# Complex Distribution of Avian Color Vision Systems Revealed by Sequencing the SWS1 Opsin from Total DNA

Anders Ödeen<sup>1</sup> and Olle Håstad

Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

To gain insights into the evolution and ecology of visually acute animals such as birds, biologists often need to understand how these animals perceive colors. This poses a problem, since the human eve is of a different design than that of most other animals. The standard solution is to examine the spectral sensitivity properties of animal retinas through microspectophotometry—a procedure that is rather complicated and therefore only has allowed examinations of a limited number of species to date. We have developed a faster and simpler molecular method, which can be used to estimate the color sensitivities of a bird by sequencing a part of the gene coding for the ultraviolet or violet absorbing opsin in the avian retina. With our method, there is no need to sacrifice the animal, and it thereby facilitates large screenings, including rare and endangered species beyond the reach of microspectrophotometry. Color vision in birds may be categorized into two classes: one with a short-wavelength sensitivity biased toward violet (VS) and the other biased toward ultraviolet (UVS). Using our method on 45 species from 35 families, we demonstrate that the distribution of avian color vision is more complex than has previously been shown. Our data support VS as the ancestral state in birds and show that UVS has evolved independently at least four times. We found species with the UVS type of color vision in the orders Psittaciformes and Passeriformes, in agreement with previous findings. However, species within the families Corvidae and Tyrannidae did not share this character with other passeriforms. We also found UVS type species within the Laridae and Struthionidae families. Raptors (Accipitridae and Falconidae) are of the violet type, giving them a vision system different from their passeriform prey. Intriguing effects on the evolution of color signals can be expected from interactions between predators and prey. Such interactions may explain the presence of UVS in Laridae and Passeriformes.

### Introduction

Insights into color perception are often crucial to understanding animal behavior, ecology, and speciation. The sensitivity maxima of color receptors (single cones) are located in different spectral positions among animals, so that individual colors may be perceived very differently, even among related species. Unfortunately, the human eye is of an uncommon type, only shared by Old World monkeys and apes (Jacobs 1993) and therefore unfit to mirror the color perception of most other animals. The human eye is trichromatic, as our color vision involves three distinct classes of cones. Retinas with four classes of cones involved in color perception (tetrachromatic vision) have been reported in birds (Goldsmith 1990), fish (Palacios et al. 1998), and reptiles (Fleishman, Loew, and Leal 1993). Due to an additional class of cones, tetrachromats have the theoretical ability to see twice the number of colors compared with trichromats. Humans may hence be blind to many critical aspects of animal coloration and perception (Losey et al. 1999). We may not only perceive slightly different hues compared with other animals but also are possibly missing major components of animal coloration.

Compared with humans, birds have an additional color channel located in the ultraviolet (UV) to near ultraviolet range. The UV waveband is unperceivable by humans, but it has been shown to be ecologically important to birds. Experimental alterations of the UV component in the plumage have significantly affected sexual

Key words: chromatic ocular disposition, color vision, ultraviolet, opsin.

E-mail: olle.hastad@ebc.uu.se.

Mol. Biol. Evol. 20(6):855–861. 2003 DOI: 10.1093/molbev/msg108

© 2003 by the Society for Molecular Biology and Evolution. ISSN: 0737-4038

signals in many bird species (Maier and Bowmaker 1993; Bennett et al. 1996, 1997; Andersson and Amundsen 1997; Hunt et al. 1997, 1998, 1999), and it has been demonstrated a number of times that UV plays an important role in prey detection and foraging (Goldsmith 1980; Viitala et al. 1995; Church et al. 1998; Siitari, Honkavaara, and Viitala 1999). Still, UV does not seem to be more important to birds than does other parts of the spectrum (Hunt et al. 2001; Maddocks, Church, and Cuthill 2001). The focus on UV as a separate communication channel that has imbued behavioral studies in recent years ignores potentially important differences in color perception arising from tetrachromacy.

An important step towards an understanding of how animals perceive color is knowledge of their chromatic ocular disposition (COD), meaning the composite effect of the cone visual pigments' (opsin's) wavelength of maximum absorbance ( $\lambda$ -max), the filtering by the ocular media (including lens and cornea) and the oil droplets of the cones, and the relative abundance of different cone types. There appears to be two main CODs in birds. The most pronounced difference is in the  $\lambda$ -max of the opsin in the UV/violet (SWS1) and short-wavelength sensitive (SWS2) cones. One large group (violet sensitive, or VS [Hart et al. 2000b]) possesses SWS1 cones with a  $\lambda$ -max ranging from 403 to 426 nm (Hart, Partridge, and Cuthill 1999). A systematically more restricted group (ultraviolet sensitive, or UVS [Hart et al. 2000b]) has a more UVbiased SWS1 with a  $\lambda$ -max between 355 and 380 nm (Hart, Partridge, and Cuthill 1999). The VS system has been demonstrated throughout the avian phylogeny, in Anas platyrhyncos (Jane and Bowmaker 1988), Gallus gallus (Bowmaker et al. 1997), Spheniscus humboltii (Bowmaker and Martin 1985), Coturnix coturnix japonica (Bowmaker et al. 1993), Meleagris gallopavo (Hart, Partridge, and Cuthill 1999), Pavo cristatus (Hart 1998),

<sup>&</sup>lt;sup>1</sup> Present address: Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada.

