 s, 72 °C for 20 s (×45). Amplified DNAs were detected by agarose gel electrophoresis in Tris–borate–EDTA buffer (TBE), stained with 50 ng/ml ethidium bromide, and then visualized over UV light. Positive amplifications were purified by centrifugation through ~100 µl of dry Sephacryl™ S200HR and then sequenced at the Allan Wilson Centre Genome Sequencing Service using Applied Biosystems (ABI) BigDye® Terminator v3.1 chemistry and an ABI3730 Genetic Analyzer.

3. Results

Approximately 50 bp of the SWS1 opsin gene was amplified for 16 different seabird species from eight families for which ultraviolet or violet sensitivity was unknown (Table 2, Fig. 1). A serine to cysteine substitution at position 90 (S90C) confirmed UVSs in the Black-backed gull (*Larus dominicanus*). As previously described (Ödeen & Håstad, 2003) we confirm the presence of isoleucine (I) at position 93 characteristic for the Laridae (genus *Larus*) family. In addition, our results showed for the first time VSs for members of the Diomedidae and also confirmed VSs for additional members of Sulidae, Spheniscidae, Procellariidae, Phalacrocoracidae, Stercorariidae, and Sternidae families. The results suggest that UVS is present in only 1 of 16 species of seabird tested. For two members of the Stercorariidae (the Southern great skua and the Arctic skua) a serine to alanine shift was observed at amino acid position 86, while for members of the Phalacrocoracidae family there is a serine to cysteine change also at position 86 (Fig. 1). Spectral tuning amino acid changes for two members of the Sternidae (the White-fronted tern and the Caspian tern) support results obtained for other members of this family where amino acids Ala86, Cys90, and Thr93 have partially reverted to the ancestral VSs state of Thr86, Ser90, and Thr93 (Ödeen et al., 2010). In these species the position 90 coding triplet has evolved from AGC (Ser) by a single A > T transversion to TGC (Cys) and then reverted back to Ser (TCC) by another single transversion of G > C (Fig. 1).

4. Discussion

Ultraviolet vision is widespread in the animal kingdom (Hunt et al., 2001; Jacobs, 1992). Furthermore, anatomical and physiological (Bowmaker, 1991; Chen, Collins, & Goldsmith, 1984; Hart, 2004), behavioral (Burkhardt, 1982; Church, Bennett, Cuthill, &

Table 1
Seabird species previously reported to be ultraviolet sensitive.

Family	Common name	Scientific name	aa Sequence 84–94	Type	Reference
Laridae	Herring Gull	<i>Larus argentatus</i>	F I I C V F C I S I V	UVS	Ödeen and Håstad (2003)
	Lesser Black-backed Gull	<i>Larus fuscus</i>	F I I C V F C I S I V	UVS	Ödeen and Håstad (2003)
	Greater Black-backed Gull	<i>Larus marinus</i>	F I I C V F C I S I V	UVS	Ödeen and Håstad (2003)
	Hartlaub's Gull	<i>Larus hartlaubii</i>	F I I C V F C I S I V	UVS	Håstad et al. (2005)
	Sooty Gull	<i>Larus hemprichii</i>	F I I C V L C I S I V	UVS	Håstad et al. (2005)
	Black-headed Gull	<i>Larus ridibundus</i>	F I I C V L C I S I V	UVS	Håstad et al. (2005)
	Black-legged Kittiwake	<i>Rissa tridactyla</i>	F I I C V F C I S I V	UVS	Håstad et al. (2005)
	Ivory Gull	<i>Pagophila eburnea</i>	F I I C V F C I S I V	UVS	Ödeen et al. (2010)
	Sabine's Gull	<i>Xema sabini</i>	F I I C V F C I S I V	UVS	Ödeen et al. (2010)
	Shallow-tailed Gull	<i>Creagrus furcatus</i>	F I I C V F C I S I V	UVS	Ödeen et al. (2010)
	Franklin's Gull	<i>Leucophaeus pipixcan</i>	F I I C V F C I S I V	UVS	Ödeen et al. (2010)
	Olrog's Gull	<i>Larus atlanticus</i>	F I I C V F C I S I V	UVS	Ödeen et al. (2010)
	Ross's Gull	<i>Rhodostethia rosea</i>	F V I C V F C I S L V	UVS	Ödeen et al. (2010)
	Sternidae	White Tern	<i>Gygis alba</i>	F I A C I F C I F T V	UVS
Lesser Noddy		<i>Anous tenuirostris</i>	F I A C I F C I F T V	UVS	Ödeen et al. (2010)
Black Noddy		<i>Anous minutus</i>	F I A C I F C I F T V	UVS	Ödeen et al. (2010)

Table 2
Seabirds SWS1 opsin sequences and their key tuning sites, in bold (as in Wilkie et al. (2000)).

