Chinese Birds 2012, 3(4):295–301
DOI 10.5122/cbirds.2012.0035

ORIGINAL ARTICLE

Predicted visual sensitivity for short-wavelength light in the brood parasitic cuckoos of New Zealand

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Abstract Different lineages of birds show varying sensitivity to light in the ultraviolet (UV) wavelengths. In several avian brood parasite-host systems, UV-reflectance of the parasite eggs is important in discriminating own from foreign eggs by the hosts. In turn, for parasitic females it may be beneficial to lay eggs into host clutches where eggs more closely match the parasite's own eggs. While the visual sensitivities of numerous cuckoo- and cowbird-host species have been described, less is known about those of their respective parasites. Such sensory characterization is important for understanding the mechanisms underlying potential perceptual coevolutionary processes between hosts and parasites, as well as for better understanding each species' respective visual sensory ecology. We sequenced the short wavelength-sensitive type 1 (SWS1) opsin gene to predict the degree of UV-sensitivity in both of New Zealand's obligate parasitic cuckoo species, the Shining Cuckoo (*Chalcites [Chrysococcyx] lucidus*) and the Long-tailed Cuckoo (*Urodynamis [Eudynamis] taitensis*). We show that both species are predicted to possess SWS1 opsins with maximal sensitivity in the human-visible violet portion of the short-wavelength light spectrum, and not in the UV. Future studies should focus on the (mis)matching in host-parasite visual sensitivities with respect to host-parasite egg similarity as perceived by the avian visual system and the behavioral outcomes of foreign egg rejection.

Keywords brood parasitism, coevolution, Cuculiformes, SWS1 opsin, ultraviolet vision, visual ecology

Introduction

Interactions between avian obligate brood parasites and their hosts remain one of the most robust examples of coevolutionary arms races (Davies, 2000; Stoddard and Stevens, 2010; Kilner and Langmore, 2011). The best studied and historically most prominent example of such interactions is the evolved mimicry of host eggs by parasites (Moksnes and Røskaft 1995; Cherry et al., 2007a; Moskát et al., 2008, 2010; Spottiswoode and Stevens, 2010; Soler et al., 2012). Despite the extensive similarities in the appearance of host and parasitic eggs (Grim, 2005), many host species possess the ability to discriminate between own and foreign eggs (Stoddard and Stevens, 2011). Much attention has recently been given to the functional roles of light wavelengths beyond the human perceptual range in avian egg discrimination, including the role of the shorter, ultraviolet (UV) wavelengths (< 400 nm) (e.g. Honza et al., 2007),

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Received 10 October 2012; accepted 02 December 2012

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to which different species of birds within distantly related lineages are varyingly sensitive (e.g. Ödeen and Håstad, 2003; Machovsky Capuska et al., 2011; Aidala et al., 2012). For example, UV-reflectance is important in recognizing and rejecting foreign eggs in the Blackcap (*Sylvia atricapilla*) (Honza and Polačiková, 2008) and the Song Thrush (*Turdus philomelos*) (Honza et al., 2007). However, comparatively less emphasis has been given to describing the visual sensitivities, UV or otherwise, of avian obligate brood parasites themselves.

Describing the visual sensitivities of specific bird species is vital, especially because the avian visual world differs substantially from that of humans. For example, unlike trichromatic humans, who possess only three classes of cone photoreceptor, birds possess five classes, four of which are directly responsible for color perception (Hunt et al., 2009). The short wavelength-sensitive type 1 (SWS1) photoreceptor, which is responsible for short-wavelength light detection, differs in its maximal sensitivity depending on the amino acids present at key 'spectral tuning' sites 86, 90, and 93 (following the bovine *Bos taurus* rhodopsin numbering) (Wilkie et al., 2000; Yokoyama et al., 2000; Shi et al., 2001). Of these, amino acid residue 90 is particularly important for mediating the degree of UV-sensitivity in avian species (Wilkie et al., 2000; Hunt et al., 2009). Those species possessing serine at site 90 (S90) are designated as having violet-sensitive (VS) pigments with a maximal sensitivity > 400 nm, and those possessing cysteine (C)90 are designated as having UV-sensitive (UVS) pigments with a maximal sensitivity < 400 nm (Hart, 2001). Site 90 is also highly conserved, with S90 proposed to be the ancestral state in all birds (Yokoyama and Shi, 2000; Hunt et al., 2009), though recent analyses of basal paleognaths (which were not included in these earlier analyses) including extinct moa from New Zealand, predicted a uniform UVS SWS1 for all ratites and tinamou allies (Aidala et al., 2012). Therefore, it is likely that C90 has (re-)evolved independently several times among avian lineages (Hunt et al., 2009; Ödeen et al., 2010; Machovsky Capuska et al., 2011; Ödeen et al., 2011, Aidala et al. 2012). Because microspectrophotometric and genetic data are in accord with one another in avian taxa for which both types of data are available (i.e. those possessing S90 have VS SWS1 opsins and those possessing C90 have UVS SWS1 opsins), DNA sequencing of the SWS1 opsin gene therefore permits accurate assessment of the degree of UV-sensitivity in any given avian species (Ödeen and Håstad, 2003) before the need for invasive and terminal physiological experimentation to confirm the sequence-based predictions (Aidala and Hauber, 2010).