Table 1 Type of Color Vision in Examined Bird Species

A conjection         A conjection         Multard duck         V/S         FV9CTESTIFTY         405         420         420           A conjectida         A conject gentific         Longon games bank         V/S         ETECTESTIFTY         405         406         420         420           A conjectida         Control originates         Characterida         Characterida         Characterida         Characterida         405         405         406	Order	Family	Name	Common Name	Type	Amino Acid Sequence	Calc. λ-max <sup>a</sup>	Meas. λ-max <sup>b</sup>	Reference
Accipitation         Accipitation<	Anseriformes	Anatidae	Anas platyrhynchos	Mallard duck	SA	FVSCIFSVFIV	405°	420	Jane and Bowmaker 1988
Accipitridae         Acciditae	Ciconiiformes	Accipitridae	Accipiter gentilis	Northern goshawk	SA	FIXCIFSVFTV	406		
Accipititate         Button button         Common bizzard         VS         FISELIFESTYTY         405           Accipititate         Circus acragatoms         Common bizzard         VS         FISELIFESTYTY         405           Accipititate         Parallor bilinearies         Opprey beron         VS         FISELIFESTYTY         406           Chendridate         Chanchique diversuches         VS         FISELIFESTYTY         406           Falconidate         Chanchique diversuches         VS         FISELIFESTYTY         406           Falconidate         Grain stream         Red-throad diver         VS         FISELIFESTYTY         406           I and the         Lann argentum         Red-throad diver         VS         FISELIFESTYTY         406           I and the         Lann argentum         Red-throad diver         VS         FISELIFESTYTY         406           I and the         Lann argentum         Red-throad diver         VS         FISELIFETY         406           I and the         Lann argentum         Red-throad diver         VS         FISELIFETY         406           I and the         Lann argentum         Red-throad diver         VS         FISELIFETY         407           I and the         Lann dige         <	Ciconiiformes	Accipitridae	Accipiter nisus	European sparrow hawk	NS	FISCIFSVFTV	405		
Accipitidae         Circa arangenous         Mash harier         VS         FISELIESUPTY         405           Accipitidae         Pranden haliacue         Grey heren         VS         FISELIESUPTY         406           Charachitidae         Ardeidae         Ardeidae         Grey heren         VS         FISELIESUPTY         406           Charachitidae         Himanopus savadegas         Common pied oystecatchen         VS         FISELIESUPTY         406           Charachitidae         Himanopus himanopus         Prescriber falso         VS         FISELIESUPTY         406           Gavidae         Acta orda         Common pied oystecatchen         VS         FISELIESUPTY         406           Landae         Lara de great         Reachtomied diver         VS         FISELIESUPTY         406           Landae         Lara de great         Reachtomied diver         VS         FISELIESUPTY         406           Landae         Lara diversity         Recent hale-backed gall         VS         FISELIESUPTY         406           Landae         Lara diversity         Greater black-backed gall         VS         FISELIESUPTY         406           Landae         Lara diversity         Greater black-backed gall         VS         FISELIESUPTY         <	Ciconiiformes	Accipitridae	Buteo buteo	Common buzzard	SA	FISCIFSVFTV	405		
Accipitation         Postularious plantanes         Opproper         VS         FIGEISTREPT         405           Actionidate         Charactifica         Charactifica         Charactifica         Charactifica         406           Charactifica         Charactifica         Charactifica         1 Jule ringed plower         VS         FIALISTREPT         406           Charactifica         Himanopus himanopus         Black-winged stift         VS         FIALISTREPT         406           Gavidas         Garia steflana         Reachineaed discon         VS         FIALISTREPT         406           Lunidae         Aria steflana         Represented falcon         VS         FIALISTREPT         406           Lunidae         Luris media         Razorbill         VS         FIALISTREPT         406           Lunidae         Luris media         Razorbill         VS         FIALISTREPT         406           Lunidae         Luris media         Recent black-backed gull         VS         FIALISTREPT         406           Lunidae         Luris mediga         Common numer         VS         FIACITESTREPT         406           Phulacrocracrac crabe         Common numer         VS         FIACITESTREPT         407           Proceilaridae </td <td>Ciconiiformes</td> <td>Accipitridae</td> <td>Circus aeruginosus</td> <td>Marsh harrier</td> <td>SA</td> <td>FISCIFSVFTV</td> <td>405</td> <td></td> <td></td>	Ciconiiformes	Accipitridae	Circus aeruginosus	Marsh harrier	SA	FISCIFSVFTV	405		
Autocidate Ardica circure as Circy heron VS FIGCIESTEPY 406 Charachicidae Hemanopus sorradegus Charachicidae Gavis sedelura Red-kancked gull UNS FIGCIESTEPY 406 Lancidae Larra sourina Red-kancked gull UNS FIGCIESTEPY 416 Lancidae Larra sourina Charachicidae Physiciacus common nume VS FIGCIESTEPY 406 Physiciacidae Physiciacus Charachicidae Charachicidae Adelic pengini VS FIGCIESTEPY 406 Physiciacidae Physiciacus humboldi Humboldi pengini VS FIGCIESTEPY 405 Spheniscidae Physiciacus humboldi Humboldi pengini VS FIGCIESTEPY 405 Accollaridae Charachicidae Adelic pengini VS FIGCIESTEPY 405 Accollaridae Charachicidae Adelic pengini VS FIGCIESTEPY 405 Accollaridae Charactica guradus Charachicidae Adelic pengini VS FIGCIESTEPY 405 Accollaridae Charactica guradus Charachicidae Charactica guradus Charachicidae Charactica guradus Charactica guradus Charachicidae Charactica guradus Charachicidae Charactica guradus Charachicidae Charactica guradus Charactica guradus Charactica guradus Charactica guradus Charactica guradus Charactica charachicidae Charactica guradus Charactica charachicidae Charactica guradus Charactica	Ciconiiformes	Accipitridae	Pandion haliaetus	Osprey	NS	FISCIFSVFTV	405		
Charachidide Charachidide Alexandres Charachidide Nover Charachidide Hemanagus orandres Preggine shoom Progressive Hoom Progressive Hoom Charachidide Alexandres Hemanagus Charachidide Charachidide Alexandres Charachidide Charachidide Progressive Hemanagus Charachidide Chara	Ciconiiformes	Ardeidae	Ardea cinerea	Grey heron	ΛS	FICCIFSVFTV	$406^{\rm d}$		
Chrandridiae         Humanopus himanopus him	Ciconiiformes	Charadriidae	Charadrius dubius	Little ringed plower	NS	FIACIFSVFTV	406		
Electronic control to the Internation of the Internation forms from the Engine forms of the Engine forms of the Engine forms of Carita stellara (Savidae Gavita stellara Herring gall to VS FIGUESUPTY 406 Act and the Act and the Larus argundums (Tarach gall UVS FIGUESUPTY 406 Act and the Larus internation of Creater black-backed gall UVS FIGUESUPTY 406 Act and the Larus internation of Creater black-backed gall UVS FIGUESUPTY 406 Act and the Larus internation of Creater flaming VS FIGUESUPTY 406 Act and the Engineering of Common mure et al. VS FIGUESUPTY 406 Act and the Engineering of Common mure et al. VS FIGUESUPTY 406 Act and the Engineering of Common mure et al. VS FIGUESUPTY 406 Act and Engineering Photosicoperidae Oceanochus flaming Common mure et al. VS FIGUESUPTY 406 Act and Engineering Engineering Procellaridae Oceanochus flaming Engineering VS FIGUESUPTY 405 Act and Act and the Engineering Spheriscide Spheriscide Columbi fivia Domestic pigeon VS FIGUESUPTY 405 Act and Act and the Engineering Spheriscide Spheriscide Columbi fivia Domestic pigeon VS FIGUESUPTY 405 Act and Act and the Engineering Spheriscide Columbi fivia Common moler VS FIGUESUPTY 405 Act and Act and the Engineering Spheriscide Spheriscide Spheriscide Spheriscide Common moler VS FIGUESUPTY 405 Act and Act and action and Engineering VS FIGUESUPTY 405 Act and Engineering Act and Common moler VS FIGUESUPTY 405 Act and Engineering Engineering Engineering Engineering Spheriscide Spheriscide Spheriscide Spheriscide Spheriscide Spheriscide Covers monetalis Common cont VS FIGUESUPTY 406 Act and Covers monetalis Engineering VS FIGUESUPTY 406 Act and Covers monetalis Engineering Eng	Ciconiiformes	Charadriidae	Haematopus ostralegus	Common pied oystercatcher	NS	FIACIFSVFTV	406		
Gavindae         Factor persegnius         Persegniue Inform         VS         FIGGERSPETE         405           Lanidae         Acta torda         Reachina         VS         FIGGERSPETE         406           Lanidae         Lanidae         Lanidae         Lanidae         100         FIGUERSPETE         406           Lanidae         Lanidae         Lanidae         Lanidae         100         FIGUERSPETE         371 cd           Lanidae         Lanidae         Lanidae         Common murre         VS         FIGUERSPETE         406           Indidenciopleridae         Protein sometra         Common murre         VS         FIGUERSPETE         406           Procellariidae         Proteincoprenta         VS         FIGUERSPETE         407           Procellariidae         Proteincoprenta         VS         FIGUERSPETE         403           Spheniscolae         Phygoscelis addiae         Adelie perguin         VS         FIGUERSPETE         403           Spheniscolae         Proteininde         Common perform         VS         FIGUERSPETE         403           Spheniscolae         Proteininde         Adelie perguin         VS         FIGUERSPETE         403           Spheniscolae         Proteininde	Ciconiiformes	Charadriidae	Himantopus himantopus	Black-winged stilt	NS	FVACIFSVFTV	406		
Gaviidae Gavia setlata Rachina VS FIGUESSTEW 406* Lanidae Lana gentatus Rachina VS FIGUESSTEW 406* Lanidae Lana gentatus Hering gull UVS FITCYPECISTY 371°-d Lanidae Lana gentatus Hering gull UVS FITCYPECISTY 371°-d Lanidae Lana maria Greater black-backed gull UVS FITCYPECISTY 371°-d Lanidae Lana agentatus Creater black-backed gull UVS FITCYPECISTY 406 Lanidae Common murre VS FITCYPECISTY 406 Phoeticopteridae Phalaterocoax carbo Common murre VS FITCYPECISTY 406 Phoeticopteridae Phalaterocoax carbo Common murre VS FITCYPECISTY 406 Phoeticopteridae Phalaterocoax carbo Common murre VS FITCYPECISTY 406 Procellaridae Phylaterocoax carbo Common murre VS FITCYPECISTY 406 Procellaridae Adelie penguin VS FITSCIPSTYPY 405 Spheniscidae Domestic phylaterocoax adeliae Adelie penguin VS FITSCIPSTYPY 405 Spheniscidae Spheniscidae Domestic pipcon VS FITSCIPSTYPY 405 Concide Concisto gunthin Marx shearwater VS FITSCIPSTYPY 405 Phasianidae Adelie penguin VS FITSCIPSTYPY 405 Phasianidae Columb Inia Domestic turkey VS FITSCIPSTYPY 405 Phasianidae Adelie promino coat VS FITSCIPSTYPY 406 Covidae Convincia goundina Lackaw VS FITSCIPSTYPY 406 Covidae Convince councied Lackaw VS FITSCIPSTYPY 406 Covidae Convince conne conix Hooded crow VS FITSCIPSTYPY 406 Covidae Convince conne conix Hooded crow VS FITSCIPSTYPY 406 Proceidae Furlica area Common pealo con VS FITSCIPSTYPY 406 Covidae Convince conne conix Hooded crow VS FITSCIPSTYPY 406 Proceidae Furlica area Common pealo con VS FITSCIPSTYPY 406 Covidae Convince conne conix Hooded crow VS FITSCIPSTYPY 406 Proceidae Furlica area Common pealo con VS FITSCIPSTYPY 406 Proceidae Furlica area Common pealo con VS FITSCIPSTYPY 406 Proceidae Furlica area Common cont VS FITSCIPSTYPY 406 Proceidae Furlica area Common cont Real Condition finch UVS FITSCIPSTYPY 406 Proceidae Furlica area Control finch My FITSCIPSTYPY 406 Proceidae Furlica area Control finch My FIT	Ciconiiformes	Falconidae	Falco peregrinus	Peregrine falcon	ΛS	FISCIFSVFTV	405		