Family	Common name	Scientific name	aa Sequence 84–94	Type
Laridae	Black-backed Gull	<i>Larus dominicanus</i>	F I I C V F C I S I V	UVS
Procellariidae	White-faced Storm Petrel	<i>Pelagodroma marina</i>	F I S C I F S V F T V	VS
	Gray-faced Petrel	<i>Pterodroma macroptera</i>	F I S C I F S V F T V	VS
Spheniscidae	King Penguin	<i>Aptenodytes patagonicus</i>	F I S C I F S V F T V	VS
	Little Blue Penguin	<i>Edyptura minor</i>	F I S C I F S V F T V	VS
Sternidae	Caspian Tern	<i>Hydroprogne caspia</i>	F V T C I F S I F T V	VS
	White-fronted Tern	<i>Sterna striata</i>	F V T C I F S I F T V	VS
Sulidae	Australasian Gannet	<i>Morus serrator</i>	F I S C I F S V F T V	VS
Phalacrocoracidae	Little Pied Shag	<i>Phalacrocorax melanoleucus</i>	F I C C L F S V F T V	VS
	Little Black Shag	<i>Phalacrocorax sulcirostris</i>	F I C C L F S V F T V	VS
	Great Black Shag	<i>Phalacrocorax carbo</i>	F I C C L F S V F T V	VS
Diomedeidae	Wandering Albatross	<i>Diomedea exulans</i>	F I S C I F S V F T V	VS
	Southern Royal Albatross	<i>Diomedea epomophora</i>	F I S C I F S V F T V	VS
	Yellow-nosed Albatross	<i>Diomedea chlororhynchus</i>	F I S C I F S V F T V	VS
Stercorariidae	Southern Great Skua	<i>Catharacta lonnbergi</i>	F V A C I F S V F T V	VS
	Arctic Skua	<i>Stercorarius parasiticus</i>	F V A C I F S V F T V	VS

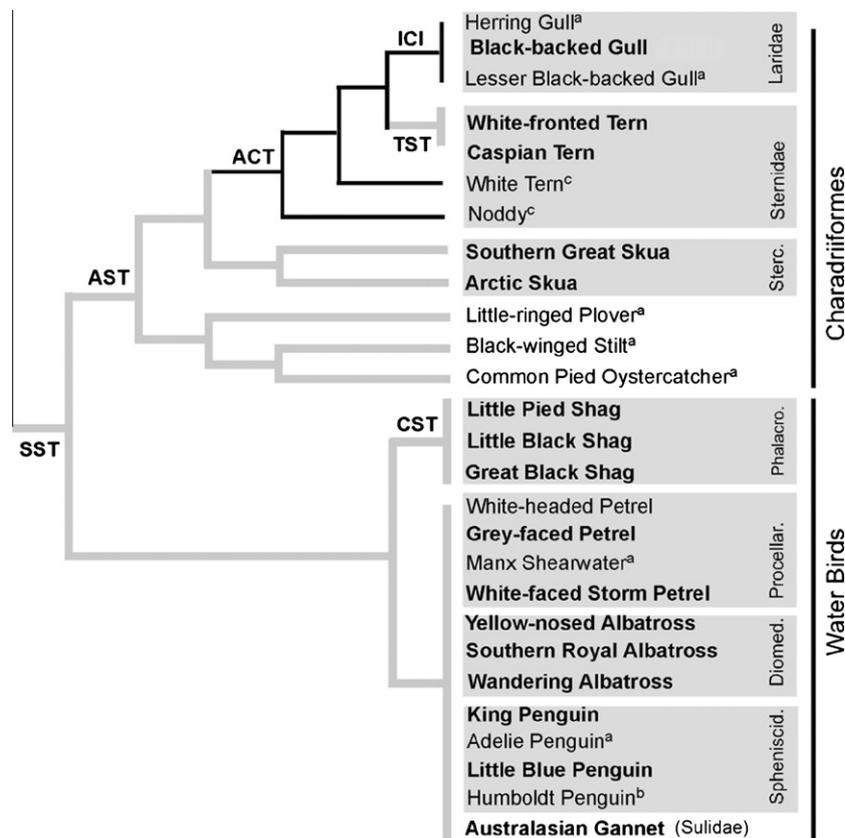


Fig. 1. Phylogenetic relationships among the water birds and Charadriiformes showing VS/UVS SWS1 pigments and their amino acid substitutions (represented as single letter code) at positions 86, 90, and 93 respectively. Gray lines reflect lineages with VS and black lines are lineages with UVS. The 17 species (bold) representing the eight families tested in this work are shown in gray boxes. Spheniscid. – Spheniscidae, Diomed. – Diomedeidae, Procellar. – Procellariidae, Phalacro. – Phalacrocoracidae, Sterc. – Stercorariidae, Stern. – Sternidae. Tree topology was obtained from the Tree of Life (<http://tolweb.org/tree/>). ^aÖdeen and Håstad (2003). ^bWilkie et al. (2000). ^cÖdeen et al. (2010).