Much of the work on the functional role of UV-reflectance and sensitivity in brood parasitic birds has focused on explaining the lack of eggshell color-based egg rejection to seemingly non-mimetic parasitic eggs. Cherry and Bennett's (2001) UV-matching hypothesis suggests that matching host/parasitic egg reflectance along a UV-green opponency (which humans cannot see) may explain the lack of rejection in acceptor host species. Empirical support for this hypothesis, however, is equivocal. For example, blocking-the UV-reflectance of Great-spotted Cuckoo (*Clamator glandarius*) eggs does not affect rejection in Common Magpies (*Pica pica*) (Avilés et al., 2006). However, the UVS/VS SWS1 sensitivity in this parasite-impacted host species has not been described, although other Corvidae species are predicted to be VS based on SWS1 DNA sequencing (Ödeen and Håstad, 2003). More critically, no apparent relationship between accepter/rejecter status and UVS/VS SWS1 sensitivity appears to exist among hosts of the North American generalist brood parasite, the Brown-headed Cowbird (*Molothrus ater*) and many of its hosts (Underwood and Sealy, 2008; Aidala et al., 2012).

The degree of UV egg color-matching/UV light sensitivity in New Zealand obligate brood parasite-host systems is not yet described using reflectance spectrophotometric or avian perceptual modeling data. The endemic Grey Warbler (*Gerygone igata*) is an accepter host of the local subspecies of the native Shining Cuckoo (in Australia, called the Shining-bronze Cuckoo; *Chalcites [Chrysococcyx] lucidus*) (McLean and Waas, 1987; also reviewed in Grim, 2006). In turn, the Whitehead (*Mohoua albicilla*), Yellowhead (*M. ochrocephala*), and Brown Creeper (*M. novaeseelandiae*) are endemic hosts of the also endemic Long-tailed Cuckoo (*Urodynamis [Eudynamis] taitensis*) (Payne, 2005). The Whitehead and Yellowhead are both considered accepter hosts (McLean and Waas, 1987; Briskie, 2003), while the Brown Creeper ejects artificial Long-tailed Cuckoo eggs at a rate of 67% (Briskie, 2003). DNA sequencing of the SWS1 photoreceptor in the Grey Warbler and the Whitehead predicted a VS and a UVS SWS1 maximal sensitivity, respectively (Aidala et al., 2012), whereas the predicted sensitivities of their respective parasites are not well known.

Compared to the large amount of effort spent characterizing the visual sensitivities of host species, those of brood parasites themselves, especially to UV-wavelengths, have received considerably less attention. To date, the SWS1 sensitivities have not been described in any Cuculiformes species, although a study measuring UV-reflectance in feather patches of 24 of 143 (17%) total cuckoo species showed that 5 of the species (21% of those measured) showed peaks in UV-reflectance (Mullen and Pohland, 2008). As there are increasingly more known inter-and intra-order variations in avian UV-sensitivity (Ödeen and Håstad, 2003; Machovsky Capuska et al., 2011; Aidala et al., 2012; Ödeen et al., 2012), and because visual systems among closely related species may vary widely, and are likely to reflect species-specific sensory ecologies (Machovsky Capuska et al., 2012), reliance on species for which SWS1 sensitivity data are available even within a lineage to approximate the degree of UV-sensitivity may be inaccurate.