Laridate         Arta tortuta         Razorbill         UNS         FIXTCRESTRY         4106           Laridate         Common normorant         VS         FIZCUEGISTY         371°-d           Laridate         Driva angre         Common comorant         VS         FIZCUEGISTY         400°           Phoenicopretars procellaridate         Phoenicopretars processor         VS         FISCUEGISTY         400°           Procellaridate         Procellaridate         Procellaridate         VS         FISCUEGISTY         400°           Procellaridate         Procellaridate         Procellaridate         VS         FISCUEGISTY         400°           Spheniscidae         Spheniscidae         Spheniscidae         Spheniscidae         VS         FISCUEGISTY         400°           Spheniscidae         Spheniscidae         Columbidae         Columbidae         VS         FISCUEGISTY         400°           Recordidate         A	Ciconiiformes	Gaviidae	Gavia stellata	Red-throated diver	ΛS	FICCIFSVFTV	$406^{d}$		
Laridate   Larus argentum: Herring gull   UVS   FILCYPECISTY   371cd     Laridate   Larus argentum: Herring gull   UVS   FILCYPECISTY   371cd     Laridate   Larus normins   Greater black-backed gull   UVS   FILCYPECISTY   371cd     Laridate   Larus normins   Greater black-backed gull   UVS   FILCYPECISTY   371cd     Laridate   Larus normins   Greater black-backed gull   UVS   FILCYPECISTY   406     Phalactroconacidate   Phalactrocoperac carbo   Common normins   VS   FILSCITESTYPY   406     Procellaridate   Phalactrocoperac carbo   Common normins   VS   FILSCITESTYPY   406     Procellaridate   Physicalization   Columbol to paguin   VS   FILSCITESTYPY   405     Spheniscidate   Spheniscus humboldi   Domestic paguin   VS   FILSCITESTYPY   405     Abbeniscidate   Columbol trivia	Ciconiiformes	Laridae	Alca torda	Razorbill	ΛS	FVACIFSVFTV	406		
Latindac   Latindaca   Latindacacoatac carbo   Common nutric   VS   FILACIISTIFT   406	Ciconiiformes	Laridae	Larus argentatus	Herring gull	OVS	FIICVFCISIV	$371^{c,d}$		
Luridae Larius marinius Greater Back-backed gull UVS FTLECTESUFTY 406 Phalacroconacidae Phalacrocorax carbo Common comorant VS FTLECTESUFTY 406 Phalacroconacidae Phalacrocorax carbo Common comorant VS FTLECTESUFTY 406 Phalacroconacidae Phalacrocorax carbo Greater Hamingo VS FTLECTESUFTY 406 Procellariidae Phalacrocorax carbo Greater Hamingo VS FTLECTESUFTY 406 Procellariidae Phygoseclis adeliae Adelie penguin VS FTLECTESUFTY 405 Spheniscidae Spheniscidae Adelie penguin VS FTLECTESUFTY 405 Spheniscidae Spheniscidae Adelie penguin VS FTLECTESUFTY 405 Columbidae Corraxia gorrulus Common roller VS FTLECTESUFTY 405 Alcedinidae Alcedo arthix Common roller VS FTLECTESUFTY 405 Phasianidae Corraxia gorrulus Spoebacked pulfind VS FTLECTESUFTY 405 Phasianidae Columnix japonica Japanese quail VS FTLECTESUFTY 405 Phasianidae Columnix japonica Japanese quail VS FTLECTESUFTY 405 Phasianidae Columnix japonica Japanese quail VS FTLECTESUFTY 405 Phasianidae Alcedo arthix Common peafowl VS FTLECTESUFTY 406 Phasianidae Anadina Jacciana Common peafowl VS FTLECTESUFTY 406 Corvidae Corrus corona comita Common coot VS FTLECTESUFTY 406 Corvidae Corrus corona comita Hooded crane VS FTLECTESUFTY 406 Corvidae Corrus corona Common coot VS FTLECTESUFTY 406 Corvidae Corrus corona comita Hooded crane VS FTLECTESUFTY 406 Corvidae Corrus corona comita Jacciana Canary UVS FTLECTESUFTY 406 Phasientidae Puras carnelias Bhackbird UVS FTLECTESUFTY 406 Phasiende Puras corona comita Jacciana Cun-throat finch UVS FTLECTESUFTY 406 Phaseridae Dryhtrangian Chanary UVS FTLECTESUFTY 406 Ph	Ciconiiformes	Laridae	Larus fuscus	Lesser black-backed gull	NNS	FITCVFCISIV	$371^{c,d}$		
Luidee Dria aulge Common nurre VS FFACIESSFEW 406 Phalacrocoractae Phalacrocorac arp. Common common of Common common common of Phalacrocorac arp. Common common common of Phalacrocorac arp. Common	Ciconiiformes	Laridae	Larus marinus	Greater black-backed gull	OVS	FIICVFCISIV	$371^{c,d}$		
Phalactoconcides Planarocome commorant VS FYGCLIESTETY 406° Photeitopperate Pocellaridae Planarocome Common commorant VS FYGCLIESTETY 406 Procellaridae Oceanodroma leucorhoa Leach's storm-petrel VS FYGCLIESTETY 405 Procellaridae Photeitopperas p. Publinus pulfinus	Ciconiiformes	Laridae	Uria aalge	Common murre	ΛS	FLACIFSVFTV	406		
Procellaridae Phenicopterus sp. Greater flamingo VS FUSCIESUFWY 408 Procellaridae Oceanodrona leucorhoa Leach's storm-petrel VS FUSCIESUFWY 405 Procellaridae Puginus puginus Spheniscidae Spheniscidae Adelie penguin VS FUSCIESUFWY 405 Spheniscidae Columba livina Domestic pigeon VS FUSCIESUFWY 405 Alcedinade Alcedo atthis Coraciidae Columba livina Domestic pigeon VS FUSCIESUFWY 405 Alcedinade Mystalus moraduna Spot-backed puffitied VS FUSCIESUFWY 405 Phasianidae Gallus gallus Checken Japanese quail VS FUSCUESUFWY 405 Phasianidae Gallus gallus Chicken Domestic turkey VS FUSCUESUFWY 408 Phasianidae Pavo crisvatus Common peafowl VS FUSCUESUFWY 408 Phasianidae Pavo crisvatus Common peafowl VS FUSCUESUFWY 406 Rallidae Fulfica ara Domestic turkey VS FUSCUESUFWY 406 Covidae Corvus corone cornix Hooded crow VS FUNCIESUFWY 406 Covidae Corvus corone cornix Hooded crow VS FUNCIESUFWY 406 Covidae Corvus corone cornix Hooded crow VS FUCCIESUFWY 406 Covidae Corvus corone cornix Hooded crow VS FUNCIESUFWY 406 Prasceridae Houst mendalua Jackdaw UVS JUVS JUCCIESUFWY 371 Passeridae Fulfus ara Gandina fasciara Cuartheros finch UVS JUVS JUCCIESUFWY 371 Passeridae Parascondus White-beaded mich UVS JUCCIESUFWY 371 Passeridae Passeridae Corrus mordesta Zeba finch UVS JUCCIESUFWY 371 Passeridae Passeridae Corrus Corruleus Common osating UVS JUCCIECIFFY 371 Passeridae Passeridae Jurius mordesta Zeba finch UVS JUCCIECIFFY 371 Passeridae Passeridae Corrus corruleus Surmato valed mich Surmato Valed Valed Surmato Valed Surmato Valed Surmato Valed Surmato Valed Valed Valed Valed Surmato Valed Va	Ciconiiformes	Phalacrocoracidae	Phalacrocorax carbo	Common cormorant	ΛS	FYCCLFSVFTV	$406^{\rm d}$		
Procellariidae Orcanodroma leucorhoa Leach's storm-petrel VS FISCIFSVETV 405 Procellariidae Puffnus puffnus Manx shearwater VS Spheniscidae Spheniscus humboldit Humbold proguin VS Spheniscidae Spheniscus humboldit Domestic pigeon VS Alcedinidae Columbi tivia Domestic pigeon VS Alcedinidae Alcedo atthis Ringfisher VS Alcedinidae Alcedo atthis Columbi tivia Common roller VS Bucconidae Coturmix japonica Japanese quail Phasianidae Meleagris galloparvo Domestic turkey VS Phasianidae Parvo cristatus Common coot VS Pringfisher Coturus corner cornix Covindae Corvus corne cornix Hooded crow VS Ralifidae Fulfica atra Corvus Corone cornix Hooded crow VS FUGCIFSVETV 406 Covidae Corvus corne cornix Hooded crow VS FUGCIFSVETV 406 Covidae Corvus cornectinic Jackdaw VS FUGCIFSVETV 406 Covidae Corvus cornectinic Jackdaw VS FUGCIFSVETV 406 Funds mendel Jackdaw VS FUGCIFSVETV 4	Ciconiiformes	Phoenicopteridae	Phoenicopterus sp.	Greater flamingo	ΛS	FVSCVLSVFV	408		
Procellariidae Puffinus puffinus Manx shearwater VS FVBCIFBNETV 405  Spheniscidae Spheniscus humboldti penguin VS FVBCIFBNETV 405  Spheniscidae Columbida Guantu II Humboldti penguin VS FIBCIFBNETV 405  Coraciidae Acedo antalia Kiingisher VS FIBCIFBNETV 405  Coraciidae Acedo antalia Kiingisher VS FIBCIFBNETV 405  Coraciidae Courant japonica Japanese quall VS FIBCIFBNETV 405  Phasianidae Columni japonica Comenon roller VS FIBCIFBNETV 408  Phasianidae Columni japonica Domestic turkey VS FIBCIFBNETV 408  Phasianidae Acedo antalia Sallus Chicken VS FIBCIFBNETV 408  Phasianidae Acedo antalia Common peatowl VS FIBCIFBNETV 408  Phasianidae Balearica paronima Common coot VS FIBCIFBNETV 406  Corvidae Corviscus mendal Jackdaw VS FIBCIFBNETV 406  Corvidae Corviscus mendal Jackdaw VS FIBCIFBNETV 371  Passeridae Annadina faxciata Cut-throat finch UVS FIBCIFBNETV 371  Passeridae Annadina faxciata Plumina modesta Plumi-headed munia UVS JACCNETETEV 371  Passeridae Annadina faxciata Common stating UVS JA	Ciconiiformes	Procellariidae	Oceanodroma leucorhoa	Leach's storm-petrel	ΛS	FISCIFSVFTV	405		
Spheniscidae         Pygoscelis adeliae         Adelie penguin         VS         FVSCIESVFTV         405           Spheniscidae         Spheniscus humboldti         Humboldt penguin         VS         FISCIESVFTV         405         409           Acloumbidae         Columbidae         Columbidae         Domestic pigeon         VS         FISCIESVFTV         405         409           Rucconidae         Alvacido authis         Common roller         VS         FISCIESVFTV         405         419           Phasianidae         Corumix japonica         Japanese quall         VS         FVSCVLSVFTV         405         415, 418           Phasianidae         Corumix japonica         Chicken         VS         FVSCVLSVFTV         408         415, 418           Phasianidae         Gallus gallopavo         Domestic turkey         VS         FVSCVLSVFTV         408         421           Phasianidae         Paleagriz gallopavo         Domestic turkey         VS         FVSCVLSVFTV         406         421           Phasianidae         Paleagriz gallopavo         Domestic turkey         VS         FVSCVLSVFTV         406         421           Rallidae         Fullica araa         Corvus corone cornix         Cowned crane         VS         FVSCVLSVFTV </td <td>Ciconiiformes</td> <td>Procellariidae</td> <td>Puffinus puffinus</td> <td>Manx shearwater</td> <td>S</td> <td></td> <td></td> <td>402</td> <td>(unpublished in Bowmaker</td>	Ciconiiformes	Procellariidae	Puffinus puffinus	Manx shearwater	S			402	(unpublished in Bowmaker