Partridge, 1998; Wright, 1972), and molecular evidence (Carvalho, Cowing, Wilkie, Bowmaker, & Hunt, 2007; Carvalho, Knott, Berg, Bennett, & Hunt, 2010; Ödeen & Håstad, 2003; Wilkie et al., 2000) has established that visual sensitivity to ultraviolet light is widespread among terrestrial birds. In contrast, our results expand previous suggestions that UVS is uncommon in seabird families (Håstad et al., 2005; Ödeen et al., 2010), with evidence existing

for the occurrence of UVS in only 17 (6%) of the estimated 300 species of seabirds (Croxall, 1987). Seabirds are continually exposed to variable levels of ultraviolet radiation from the sky (Terjung & Louie, 1971), snow (Honkavaara, Koivula, Korpimäki, Siitari, & Viitala, 2002), ice (Godar, 2005), sand (Frohlich, 1976) and the ocean (Lythgoe, 1979). UV radiation varies with time of day, season, latitude and altitude (Silberglied, 1979) and it is

greatest during summer in polar regions where the ozone level is high and seasonal in the tropics, where the ozone concentration is low (Meyer-Rochow & Shimoyama, 2008).

UV light is thus available to seabirds, as it is to terrestrial animals, giving rise to the question of why their sensory systems appear not to have capitalized more widely on this potential source of information. One possibility concerns the potential costs of exposure to high-levels of UV. As radiation in the UV range of the spectrum is well known to cause photo oxidation of the retinal tissues in the absence of adequate optical filters (Burkhardt, 1982; Chen et al., 1984; Siebeck & Marshall, 2001), it is possible that selection has favored filtration devices such as oil droplets which remove UV light for protective purposes. On the other hand, this would suggest that UV sensitivity would be retained only if it had an important adaptive function, for example in foraging, orientation or sexual selection (Bennett & Cuthill, 1994), which more than counter-balanced the risk of retinal damage. What might these functions be?

4.1. UVS from a functional perspective

Seabirds spend most of their lives over the ocean foraging in diverse marine environments (Lack, 1968), preying mainly on fish. To date, over a hundred marine fish species are known to exhibit colors that include UV wavelengths (Losey et al., 1999). Near the surface of the ocean the intensity of UV radiation is high; however particles and dissolved organics in the water will attenuate the UV light penetrating the sea (Losey et al., 1999). The reflection and refraction of the light at the interface between the air and water plays an important role in the detection of prey by diving seabirds (Lythgoe, 1979), including members of the Sulidae, Phalacrocoracidae, Procellariidae and Diomedidae. Although the use of ultraviolet vision by some of these birds to break camouflage during fish capture has been suggested, as yet violet sensitivity but not ultraviolet sensitivity has been shown in the Sulidae and Phalacrocoracidae (Håstad et al., 2005). Experiments on cormorants suggest that these birds have poor visual resolution for detail in water (Martin, White, & Butler, 2008). Australasian gannets (*Morus serrator*) plunge dive from aerial heights of 9–15 m (Wodzicki & Robertson, 1955), whereas the effective distance for UVS detection is reported to be approximately 5 m (Håstad et al., 2005). We also found evidence for VS vision in members of the Procellariidae and the Diomedidae. In addition to vision (Martin & Katzir, 1995; Martin & Prince, 2001), members of both families strongly rely on olfactory cues to forage (Mardon, Nesterova, Traugott, Saunders, & Bonadonna, 2010; Nevitt, Reid, & Trathan, 2004).

To date the only seabird species shown to have ultraviolet vision are members of the Laridae (Table 1). Members of this family forage over large areas including terrestrial and coastal environments, using a variety of techniques such as surface seizing, dipping, kleptoparasitism, and scavenging, and have a wide variety of prey in their diet (Shealer, 2002). The pattern of light distribution is significantly different in a vertical compressed terrestrial environment and an expanded aquatic ecosystem (Lythgoe, 1979). UV coloration effects are background-dependent, and more relevant in terrestrial than aquatic environments (McFall-Ngai, 1990). Thus, UVS in this group may enhance their ability to forage in terrestrial as well as aquatic environments, allowing a varied omnivorous diet (Håstad et al., 2005), including caterpillars from terrestrial environments (Vernon, 1972) that reflect their coloration in the UV range of the spectrum (Bradley & Tye, 2001).