Characterization of the UV-sensitivities of brood parasitic species is important for several reasons. First, it will allow for stronger analysis of comparative perceptual coevolution between hosts and parasites (Anderson et al., 2009). For example, recent egg color work using spectrophotometric measurements across the entire avian visible range have provided new insights into the direction of coevolutionary processes between hosts and parasites. Great Reed Warblers (*Acrocephalus arundinaceus*) are more likely to reject mimetic Common Cuckoo (*Cuculus canorus*) eggs when this hosts' own eggs exhibit higher intraclutch variation, a finding not in line with traditional predictions of coevolutionary theory, but validated by spectrophotometric measurements of host eggs (Cherry et al., 2007a; see also Antonov et al., 2012). Similarly, Common Cuckoos may preferentially parasitize host nests with eggs more closely resembling their own, also out of line with the theoretical assumption that female cuckoos randomly choose local nests to parasitize (Cherry et al., 2007b). Second, describing the visual sensitivities of brood parasitic cuckoo species will better inform studies examining cuckoo-cuckoo competition (Brooker et al., 1990) over host nesting sites using visual modeling analyses. Third, it will allow for more accurate analysis of VS/UVS SWS1 opsin ancestral states among avian species (Hunt et al., 2009; Aidala et al., 2012). Here, we report the predicted maximal sensitivities of the SWS1 opsins in two New Zealand native brood parasitic cuckoos based on DNA sequencing of the SWS1 'spectral tuning' region. In keeping with the general theoretical framework that host egg rejection selects for egg color matching, and in turn, favors UV-sensitivity in hosts, which in turn selects for UV-sensitivity in parasites, we expect the Shining Cuckoo that parasitizes the VS-predicted Grey Warbler to possess VS SWS1 opsins and the Long-tailed Cuckoo that parasitizes the UVS-predicted Whitehead to possess UVS SWS1 opsins.

Methods

We collected ~100 μL blood samples that were stored in Queen's lysis buffer from live Shining Cuckoos captured in mistnets during our field studies on avian host-parasite interactions (Anderson et al., 2009). We also obtained tissue samples from frozen Long-tailed Cuckoos that died from migration-related window-collisions and were stored in the Auckland Museum collection (Gill and Hauber, 2012). Our collecting protocols were approved by governmental and institutional animal research committees. Total genomic DNA was extracted from tissue samples stored in ethanol using the DNeasy Blood and Tissue Kit (Qiagen) according to manufacturer's instructions. DNA concentration ($ng \cdot \mu L^{-1}$) was estimated using Nanodrop spectrophotometer.

Forward primers SU149a (Shining Cuckoo) or SU193 (Long-tailed Cuckoo) and reverse primer SU306b (Ödeen and Håstad, 2003), modified to include M13-tails, were used to sequence the SWS1 opsin gene. PCR amplifications were carried out in 25 μL reaction volumes of 60 $mmol \cdot L^{-1}$ Tris-HCl ph 8.5, 15 $mmol \cdot L^{-1}$ $(NH_4)_2SO_4$, 2.5 $mmol \cdot L^{-1}$ $MgCl_2$, 0.3 $mmol \cdot L^{-1}$ of each dNTP, 0.2 $\mu mol \cdot L^{-1}$ of each primer and 0.5 U of Platinum *Taq* polymerase (Invitrogen). Thermal cycling followed conditions outlined in Ödeen and Håstad (2003) and was conducted in an ABI GeneAmp 9700 thermocycler.

An Exo/SAP treatment was used to purify PCR products: 5 μL PCR product was added to 0.2 μL of Exo I (GE Healthcare), 0.1 μL Shrimp Alkaline Phosphatase (GE Healthcare) and 1.7 μL UltraPure water (Invitrogen). We incubated mixtures for 30 min at 37°C, then for 15 min at 80°C to ensure enzyme inactivation. A BigDye Terminator Cycle Sequencing kit v3.1 (Applied Biosystems) was used to sequence samples in both directions with M13 forward and reverse primers. Each sequencing reaction consisted of 1 μL BigDye Terminator Mix, 3.5 μL 5× sequencing buffer, 0.2 $\mu mol \cdot L^{-1}$ primer, 1 μL DMSO and 2 μL PCR product. Agencourt CleanSeq (Beckman Coulter) was used according to manufacturer's instructions to purify sequencing reactions and analyzed using an ABI 3100 automated sequencer. Chromas Pro (Technelysium Pty. Ltd.) was used to edit sequences following which they were exported to BioEdit (Hall, 1999) for alignment and translation.