Spheniscidae         Pygoselis adeliae         Adelle pengun         VS         FV8CTESTFT         4DS           Spheniscidae         Spheniscus humboldit         Humboldit penguin         VS         FL8CIESUFT         4DS         403           Alcedinidae         Columbat livia         Domestic pigen         VS         FL8CIESUFT         4DS         409           Alcedinidae         Columbat livia         Conacios granulus         Conmon roller         VS         FL8CIESUFT         4DS         405           Bucconidae         Ovacaios granulus         Conmon roller         VS         FL8CIESUFT         4DS         419           Phasianidae         Cotumix japonica         Japanese quail         VS         FV8CVLSVEV         408         419           Phasianidae         Cotumix japonica         Domestic turkey         VS         FV8CVLSVEV         408         418           Phasianidae         Mclagris gallopavo         Domestic turkey         VS         FV8CVLSVEVT         408         418           Phasianidae         Paro cristatus         Common peafowl         VS         FUACCIESVET         406 <sup>d</sup> Guildae         Balearica paronina         Corvus corner cornix         Hooded crow         VS         FUACCIESVET         406 <sup>d</sup> <	:		;		,				c a.: 1771)
Spheniscidae Sphenistidae Sphenistidae Columboldii Humboldi penguin VS EISCIESUFEV 405 409 Alcedinidae Alcedo athiis Kingifisher VS EISCIESUFEV 405 Bucconidae Alcedo athiis Spot-backed putford VS EISCIESUFEV 405 Phasianidae Couracius garrutus Spot-backed putford VS EISCIESUFEV 405 Phasianidae Couracius garrutus Igonica Japanese quail VS EVSCVILSUFEV 408 419 Phasianidae Columnix japonica Japanese quail VS EVSCVILSUFEV 408 415, 418 Phasianidae Meleagris gallopavo Domestic turkey VS EVSCVILSUFEV 406 415, 418 Phasianidae Parvo cristatus Common peafowl VS EVACCIESUFEV 406 415, 418 Rallidae Corvus monedula Common peafowl VS ELECTESUFEV 406 415, 418 Rallidae Corvus corone comix Hooded crow VS ELECTESUFEV 406 717 371 373 Paridae Parina canaria Canary UVS ELECTESUFEV 406 717 371 373 Paridae Parina canaria Blue tit UVS LACCVECIETY 371 373 Passeridae Lonchura maja Mhiti-headed munia UVS LACCVECIETY 371 360-380 Suurnidae Suurnia guttata Zebra finch UVS LACCVECIETY 371 360-380 Suurnidae Suurnia modesta Purna cominon satting UVS LACCVECIETY 371 350-380 Suurnidae Suurnins vulgaris Common stating UVS LACCVECIETY 371 350-380	Ciconitomes	Spheniscidae	Pygoscelis adeliae	Adelie penguin	S>	FVSCIFSVFTV	405		
Secritidae Alcedo authis Domestic pigeon VS FIECIESVETY 405 409 Alceduindae Alcedo authis Ringisher VS FIECIESVETY 405 409 Alceduindae Alcedo authis Spot-backed putfibird VS FIECIESVETY 405 A199 Phasianidae Coturità japonica Japanese quail VS FIECIESVETY 405 A199 Phasianidae Coturità japonica Japanese quail VS FIECIESVETY 406 415,418 Phasianidae Gallus gallus Chieken VS FYSCVLSVETY 408 415,418 Phasianidae Meleagris gallopavo Domestic turkey VS FYSCVLSVETY 408 415,418 Cruide Belearica pavonina Crowned crane VS FIECIESVETY 406 <sup>4</sup> Corvus corone cornix Hooded crow VS FIECIESVETY 406 <sup>4</sup> Corvus monedula Jackdaw VS FIECIESVETY 406 <sup>4</sup> And Muscicapidae Turdus merula Bue tit UVS INCCVECIETY 371 <sup>4</sup> 369 Passeridae Erythrura gouldiae Gouldian finch UVS INCCVECIETY 371 <sup>4</sup> 369 Passeridae Passeridae Chambra angia White-headed munia UVS INCCVECIETY 371 <sup>4</sup> 360-380 Sumin develugia guttata Zeban finch UVS INCCVECIETY 371 <sup>4</sup> 350-380 Sumindee Sumins valigaris Common starling UVS INCCVECIETY 371 <sup>4</sup> 350-380 Sumindee Sumins valigaris Common starling UVS INCCVECIETY 371 <sup>4</sup> 350-380	Ciconiiformes	Spheniscidae	Spheniscus humboldti	Humboldt penguin	S/		1	403	Bowmaker and Martin 1985
Alcedinidae Alcedo atthis Kingfisher VS FISCIFSUFTY 405  Coracidae Coracias garrulus Common roller VS FISCIFSUFTY 405  Buccoiidae Cotumix japonica Japanese quail VS FISCIFSUFTY 405  Phasianidae Cotumix japonica Japanese quail VS FUSCULSUFTY 408 415, 418  Phasianidae Gallus gallus Chicken VS FUSCULSUFTY 408 415, 418  Phasianidae Meleagris gallopavo Domestic turkey VS FUSCULSUFTY 406 415, 418  Phasianidae Balearica pavonina Crowned crane VS FUACLIFSUFTY 406 406 400 400 400 400 400 400 400 400	Columbiformes	Columbidae	Columba livia	Domestic pigeon	ΛS	FISCIFSVFTV	405	409	Bowmaker et al. 1997
Coracitate         Coracia garrutus         Common roller         VS         FISCIESVETV         405           Bucconidae         Nysalus maculans         Spot-backed puffyird         VS         FISCIESVETV         405           Phasianidae         Callus gallus         Chicken         VS         FVSCVLSVFV         408         415, 418           Phasianidae         Gallus gallus         Chicken         VS         FVSCVLSVFV         408         415, 418           Phasianidae         Meleagriz gallopavo         Domestic turkey         VS         FVSCVLSVFV         408         415, 418           Phasianidae         Meleagriz gallopavo         Domestic turkey         VS         FVSCVLSVFV         406         418           Phasianidae         Pavo cristatus         Common peafowl         VS         FVGCIESVFT         406 <sup>d</sup> 421           Rallidae         Fulica atra         Common coot         VS         FLCCIESVFT         406 <sup>d</sup> 421           Covidae         Corvidae         Corvidae         Corvidae         Canay         VS         FLCCIESVFT         406 <sup>d</sup> Covidae         Serinus corneleus         Bune it         UVS         LocCIESVFT         406 <sup>d</sup> Pariscapidae         Prantina	Coraciiformes	Alcedinidae	Alcedo atthis	Kingfisher	ΛS	FISCIFSVFTV	405		
Bucconidae         Nysadus macudatus         Spot-backed puffbird         VS         FISCIFSUET         405           Phasianidae         Cotumix japonica         Japanese quail         VS         FVSCVLSVEV         408         419           Phasianidae         Gallus gallus         Chicken         VS         FVSCVLSVEV         408         415, 418           Phasianidae         Meleagris gallopavo         Domestic turkey         VS         FVSCVLSVEV         408         421           Phasianidae         Pavo cristatus         Common peafowl         VS         FUNCIFSVET         406 <sup>d</sup> 421           Ralidae         Balearica pavonina         Crowned crane         VS         FUNCIFSVET         406 <sup>d</sup> 421           Covilidae         Corvus monedula         Jackdaw         VS         FUNCIFSVET         406 <sup>d</sup> 421           Corvus monedula         Jackdaw         VS         FUCCIFSVET         406 <sup>d</sup> 433           Fringillidae         Serinus canaria         Canary         UVS         MCCVFCIFSVET         408 <sup>d</sup> Passeridae         Parus carelleus         Blue it         UVS         MCCVFCIFSVET         371           Passeridae         Erythrura gouldiae         Gouldian finch	Coraciiformes	Coraciidae	Coracias garrulus	Common roller	ΛS	FISCIFSVFTV	405		
Phasianidae         Coturnix japonica         Japanese quail         VS         FVSCVLSVFVV         408         419           Phasianidae         Gallus gallus         Chicken         VS         FVSCVLSVFVV         408         415, 418           Phasianidae         Meleagris gallopavo         Domestic turkey         VS         FVSCVLSVFVV         408         421           Phasianidae         Pavo cristatus         Common peafowl         VS         FIGCIFSVFTV         406 <sup>d</sup> 421           Rallidae         Fulica arra         Common cont         VS         FIGCIFSVFTV         406 <sup>d</sup> 421           Corvidae         Corvus monedula         Jackdaw         VS         FIGCIFSVFTV         406 <sup>d</sup> 421           Fringillidae         Serinus canaria         Canary         UVS         FIGCIFSVFTV         406 <sup>d</sup> 421           Musicapidae         Pariscicapidae         Corvus monedula         Lucha         UVS         FIGCIFSVFTV         371         373           Pariscicapidae         Pariscicapidae         Burasian blackbird         UVS         LMCCVFCIFT         377           Passeridae         Lonchura maja         White-headed munia         UVS         LMCCVFCIFT         373           Passer	Galbuliformes	Bucconidae	Nystalus maculatus	Spot-backed puffbird	ΛS	FISCIFSVFTV	405		
Phasianidae         Gallus gallus         Chicken         VS         FVSCVLSVEV         408         415,418           Phasianidae         Meleagris gallopavo         Domestic turkey         VS         FTCCIFSVFTV         406 <sup>d</sup> 421           Phasianidae         Pavo cristatus         Common peafowl         VS         FTCCIFSVFTV         406 <sup>d</sup> 421           Guidae         Balearica pavonina         Crowned crane         VS         FTGCIFSVFTV         406 <sup>d</sup> 421           Rallidae         Fullica atra         Corvus corone cornix         Hooded crow         VS         FMCCIFSVFTV         406 <sup>d</sup> 421           Corvidae         Corvus corone cornix         Hooded crow         VS         FMCCIFSVFTV         406 <sup>d</sup> 431           Corvidae         Corvus corone cornix         Cornus         VS         FMCCIFSVFTV         406 <sup>d</sup> 437           Corvidae         Corvus corone cornix         Cornus         VS         FMCCIFSVFTY         408 <sup>d</sup> 437           Muscicalidae         Fringillidae         Serinus carnelus         Bue tit         UVS         McCVFCIFTY         371         373           Passeridae         Amadina fasciata         Plum-headed finch         UVS         LMCCVFCIFTY<	Galliformes	Phasianidae	Coturnix japonica	Japanese quail	ΛS	FVSCVLSVFV	408	419	Bowmaker et al. 1993
Phasianidae         Meleagris gallopavo         Domestic turkey         VS         FICCIESVETY         406 <sup>d</sup> 421           Phasianidae         Balearica pavonina         Crowned crane         VS         FICCIESVETY         406 <sup>d</sup> 421           Guidae         Balearica pavonina         Crowned crane         VS         FICCIESVETY         406 <sup>d</sup> 421           Corvidae         Corvus corone cornix         Hooded crow         VS         FICCIESVETY         406 <sup>d</sup> 433           Corvidae         Corvus monedula         Jackdaw         VS         FICCIESVETY         406 <sup>d</sup> 373           Fringillidae         Serinus canaria         Canary         UVS         IMCCVECIETY         408 <sup>d</sup> 373           Muscicapidae         Parus sceruleus         Blue tit         UVS         IMCCVECIETY         371 <sup>d</sup> 370           Passeridae         Amadina fasciata         Cut-throat finch         UVS         Erythrur agouldae         White-headed munia         UVS         370           Passeridae         Neochhua maja         White-headed munia         UVS         Amadina fasciata         2eba finch         2eba finch         UVS         1MCCVECIETY         371 <sup>d</sup> 350-380           Passeridae	Galliformes	Phasianidae	Gallus gallus	Chicken	SA	FVSCVLSVF <b>v</b> V	408	415, 418	Okano et al. 1992, Bowmaker