For many years Terns were included as a Tribe Sternini of the sub family Laridae (Sibley, Jon, & Monroe, 1988). This group has now been included in the Sternidae family, with most members having violet vision, as our data suggest for the Caspian tern (*Hydroprogne caspia*) and White-fronted tern (*Sterna striata*). Some,

however, including the Black noddy (*Anous minutus*), Lesser noddy (*Anous tenuirostris*) and the White tern (*Gygis alba*), have UV sensitive pigments and thus likely UVS vision (Ödeen et al., 2010). Although members of the Sternidae are mainly dip or plunge divers, intertidal foraging strategies have also been described (Naves, Ferreira Brusque, & Vooren, 2002). Birds sharing similar environments do not necessarily have the same visual capabilities. For example, although sharing ecological similarities with gulls, the Southern Great skua (*Catharacta lonnbergi*) and Arctic skua (*Stercorarius parasiticus*) from the Stercorariidae family (Bonadonna, Hesters, & Jouventin, 2003) have violet sensitive vision.

With regard to plumage, members of the Laridae and Sternidae have been demonstrated to have UV light reflection from the feathers, which is thought to play a role in sexual selection (Bridge & Eaton, 2005; Burkhardt, 1989). Initial work with Spheniscidae suggested they utilized the invisible spectrum for communication (Bowmaker, Heath, Wilkie, & Hunt, 1997). Humboldt penguins were shown to have a wavelength sensitivity of 403 nm that was thought to extend into the ultraviolet range (Bowmaker & Martin, 1985). Our study shows that Little blue penguins and King penguins, along with Adélie penguins (*Pygoscelis adeliae*) (Ödeen & Håstad, 2003), have violet sensitive pigments. Further analysis of how transparent the ocular media is in these species will revealed the extent to which a UV reflective beak in King penguins (*A. patagonicus*) and feathers from Emperor penguins (Dresp et al., 2005; Jouventin, Couchoux, & Dobson, 2009; Jouventin et al., 2005) may play a role in sexual selection (Dresp et al., 2005). Considering that most birds have plumage that reflects to some degree in the UV range (Bennett & Cuthill, 1994), it is presently unknown whether this is important for sexual selection or intraspecific communication.

4.2. VS / UVS from a phylogenetic perspective

The phylogenetic relationship between VS/UVS SWS1 pigments in water birds and Charadriiformes show, as previously suggested, a common violet sensitive avian ancestor with amino acids serine, serine, and threonine at SWS1 positions 86, 90, and 93 respectively (Fig. 1) (Ödeen & Håstad, 2003). A single change of alanine for serine at position 86 marks an evolutionary split of Charadriiformes from the ancestral state. Within the water birds, a cysteine to serine shift at position 86 separates the Phalacrocoracidae family from the Procellariidae, Diomedidae, and Spheniscidae and the only member of the Sulidae studied in present work. Regarding the Charadriiformes, our results confirmed that a single amino acid change divides the Stercorariidae from the Laridae and Sternidae. For a member of the Laridae, the Black-backed gull (*L. dominicanus*), a single Ser to Cys change at position 90, resulting in UVS, was found and is shared by other members of this family (Wilkie et al., 2000; Ödeen et al., 2010). Our results also demonstrate VS for the Caspian tern (*H. caspia*) and White-fronted tern (*S. striata*), suggesting a partial reversion to this ancestral state had occurred. The same conclusion was reached by Ödeen et al. (2010) regarding other members of the Sternidae. In addition, the evolution of the 90th codon in terns showed by our results reinforces the evidence of a single acquisition of VS vision from a UVS ancestor.

In conclusion, our molecular analysis of 8 of the 15 seabird families (Shealer, 2002) provided evidence of ultraviolet sensitivity in only one. The results expand previous observations that UV sensitivity is not widespread among seabird families, although little is known of the remaining seven families. What is, however, clear is that UVs is widespread within the Laridae and present, although inconsistently so, in the Sternidae. A priority for future research is to expand the database to the extent that the phylogeny of VS and UVS in seabirds can be definitively resolved. Further work is needed to definitively establish that the presence of sequences

associated with UVS pigments in seabirds does indeed imply functional UVS vision, including studies on behavior and ocular media transparency to UV wavelengths.

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