Results

The two Shining Cuckoo samples generated a sequence length of 119 base pairs (bp) each. The two Long-tailed Cuckoo samples generated a sequence length of 74 bp each. All sequences have been made available on GenBank (Accession numbers HM159121–HM159124). We detected no intraspecific or intrafamilial variation in either the gene or amino acid sequences, except for the codons at residue 95; however, both of these code for the amino acid phenylalanine (Table 1). We found only two ambiguities in one Long-tailed Cuckoo sample, whereas the other Long-tailed Cuckoo possessed the same codons and amino acid residues as the two Shining Cuckoo samples (Table 1). After alignment, all samples possessed S86, S90, and T93, which predict VS for both of these cuckoo species' SWS1 opsin photoreceptors.

Discussion

This is the first study to report on the sequence of SWS1 receptors and to predict short-wavelength visual sensitivities of New Zealand's brood parasitic native Shining Cuckoos and endemic Long-tailed Cuckoos. Substituting S for A at amino acid residue 86 (A86S substitution) produces a short-wave shift of 1 nm, a T93V substitution produces a long-wave shift of 3 nm, and a C90S substitution produces a 35 nm long-wave shift in the UVS SWS1 opsin of the Budgerigar (*Melopsittacus undulatus*) (Wilkie et al. 2000). The same C90S substitution in the Zebra Finch (*Taeniopygia guttata*) produces a similar-magnitude long-wave shift of SWS1 maximal sensitivity from 359 to 397 nm (Yokoyama et al., 2000). Thus, despite possessing S86 and T93 in both species, the presence of S90 predicts that the SWS1 maximal sensitivities of our cuckoo samples should be well within the visible-violet portion of the light spectrum, or VS (Table 1).

This finding is contradictory to our original prediction that only the Long-tailed Cuckoo should possess UVS SWS1 opsins due to the predicted UVS SWS1 of its Whitehead host (in contrast with the VS SWS1 of the Shining Cuckoo's Grey Warbler host; Table 1). Accordingly, we did not observe a distinct pattern between predicted SWS1 sensitivities of our cuckoo samples and those of their hosts. Both the Grey Warbler and Whitehead are non-ejector hosts of the Shining and Long-tailed Cuckoos respectively, yet these host species differ in their predicted SWS1 maximal sensitivities; DNA sequencing of the SWS1 photoreceptor gene predicted a VS SWS1 in the Grey Warbler but a UVS SWS1 in the Whitehead (Aidala et al., 2012). Predicted sensitivities of the other two Long-tailed Cuckoo hosts, the non-ejector Yellowhead, and the artificial egg-ejecting Brown Creeper are not yet described from molecular sequencing data. Also undocumented is the degree of physical or perceptual host-parasite egg color matching, in the UV-portion specifically, and in the avian-visible spectrum overall, in these two host-parasite systems. Nonetheless, human-visible assessment suggests

Table 1 Predicted VS/UVS SWS1 opsin state of two New Zealand cuckoo species based on SWS1 amino acid sequences. Passerine host species are shown below each cuckoo species and were adapted from Aidala et al. (2012). Spectral tuning sites 86, 90, and 93 are underlined.

Scientific name	Common name	GenBank Accession Number	Amino acid sequence	Predicted SWS1 sensitivity
			86 90 93	
Chrysococcyx lucidus	Shining-bronze Cuckoo	HM159121	VKYKKLRQPLNYILVNISFSGFISCIFSVFTVFVSSSQG	VS
Chrysococcyx lucidus	Shining-bronze Cuckoo	HM159122	VKYKKLRQPLNYILVNISFSGFISCIFSVFTVFVSSSQG	VS
Gerygone igata 1	Grey Warbler	HM159130	NISFSGFMCCIFSVFTVFVSSAQG	VS
Gerygone igata 2	Grey Warbler	HM159131	NISFSGFMCCIFSVFTVFVSSAQG	VS
Urodynamis taitensis	Long-tailed Cuckoo	HM159123	N?SFSGFISCIFSVFTVF?SSSQG	VS
Urodynamis taitensis	Long-tailed Cuckoo	HM159124	NISFSGFISCIFSVFTVFVSSSQG	VS
Mohoua albicilla	Whitehead	Aidala et al., 2012	VKYKKLRQPLNYILVNISVSGLMCCIFCLFTVFISSSQG	UVS

some level of mimicry between Long-tailed Cuckoos and their hosts (Briskie, 2003), whereas the dark Shining Cuckoo's eggs may be cryptic, and not mimetic, in the enclosed nests of the Grey Warbler hosts (see Langmore et al., 2009).