Phasianidae Meleagris gallopavo Domestic turkey VS Hasianidae Pavo cristatus Common peafowl VS FICCIFSVFTV 406 <sup>d</sup> Guidae Balearica pavonina Crowned crane VS FIWCIFSVFTV 406 <sup>d</sup> Rallidae Fulica atra Common coot VS FIWCIFSVFTV 406 <sup>d</sup> Corvidae Corvus monedula Jackdaw VS FICCIFSVFTV 408 <sup>d</sup> Corvidae Corvus monedula Jackdaw VS FICCIFSVFTV 408 <sup>d</sup> Corvidae Corvus monedula Burasian blackbird UVS LMCCVFCIFTV 371 <sup>d</sup> 369  Muscicapidae Furnas and Bube tit UVS LMCCVFCIFTV 371 <sup>d</sup> 370  Paridae Parus caeruleus Bube tit UVS LMCCVFCIFTV 371 <sup>d</sup> 370  Passeridae Gouldian finch UVS LMCCVFCIFTV 371  Passeridae Meaching autuata Zebra finch UVS LMCCVFCIFTV 371 <sup>d</sup> 360-380  Sturnidae Surrus vulgaris Common startling UVS LMCCVFCIFTV 371 <sup>d</sup> 359	;	:			Ç				ct al. 1997
Phasianidae         Pavo cristatus         Common peafowl         VS         FICCIFSVFTV         406 <sup>d</sup> Rulidae         Fulica atra         Crowned crane         VS         FIMCIFSVFTV         406 <sup>d</sup> Rallidae         Fulica atra         Common coot         VS         FIMCIFSVFTV         406 <sup>d</sup> Corvidae         Corvus corone cornix         Hooded crow         VS         FIMCIFSVFTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FIACIFSVFTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FIACIFSVFTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FIACIFSVFTV         406 <sup>d</sup> Muscicapidae         Corvus monedula         Busseridae         UVS         IMCCVECIFTV         371           Passeridae         Amadina fasciata         Cut-throat finch         UVS         Amadina fasciata         371           Passeridae         Lorchura maja         White-headed munia         UVS         Lorchura maja         371           Passeridae         Taeniopygia guttata         Zebra finch         UVS         LACCIFCIFTV         371 <sup>d</sup> Sturnidae <td< td=""><td>Galliformes</td><td>Phasianidae</td><td>Meleagris gallopavo</td><td>Domestic turkey</td><td>S &gt;</td><td></td><td></td><td>418</td><td>Hart, Partridge, and Cuthill 1999</td></td<>	Galliformes	Phasianidae	Meleagris gallopavo	Domestic turkey	S >			418	Hart, Partridge, and Cuthill 1999
Gruidae         Balearica pavonina         Crowned crane         VS         FICCIFSVFTV         406 <sup>d</sup> Rallidae         Fulica atra         Common coot         VS         FIMCIFSVFTV         406 <sup>d</sup> Corvidae         Corvus corone cornix         Hooded crow         VS         FIGCIFSVFTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FIGCIFSVFTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FIGCIFSVFTV         408 <sup>d</sup> Fringillidae         Serinus canaria         Canary         UVS         LMCCVECIFTV         371 <sup>d</sup> 369         17           Muscicapidae         Parus caeruleus         Blue tit         UVS         LMCCVECIFTV         371 <sup>d</sup> 370         18           Passeridae         Lorchura magina fasciata         Cut-throat finch         UVS         LMCCVECIFTV         370         19           Passeridae         Neochnia modesta         Plum-headed finch         UVS         LMCCVECIFTV         371 <sup>d</sup> 360-380         1           Passeridae         Taeniopygia guttata         Zebra finch         UVS         LMCCVECIFTV         371 <sup>d</sup> 360-380         1           Stu	Galliformes	Phasianidae	Pavo cristatus	Common peafowl	ΛS			421	Hart 1998
Rallidae         Fulica atra         Common coot         VS         FLWCIESVFTV         406 <sup>d</sup> Corvidae         Corvus corone cornix         Hooded crow         VS         FMCIESVFTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FLCCIESVFTV         406 <sup>d</sup> Fringillidae         Corvus monedula         Jackdaw         VS         FLCCIESVFTV         408 <sup>d</sup> Muscicapidae         Turdus merula         Burasian blackbird         UVS         LMCCVECIETV         371 <sup>d</sup> 373           Passeridae         Amadina fasciara         Cut-throat finch         UVS         370         370           Passeridae         Lonchura maja         White-headed munia         UVS         373         370           Passeridae         Neochnia modexta         Plum-headed finch         UVS         Amacunia         373           Passeridae         Taeniopygia guttata         Zebra finch         UVS         LMCCVECIFTV         371 <sup>d</sup> Sturnidae         Sturnidae         Common startling         UVS         LMCCVECIFTV         371 <sup>d</sup> 359	Gruiformes	Gruidae	Balearica pavonina	Crowned crane	ΛS	FICCIFSVFTV	$406^{d}$		
Corvidae         Corvus corone cornix         Hooded crow         VS         FMCLIES/FTV         406 <sup>d</sup> Corvidae         Corvus monedula         Jackdaw         VS         FLCCIFS/FTV         408 <sup>d</sup> Fringillidae         Serinus canaria         Canary         UVS         LMCCVECIFT         371 <sup>d</sup> 369         13           Muscicapidae         Turdus merula         Eurasian blackbird         UVS         LMCCVECIFT         371         373         17           Passeridae         Amadina fasciata         Cut-throat finch         UVS         370         370         17           Passeridae         Lorchura maja         White-headed munia         UVS         Amaccvecity         373         17           Passeridae         Neochma madexta         Plum-headed finch         UVS         LMCCVECIFT         373         360-380           Passeridae         Taeniopygia gutata         Zebra finch         UVS         LMCCVECIFT         371 <sup>d</sup> 360-380           Sturnidae         Sturnidae         Common startling         UVS         LMCCVECIFT         371 <sup>d</sup> 359         17	Gruiformes	Rallidae	Fulica atra	Common coot	ΝS	FIMCIFSVFTV	$406^{d}$		
Corvidae         Corvus monedula         Jackdaw         VS         FLCCIFSVFTV         408 <sup>d</sup> Fringillidae         Serinus canaria         Canary         UVS         LMCCVFCIFT         371 <sup>d</sup> 369         ]           Muscicapidae         Turdus merula         Burasian blackbird         UVS         LMCCVFCIFT         371 <sup>d</sup> 369         ]           Paridae         Parius caeruleus         Blue tit         UVS         371         ]           Passeridae         Amadina fasciata         Cut-throat finch         UVS         370         ]           Passeridae         Lorchura miga         White-headed munia         UVS         373         ]           Passeridae         Necorhura medesta         Plum-headed finch         UVS         LMCCVECIFT         373         ]           Passeridae         Taeniopygia guttata         Zebra finch         UVS         LMCCVECIFT         371 <sup>d</sup> 360-380         ]           Sturnidae         Sturnidae         Common startling         UVS         LMCCIFCIFT         371 <sup>d</sup> 359         ]	Passeriformes	Corvidae	Corvus corone cornix	Hooded crow	ΝS	FMCCIFSVFTV	$406^{d}$		
Fringillidae         Serinus canaria         Canary         UVS         LMCCVFCIFTV         371 <sup>d</sup> 369         1           Muscicapidae         Turdus merula         Eurasian blackbird         UVS         373         1           Paridae         Parus caeruleus         Blue tit         UVS         371         373           Passeridae         Amadina fasciata         Cul-throat finch         UVS         370         370           Passeridae         Lonchura maja         White-headed munia         UVS         373         373           Passeridae         Neochnia modesta         Plum-headed finch         UVS         LMCCVECIETY         371 <sup>d</sup> 360-380           Passeridae         Sturnus vulgaris         Common startling         UVS         LMCCIECIFTY         371 <sup>d</sup> 359	Passeriformes	Corvidae	Corvus monedula	Jackdaw	ΝS	FLCCIFSVFTV	$408^{d}$		
Muscicapidae         Turdus merula         Eurasian blackbird         UVS         373         373           Paridae         Parus caeruleus         Blue tit         UVS         371         371           Passeridae         Amadina fasciata         Cut-throat finch         UVS         370         370           Passeridae         Lonchura maja         White-headed munia         UVS         373         373           Passeridae         Neochmia modesta         Plum-headed finch         UVS         100         373           Passeridae         Taentopyaga guttata         Zebra finch         UVS         100         360-380           Sturnidae         Sturnidae         Common starting         UVS         LMCCIECIFT         371 <sup>d</sup> 359	Passeriformes	Fringillidae	Serinus canaria	Canary	NAS	LMCCVFCIFTV	$371^{d}$	369	Das et al. 1999
ParidaeParius caeruleusBlue titUVS371PasseridaeAmadina fasciataCut-throat finchUVS370PasseridaeErythrura gouldiaeGouldian finchUVS370PasseridaeLonchura majaWhite-headed muniaUVS373PasseridaeNeochmia modestaPlum-headed finchUVS1MCCVFCIFTV371dPasseridaeTaeniopygia guttataZebra finchUVS1MCCVFCIFTV371d360-380SturnidaeSturnidaeCommon startingUVSLMCCIFCIFTV371d3591	Passeriformes	Muscicapidae	Turdus merula	Eurasian blackbird	UVS			373	Hart et al. $2000b$
Passeridae Amadina fasciata Cut-throat finch UVS 370 370 Passeridae Erythrura gouldiae Gouldian finch UVS 370 370 Passeridae Lonchura maja White-headed munia UVS 260 260 260 260 260 260 260 260 260 260	Passeriformes	Paridae	Parus caeruleus	Blue tit	NAS			371	Hart et al. 2000 <i>b</i>
Passeridae Erythrura gouldiae Gouldian finch UVS 370 370 Passeridae Lonchura maja White-headed munia UVS 273 373 Passeridae Neochmia modesta Plum-headed finch UVS 271 <sup>d</sup> 360–380 Passeridae Sturnus vulgaris Common startling UVS 271 <sup>d</sup> 359	Passeriformes	Passeridae	Amadina fasciata	Cut-throat finch	UVS			370	Hart et al. $2000a$
Passeridae Lonchura maja White-headed munia UVS 373 3 Passeridae Neochmia modesta Plum-headed finch UVS LMCCVFCIFTV 371 <sup>d</sup> 360–380 3 Passeridae Surrnus vulgaris Common starling UVS LMCCIFCIFTV 371 <sup>d</sup> 359 3	Passeriformes	Passeridae	Erythrura gouldiae	Gouldian finch	UVS			370	Hart et al. 2000 <i>a</i>
Passeridae Neochmia modesta Plum-headed finch UVS LMCCVFCIFTV 371 <sup>d</sup> 360–380 ] Surnidae Suurnus vulgaris Common starling UVS LMCCIFCIFTV 371 <sup>d</sup> 359 ]	Passeriformes	Passeridae	Lonchura maja	White-headed munia	UVS			373	Hart et al. $2000a$
Passeridae <i>Taeniopygia guttata</i> Zebra finch UVS LMCCVFCIFTV 371 <sup>d</sup> 360–380 ] Sturnidae Sturnus vulgaris Common starling UVS LMCLFCIFTV 371 <sup>d</sup> 359 ]	Passeriformes	Passeridae	Neochmia modesta	Plum-headed finch	NNS			373	Hart et al. $2000a$
Sturnidae Sturnus vulgaris Common starling UVS LMCCIFCIFTV 371" 359	Passeriformes	Passeridae	Taeniopygia guttata	Zebra finch	CVS	LMCCVFCIFTV	371 <sup>d</sup>	360–380	Bowmaker et al. 1997
	Passeriformes	Sturnidae	Sturnus vulgaris	Common starling	UVS	LMCCIFCIFTV	$371^{\rm u}$	359	Hart et al. 1998

Continued

			Common		Amino Acid	Calc.	Meas.	
	Family	Name	Name	Type	Sequence	$\lambda$ -max $^{ m a}$	$\lambda$ -max <sup>b</sup>	Reference
asseriformes	Sylviidae	Leiothrix lutea	Pekin robin	SAN			355	Maier and Bowmaker 1993
asseriformes	Sylviidae	Phylloscopus trochilus	Willow warbler	NAS	LMMCIFCIFTV	$371^{d}$		
asseriformes	Tyrannidae	Manacus manacus	White-bearded manakin	SA	FISCIFSVFTV	405		
asseriformes	Tyrannidae	Myiarchus tyrannulus	Brown-crested flycatcher	SA	FMCCIFSVFTV	$406^{\rm d}$		
iciformes	Picidae	Dendrocopos major	Great spotted woodpecker	SA	FLSCIFSVFTV	405		
sittaciformes	Psittacidae	Melopsittacus undulatus	Budgerigar	NAS	FLACIICIFTV	371	371	Bowmaker et al. 1997
sittaciformes	Psittacidae	Psittacus erithacus	Grey parrot	NAS	FLACIFCIFTV	371		
trigiformes	Caprimulgidae	Caprimulgus europaeus	European nightjar	ΛS	FLCCVESVFTV	406		
truthioniformes	Rheidae	Rhea americana	Common rhea	NAS	FIFCFFCVFMV	$371^{d}$		
truthioniformes	Struthionidae	Struthio camelus	Ostrich	ΛS	FISCIFSVFTV	405		
rogoniformes	Trogonidae	Trogon curucui	Blue-crowned Trogon	SA	FIFCVESVFTV	$406^{\rm d}$		
Jpupiformes	Upupidae	Upupa epops	Hoopoe	SA	FMSCIFSVFTV	405		

NOTE.—Scientific and common names were retrieved (May 23, 2002) from the Integrated Taxonomic Information System online database, http://www.itis.usda.gov. Amino acids in bold represent tuning sites 86, 90, and 93 (Wilkie et al. 2000). Approximate λ-max values were calculated from these sites. Measured λ-max values were taken from published MSP studies ' Calculated λ-max.

Measured λ-max.

to this study and their effects are unknown. study and their effects are unknown. to this s new new are are 93 The mutations in position 86 <sup>c</sup> The mutations in position

Puffinus puffinus (Bowmaker et al. 1997), Struthio camelus (Wright and Bowmaker 2001), and Taeniopygia guttata (Bowmaker et al. 1997). The UVS system has so far been found only in birds of the orders Passeriformes and Psittaciformes: Leiotrix lutea (Maier and Bowmaker 1993), Melopsittacus undulatus (Bowmaker et al. 1997), Sturnus vulgaris (Hart, Partridge, and Cuthill 1998), Serinus canaria (Das et al. 1999), Parus caeruleus (blue tit) (Hart et al. 2000b), Turdus merula (Hart et al. 2000b) and four species of estrildid finches (Hart et al. 2000a) (for common names, see table 1).

The type of SWS1 opsin possessed by a bird indicates its COD. The  $\lambda$ -max of the SWS2 cone covaries with that of SWS1 (Bowmaker et al. 1997; Hart et al. 2000a) in all species studied so far. The  $\lambda$ -max of the remaining two single-cone types (medium-wavelength sensitive [MWS] and long-wavelength sensitive [LWS]) differ only little between species, barring a few species (reviewed by Hart 2001). The oil droplets of the cones, which narrow spectral sensitivity (Kawamuro, Irie, and Nakamura 1997), fall into conserved classes, each associated with a particular cone type (Bowmaker et al. 1997), and hence do not confound the functional segregation of the two avian CODs. The Tclass oil droplet associated with SWS1 has no detectable absorption between 330 and 800 nm (Hart et al. 2000a), making the SWS1 opsin gene sequence an accurate predictor of the spectral tuning of the SWS1 cone.

Microspectrophotometry (MSP) has been the standard method used to examine the COD of animals. To prepare retinas for MSP, the live subjects are held in darkness for several hours before being sacrificed and having their eyes dissected (Hart, Partridge, and Cuthill 1999). Due to the complexity of the method, the absorbance of visual pigments has only been examined in a limited number of species. From in vitro examination, Wilkie et al. (2000) was able to determine the shift in  $\lambda$ -max that results from typical between-species amino acid substitutions in five spectral tuning sites in the SWS1 amino acid sequence. Shi, Radlwimmer, and Yokoyama (2001) identified five additional tuning sites in a study on mammals. Of all amino acid changes identified, those in positions 86, 90, and 93 (following the amino acid numbering of bovine rhodopsin) are of particular importance to the spectral tuning in birds (Shi, Radlwimmer, and Yokoyama 2001). Substitutions in four of the sites described by Wilkie et al. (2000) lead to minor or no shifts in  $\lambda$ -max (A86S: -1 nm; T93V: +3; A118T: +3; S298A: 0), but a change from cysteine (C) to serine (S) in position 90 leads to a substantial change in  $\lambda$ max (35 nm). Hence a C in position 90 characterizes the UVS group, whereas the VS group has an S in the same position (Yokoyama, Radlwimmer, and Blow 2000). Based on Wilkie et al. (2000) we have developed a molecular method that can be used to quickly, easily, and cheaply assess the approximate COD in almost any bird by sequencing part of the SWS1 opsin from small samples of total DNA.

### **Materials and Methods**

We isolated total DNA from blood, muscle tissue, or quill bases with chelex extractions and using the DNeasy

Tissue Kit (QIAGEN). Standard procedures were applied, except for DNA isolated from feather with the DNeasy Tissue Kit, where the DNeasy minicolumn loaded with 35 ml of preheated water was incubated 5 min at 70°C to increase the DNA yield. Other DNA material was obtained as phenol-chloroform extractions from colleagues. We designed degenerate PCR primers based on the sequences coding for the UVS, VS, or SWS1 (synonyms) opsin gene from Serinus canaria (GenBank accession number AJ277922), Melopsittacus undulatus (Y11787), Columbia livia (AH007798), and Gallus gallus (M92039) using Primer3 (Rozen and Skaletsky 1998) and the EMBOSS (Rice, Longden, and Bleasby 2000) package. The primer pair SU193a/SU396b: 5'-CCSCTYAAYTACATCCT-GGT-3'/5'-RACRATGTARCGCTCRAA-3' (beginning at bovine rhodopsin amino acid positions 70 and 137) amplified an approximately 800 bp-long sequence in Serinus canaria, including a long intron. This intron is probably the reason for the lack of product in the other samples tested. Aligning this product with the above mentioned opsin sequences allowed us to identify the position of the intron and design a new primer pair, SU149a/SU306b: 5'-CCRTSGTSCTSDKSGTCAC-3'/5'-SYBCTTSCCGAAGAY RAAGT-3' (beginning at positions 55 and 107). SU149a, positioned 44 bp upstream from SU193a, is located outside the focus exon in some species. Therefore, SU193a was used as the forward primer in species where PCR failed with SU149a/SU306b. To overcome problems with amplifications in raptors, we also designed a third forward primer, SU161a (beginning at position 59), 5'-KSGTCACCRTYMRKTACAA-3', partially overlapping SU149a.