An alternative to perceptual coevolutionary processes mediating the detection of parasitic eggs in New Zealand hosts is that the cost of accepting parasitic eggs might be offset by recognizing and rejecting parasitic cuckoo chicks (Davies, 2000). Despite a lack of direct behavioral or sensory data in our focal systems, there is evidence of parasitic chick detection and ejection based on visual appearance in the closely related Australian Large-billed Gerygone (*Gerygone manirostris*)/Little Bronze-cuckoo (*Chalcites [Chrysococcyx] minutillus*) (Sato et al., 2010) and Superb Fairy-wren (*Malurus cyaneus*)/Shining Cuckoo host-parasite systems (Langmore et al., 2003; see also Langmore et al., 2011). Further, there is evidence of evolved call-matching of the begging calls of Grey Warblers by Shining Cuckoo chicks based on both sound recordings (McLean and Waas, 1987) and comparative phylogenetic inference (Anderson et al., 2009). Similarly, McLean and Waas (1987) noted and Ranjard et al. (2010) provided bioacoustic evidence for the evolved similarity between the begging calls of the Long-tailed Cuckoo and its *Mohoua* spp. hosts. Other parasitic cuckoo-host systems, including the Horsefield's Bronze-cuckoo (*Chalcites [Chrysococcyx] basalis*) and its Superb Fairy-wren (*Malurus cyaneus*) hosts (Langmore et al., 2003, 2008; Colombelli-Négrel et al., 2012), the Diederick Cuckoo (*Chrysococcyx caprius*) and its hosts, and the Koel (*Eudynamis scolopacea*) and its House Crow (*Corvus splendens*) hosts have also been shown to have similar begging calls (reviewed in Grim, 2006).

Characterizing the visual sensitivities of diverse avian lineages, including parasitic cuckoo species, is an important step in understanding the coevolution of visual perception/parasitic egg rejection behaviors in host-parasite interactions and sensory ecology. These studies form the basis for future visual modeling and sensory-physiological studies for more accurate description of the perceptual systems of focal cuckoo species. Future studies should investigate the behavioral significance of egg color matching in driving sensory coevolution using appropriate visual perceptual modeling analyses of both host and parasitic species (Aidala and Hauber, 2010). Additional Cuculiformes species should also be included in future analyses in order to better describe the degree of V/UV-matching in host-parasite egg color mimicry and its perception and the ecological variables that may drive or hinder the evolution of UV-sensitivity amongst parasitic and non-parasitic cuckoos (Krüger et al., 2009).

Acknowledgments All field work was conducted in accordance with local animal ethics rules and regulations in New Zealand and the University of Auckland. We thank Brian Gill for providing tissue samples of Long-tailed Cuckoos at the Auckland Museum and Andrew Fidler for advice on sequencing. We also thank the many volunteers for assistance in field work, and two anonymous reviewers for the helpful comments on our manuscript. This research was funded by the US National Science Foundation and the Graduate Center of the City University of New York (to ZA and to MEH), a Foundation for Research, Science, and Technology postdoctoral fellowship (to MGA), and the National Geographic Society, the PSC-CUNY grant scheme, and the Human Frontier Science Program (to MEH).

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新西兰寄生性杜鹃对短波光的视觉敏感性

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摘要：不同类群的鸟类对于光线中紫外波长部分的敏感程度存在差异。在一些专性巢寄生鸟类的寄生者－宿主体系中，寄生卵所反射出来的紫外光对于宿主区分外源鸟卵与自己的卵具有重要作用。反过来说，对于雌性寄主而言，宿主巢中的卵能够最大程度接近自己的卵是非常有利的。虽然视觉敏感性在大多数杜鹃和牛鹂的宿主中都有描述，这些特征在寄主中却少见报道。视觉敏感性能帮助我们理解巢寄生者与宿主之间潜在的感知共进化过程的相关机制以及更好地了解每个物种相应的视觉感知生态。本研究测定了短波长敏感型（SWS1）视蛋白基因的序列来预测两种新西兰专性巢寄生杜鹃——金鹃（*Chalcites [Chrysococcyx] lucidus*）和长尾噪鹃（*Urodynamis [Eudynamis] taitensis*）的紫外光敏感性。结果表明两种杜鹃都具有 SWS1 视蛋白基因，而其最大敏感度集中在短波长光谱中人类可见的紫光部分，而不是紫外光。未来的研究应该关注在鸟类视觉系统下所测的巢寄生者和宿主卵的相似性以及宿主拒绝寄生卵的行为后果这两个方面，来集中探究巢寄生者与宿主之间的视觉敏感度是否匹配。

关键词：巢寄生，协同进化，鹃形目，SWS1视蛋白，紫外视力，视觉生态学