Combining the forward primers SU149a, SU161a, and SU193a with the reverse primer SU306b, we conducted PCR on an Eppendorf Mastercycler Gradient. Each 25  $\mu$ l reaction volume contained 30 to 50 ng total DNA extracts, 0.125  $\mu$ l 5 U Taq-polymerase (Applied Biosystems), 2.5  $\mu$ l 10X reaction buffer, 10 pmol of each primer, 0.2 mM of each dNTP, and 50 mM MgCl<sub>2</sub>. Reaction conditions were 90 s at 94°C,  $5 \times (30 \text{ s}$  at  $94^{\circ}\text{C}$ , 30 s at  $54^{\circ}\text{C}$  and, 1 s at  $72^{\circ}\text{C}$ ),  $38 \times (15 \text{ s}$  at  $94^{\circ}\text{C}$ , 30 s at  $54^{\circ}\text{C}$ , and 5 s at  $72^{\circ}\text{C}$ ), and 10 min at  $72^{\circ}\text{C}$ . The extension time was kept very short to minimize nonspecific amplification of longer fragments.

We performed double-stranded sequencing of the PCR product with Big-Dye Terminator Cycle Sequencing v2.0 kit on an ABI-prism 310 automated sequencer following the user's manual. The same primers were used in cycle sequencing as in the PCR. PCR products for sequencing were prepared using Microcon YM-100 and YM-50 centrifugal filter devices (MILLIPORE). In case of amplification of multiple products, we purified the product from a 2% agarose gel using QIAquick Gel Purification kit (QIAGEN).

To translate our sequences we used the published amino acid sequence from *Melopsittacus undulatus* UV-sensitive opsin (Wilkie et al. 1998) as a template. From the alignment of amino acid sequences, we identified the spectral tuning sites 86, 90, and 93 (Wilkie et al. 2000) and calculated  $\lambda$ -max values from the tuning sites following Wilkie et al. (2000). We assumed the effect of these sites

on spectral tuning to be additive. Although this assumption disregards interactions between sites (see Shi, Radlwimmer, and Yokoyama 2001), additition should provide a reasonable approximation of  $\lambda$ -max.

#### Results

We amplified the target sequence in a total of 45 species of which the spectral tuning was previously unknown in 37 (table 1). The results of the remaining eight and comparisons between closely related species were consistent with MSP examinations (see table 1) and in vitro observations of cloned genes (Wilkie et al. 2000). The length of the amplified coding fragment was 74 bp with primer pair SU193a/SU306b, 107 bp with SU161a/ SU306b, and 119 bp with SU149a/SU306b. All amino acid sequences presented in table 1 are translated from sequences produced in this study. Because of an intron after amino acid position 121, we could not design a primer pair to amplify tuning site 118. Hence, our calculations disregard the potential upward shift in  $\lambda$ -max of 3 nm that a potential A118T mutation would produce. Calculated and measured λ-max values differed with 15 nm in Anas platyrhyncos and 11 nm in *Sturnus vulgaris*. Still, these differences are much smaller than that between the VS and UVS vision systems, which is at least 23 nm (Hart et al. 1999).

We found five new mutations at position 86 and one at 93, that is, mutations not described in Wilkie et al. (2000). However, since these positions only marginally contribute to the spectral tuning with their previously reported amino acids (Wilkie et al. 2000), we do not expect the new mutations to have any drastic effects on the spectral tuning of the SWS1-opsin. Nevertheless, these new findings call for further investigations using in vitro studies or MSP examination.

Our results confirm that the UV-tuned COD is present in passeriform and psittaciform birds and that most other bird taxa are violet-tuned. However, we found UVS also in the Laridae (genus *Larus*) and Rheidae families of the orders Ciconiiformes and Struthioniformes, respectively, and VS in the passeriform families Corvidae, Trogonidae, and Tyrannidae, as well as in the Struthioniform family Struthionidae.

For unknown reasons, we failed to amplify the SWS1 opsin sequence from the following species: Branta bernicla (brant), Anas crecca (green-winged teal), Apus apus (common swift), Aquila chrysaetos (golden eagle), Podiceps cristatus (great crested grebe), Mommotus mommota (blue-crowned motmot) and Strix aluco (tawny owl).

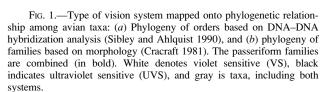
# Discussion

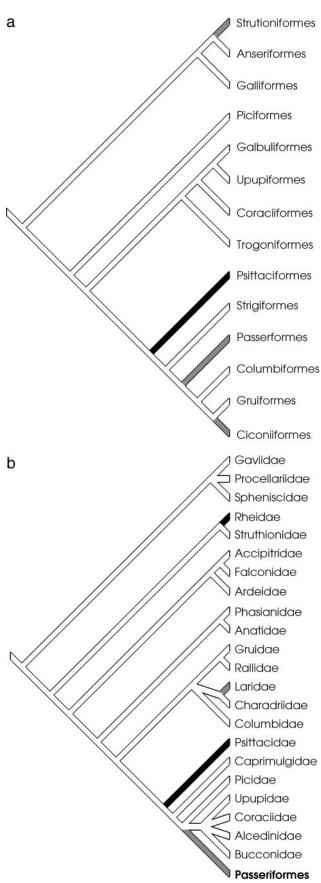
Our results support the notion that the VS type of color vision is the most common among birds, but it is also apparent that the avian distribution of vision systems is more complex than what has previously been shown. All studies to date have indicated that the VS color system is the dominating among birds and that the only bird species with a clear-cut UV-biased vision belong to the orders Psittaciformes and the Passeriformes. No previous study

shows both UVS and VS in the same taxonomic order. Although we confirm the presence of the UVS type in Passeriformes and Psittaciformes and the VS type in Anseriformes, Columbiformes, and Galliformes (table 1), we have also found species with the UVS-type vision in Ciconiiformes and Struthioniformes and species with VStype vision within Passeriformes and Struthioniformes. The variation of CODs is not restricted to high-level taxa such as orders, but varies at least within families.

The distribution of the UVS/VS character in the avian phylogeny has been considered to reflect the degree of relatedness of avian taxa and to be most parsimoniously explained by a single evolutionary split of the passeriform and psittaciform lineages from the anseriform and galliform lineages (Hart et al. 2000a). However, that UVS is present in at least nine families from four orders (table 1), interdispersed with VS taxa (fig. 1) strongly indicates that the UVS character has been acquired independently in each of these groups and that its distribution does not reflect the degree of relatedness between avian species. The vast majority of vertebrate animals studied have the amino acid serine in position 90, and this has lead Yokoyama, Radlwimmer, and Blow (2000) to suggest that having cystein in the same position is a derived state in birds. Indeed, the exclusive presence of serine in position 90 in the majority of families examined suggests that VS is the primitive state. This is also indicated by molecular and morphological phylogenies (fig. 1). However, the closest relatives to birds in which the SWS1 opsin is known are chameleon and mammals (Yokoyama, Radlwimmer, and Blow 2000), and these taxa are probably too distant relatives to provide phylogenetic resolution, as this character state varies even within avian families. Furthermore, the character state (UVS/VS) is controlled by a single-nucleotide mutation (Wilkie et al. 2000). One should therefore be careful not to draw too far-reaching conclusions from the character state in any extant outgroup. The closest living relatives to birds are the crocodilians, with which they share a common ancestor no younger than 250 Myr (Benton 1997). This provides ample time for multiple character changes.

It is more likely that the distribution of CODs in the class Aves has adaptive rather than phylogenetic explanations. The difference in peak sensitivity between UVS and VS is quite dramatic and changes not only the perception of objects that reflect light solely in the UV or violet ranges but also the perception of objects that reflect both UV/violet and longer wavelengths. This should have important consequences for foraging, habitat use, social signaling, and mate choice. We can expect intriguing effects on the evolution of color signals from interactions





between predators and prey. Such interactions may explain the presence of UVS in Laridae and Passeriformes.

Since UV scatters more under water than longer wavelengths, UV coloration and vision are only effective at short distances (< 5 m). UV may hence be useful in sexual and social signaling between fish of the same species to reduce the risk of detection by predators (Losey et al. 1999), such as other fish and swimming birds. That fish are able to make use of this private communication channel is implied by the facts that UV pigments of teleost cone receptors peak at around 360 nm (Losey et al. 1999) and that many fish species reflect UV. However, for birds like gulls (*Larus* spp.), which prey on fish just below the water surface, underwater UV scattering will be negligible and their UVS COD could be an adaptation to more effectively spot prey.

All six raptors examined are of the VS type, giving them a vision system different from many of their passeriform prey. This could enable perching birds to signal with colors that are conspicuous to members of their own species but dull or cryptic to raptors. That advantage would be common to all UVS prey species and should facilitate diversification of sexual and social signals and hence reproductive isolation and speciation. Signaling with colors that are inconspicuous to predators should reduce the cost of signaling. Selection should then favor stronger signals in the wavelengths to which predators are insensitive, that is, favor higher plumage reflectance in the SWS1 and SWS2 ranges or higher sensitivity to those parts of the spectrum.

An animal's response to a color signal depends on the signal's fit on the COD of that particular species, rather than what properties a human observer considers the signal to have. Evolutionary biologists and behavioral ecologists need to acknowledge the COD of their study animal to ask relevant questions and design experiments correctly. Indeed, the distribution of CODs is such a complex one that, when studying animal signaling, it may be necessary to verify the CODs even if they are known from related species. In bird studies, our method offers a considerably more practical tool for that purpose than does MSP. However, we do not imply that our method should replace the latter; MSP is undeniably more direct and informative. It is worth noting that some species carrying the SWS1 opsin gene might not express it, posses a very low proportion of SWS1 cones in the retina, or have ocular media absorbing ultraviolet light. So far, all our results are in agreement with those from MSP, although our  $\lambda$ -max approximations deviate by up to 15 nm, supporting a fine-tuning role for other sites (see Shi, Radlwimmer, and Yokoyama 2001). Our method can be used to quickly estimate a COD from total DNA, without the need to keep or sacrifice the animal. It thereby facilitates large screenings, including rare and endangered species, making it possible to find species with an aberrant COD suitable for MSP examination.

# **New Sequences**

The new sequences reported in this paper are available from GenBank with accession numbers AY227147 to AY227191.

#### Acknowledgments

We are grateful for Jonas Victorsson's ideas, suggestions, and comments; and we thank Anna Bartosch-Härlid, Sofia Berlin, Mats Björklund, Hans Ellegren, Fyris Zoo, Lindeberg & von Schantz Kött Chark o Deli, Göran Frisk at the Swedish Museum of Natural History, and Kristina Nilsson at the Swedish National Veterinary Institute for samples. We also thank Dr. Björklund and two anonymous reviewers for comments on an earlier draft. This study was funded by Stiftelsen för zoologisk forskning (grant to O.H.).

# Literature Cited

- Andersson, S., and T. Amundsen. 1997. Ultraviolet colour vision and ornamentation in bluethroats. Proc. R. Soc. Lond. B Biol. Sci. 264:1587–1591.
- Bennett, A. T. D., I. C. Cuthill, J. C. Partridge, and K. Lunau. 1997. Ultraviolet plumage colors predict mate preferences in starlings. Proc. Natl. Acad. Sci. USA 94:8618–8621.
- Bennett, A. T. D., I. C. Cuthill, J. C. Partridge, and E. J. Maier. 1996. Ultraviolet vision and mate choice in zebra finches. Nature **380**:433–435.
- Benton, M. J. 1997. Vertebrate palaeontology, 2nd edition. Chapman & Hall, London.
- Bowmaker, J. K., L. A. Heath, S. E. Wilkie, and D. M. Hunt. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. Vision Res. **37**:2183–2194.
- Bowmaker, J. K., J. K. Kovach, A. V. Whitmore, and E. R. Loew. 1993. Visual pigments and oil droplets in genetically manipulated and carotenoid deprived quail: a microspectrophotometric study. Vision Res. 33:571–578.
- Bowmaker, J. K., and G. R. Martin. 1985. Visual pigments and oil droplets in the penguin, *Spheniscus humboldti*. J. Comp. Physiol. [A] **156**:71–78.
- Church, S. C., A. T. D. Bennett, I. C. Cuthill, and J. C. Partridge. 1998. Ultraviolet cues affect the foraging behaviour of blue tits. Proc. R. Soc. Lond. B Biol. Sci. **265**:1509–1514.
- Cracraft, J. 1981. Toward a phylogenetic classification of the recent birds of the world (class Aves). Auk 98:681–714.
- Das, D., S. E. Wilkie, D. M. Hunt, and J. K. Bowmaker. 1999. Visual pigments and oil droplets in the retina of a passerine bird, the canary *Serinus canaria*: microspectrophotometry and opsin sequences. Vision Res. 39:2801–2815.
- Fleishman, L. J., E. R. Loew, and M. Leal. 1993. Ultraviolet vision in lizards. Nature 365:397.
- Goldsmith, T. H. 1980. Hummingbirds see near ultraviolet light. Science 207:786–788.
- ——. 1990. Optimization, constraint, and history in the evolution of eyes. Q. Rev. Biol. 65:281–322.
- Hart, N. S. 1998. Avian photoreceptors. Ph.D. thesis. University of Bristol, United Kingdom.
- ——. 2001. The visual ecology of avian photoreceptors. Prog. Retin. Eye Res. 20:675–703.
- Hart, N. S., J. C. Partridge, A. T. D. Bennett, and I. C. Cuthill. 2000a. Visual pigments, cone oil droplets and ocular media in four species of estrildid finch. J. Comp. Physiol. [A] 186: 681–694
- Hart, N. S., J. C. Partridge, and I. C. Cuthill. 1998. Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). J. Exp. Biol. **201**:1433–1446.
- 1999. Visual pigments, cone oil droplets, ocular media and predicted spectral sensitivity in the domestic turkey (*Meleagris gallopavo*). Vision Res. 39:3321–3328.
- Hart, N. S., J. C. Partridge, I. C. Cuthill, and A. T. D. Bennett.

- 2000b. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (Parus caeruleus L.) and the blackbird (Turdus merula L.). J. Comp. Physiol. [A] **186**:375–387.
- Hunt, S., A. T. D. Bennett, I. C. Cuthill, and R. Griffiths. 1998. Blue tits are ultraviolet tits. Proc. R. Soc. Lond. B Biol. Sci. **265**:451–455.
- Hunt, S., I. C. Cuthill, A. T. D. Bennett, S. C. Church, and J. C. Partridge. 2001. Is the ultraviolet waveband a special communication channel in avian mate choice? J. Exp. Biol. 204: 2499-2507.
- Hunt, S., I. C. Cuthill, A. T. Bennett, and R. Griffiths. 1999. Preferences for ultraviolet partners in the blue tit. Anim. Behav. 58:809-815.
- Hunt, S., I. C. Cuthill, J. P. Swaddle, and A. T. D. Bennett. 1997. Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*. Anim. Behav. **54**:1383–1392.
- Jacobs, G. H. 1993. The distribution and nature of colour vision among the mammals. Biol. Rev. Camb. Philos. Soc. 68:413–471.
- Jane, S. D., and J. K. Bowmaker. 1988. Tetrachromatic color vision in the duck (Anas platyrhynchos L.): microspectrophotometry of visual pigments and oil droplets. J. Comp. Physiol. [A] **162**:225–236.
- Kawamuro, K., T. Irie, and T. Nakamura. 1997. Filtering effect of cone oil droplets detected in the P-III response spectra of Japanese quail. Vision Res. 37:2829–2834.
- Losey, G. S., T. W. Cronin, T. H. Goldsmith, D. Hyde, N. J. Marshall, and W. N. McFarland. 1999. The UV visual world of fishes: a review. J. Fish Biol. 54:921-943.
- Maddocks, S. A., S. C. Church, and I. C. Cuthill. 2001. The effects of the light environment on prey choice by zebra finches, J. Exp. Biol. 204:2509-2515.
- Maier, E. J., and J. K. Bowmaker. 1993. Colour vision in the passeriform bird, Leiothrix lutea: Correlation of visual pigment absorbance and oil droplet transmission with spectral sensitivity. J. Comp. Physiol. 172:295-301.
- Okano, T., D. Kojima, Y. Fukada, Y. Shichida, and T. Yoshizawa. 1992. Primary structure of chicken cone visual pigments: vertebrate rhodopsins have evolved out of cone visual pigments. Proc. Natl. Acad. Sci. USA 89: 5932-5936.
- Palacios, A. G., F. J. Varela, R. Srivastava, and T. H. Goldsmith.

- 1998. Spectral sensitivity of cones in the goldfish, Carassius auratus. Vision Res. 38:2135-2146.
- Rice, P., I. Longden, and A. Bleasby. 2000. EMBOSS: the European molecular biology open software suite. Trends Genet. 16:276-277.
- Rozen, S., and H. J. Skaletsky. 1998. Primer3. Code available at http://www.genome.wi.mit.edu/genome\_software/other/ primer3.html.
- Shi, Y., F. B. Radlwimmer, and S. Yokoyama. 2001. Molecular genetics and the evolution of ultraviolet vision in vertebrates. Proc. Natl. Acad. Sci. USA 98:11731–11736.
- Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and classifications of birds: a study in molecular evolution. Yale University Press, New Haven, Conn.
- Siitari, H., J. Honkavaara, and J. Viitala. 1999. Ultraviolet reflection of berries attracts foraging birds: a laboratory study with redwings (Turdus iliacus) and bilberries (Vaccinium myrtillus). Proc. R. Soc. Lond. B Biol. Sci. 266:2125-2129.
- Viitala, J., E. Korpimaki, P. Palokangas, and M. Koivula. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. Nature 373:425–427.
- Wilkie, S. E., P. R. Robinson, T. W. Cronin, S. Poopalasundaram, J. K. Bowmaker, and D. M. Hunt. 2000. Spectral tuning of avian violet- and ultraviolet-sensitive visual pigments. Biochemistry **39**:7895–7901.
- Wilkie, S. E., P. M. A. M. Vissers, D. Das, W. J. Degrip, J. K. Bowmaker, and D. M. Hunt. 1998. The molecular basis for UV vision in birds: spectral characteristics, cDNA sequence and retinal localization of the UV-sensitive visual pigment of the budgerigar (*Melopsittacus undulatus*). Biochem. J. **330**: 541-547.
- Wright, M. W., and J. K. Bowmaker. 2001. Retinal photoreceptors of paleognathous birds: the ostrich (Struthio camelus) and rhea (Rhea americana). Vision Res. 41:1–12.
- Yokoyama, S., F. B. Radlwimmer, and N. S. Blow. 2000. Ultraviolet pigments in birds evolved from violet pigments by a single amino acid change. Proc. Natl. Acad. Sci. USA 97: 7366–7371.

David Irwin, Associate Editor

Accepted January 8, 2003